

·Invited Review·

Deficit Irrigation as a Strategy to Save Water: Physiology and Potential Application to Horticulture

J. Miguel Costa^{1,2}, Maria F. Ortuño¹ and M. Manuela Chaves^{1,2*}

¹Instituto Superior de Agronomia, Universidade Técnica de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal;

²Laboratório de Ecofisiologia Molecular, Instituto de Tecnologia Química e Biológica, Apartado 127, 2780-901 Oeiras, Portugal)

Abstract

Water is an increasingly scarce resource worldwide and irrigated agriculture remains one of the largest and most inefficient users of this resource. Low water use efficiency (WUE) together with an increased competition for water resources with other sectors (e.g. tourism or industry) are forcing growers to adopt new irrigation and cultivation practices that use water more judiciously. In areas with dry and hot climates, drip irrigation and protected cultivation have improved WUE mainly by reducing runoff and evapotranspiration losses. However, complementary approaches are still needed to increase WUE in irrigated agriculture. Deficit irrigation strategies like regulated deficit irrigation or partial root drying have emerged as potential ways to increase water savings in agriculture by allowing crops to withstand mild water stress with no or only marginal decreases of yield and quality. Grapevine and several fruit tree crops seem to be well adapted to deficit irrigation, but other crops like vegetables tend not to cope so well due to losses in yield and quality. This paper aims at providing an overview of the physiological basis of deficit irrigation strategies and their potential for horticulture by describing the major consequences of their use to vegetative growth, yield and quality of different crops (fruits, vegetables and ornamentals).

Key words: deficit irrigation; horticulture; partial rootzone drying; regulated deficit irrigation; water saving.

Costa JM, Ortuño MF, Chaves MM (2007). Deficit irrigation as a strategy to save water: Physiology and potential application to horticulture. *J. Integr. Plant Biol.* 49(10), 1421–1434.

Available online at www.blackwell-synergy.com/links/toc/jipb, www.jipb.net

Water is an increasingly scarce resource worldwide due to increased consumption, mismanagement and pollution. The predicted increase of dry days per year for many areas of the globe will further exacerbate the problem (Petit et al. 1999; IPPC 2001; Luterbacher et al. 2006). The agricultural sector contributes largely to this unsustainable situation. Irrigated agriculture is a major consumer of water and accounts for about two thirds of the total fresh water diverted to human uses (Feres and Evans 2006). In the global debate about water scarcity, agriculture

is commonly associated with the image of inefficiency. This derives from a poor 'irrigation water use efficiency,' understood as the ratio between the irrigation water absorbed by the crop and the amount of water actually withdrawn from its source for irrigation purposes. The increasing demand of water resources and limited availability makes water an increasingly valuable commodity. This is particularly true in regions where irrigated agriculture coexists with sectors like tourism and industry or where urban growth is high. The Pacific Northwest region in the USA, the provinces of Almeria or Murcia in southeast Spain or the Shandong province in northern China Plain are good examples of this situation (Carvalho 2000; Costa and Heuvelink 2004; Leib et al. 2006; Blanke et al. 2007; Downward and Taylor 2007). The agriculture sector is expected to lose the competition for water resources because it is less profitable than other sectors and because governmental restrictions will force growers to reduce the use of irrigation water.

As a result, improving crop water-use efficiency (WUE) has been a matter of concern to researchers and agronomists in recent years. WUE is discussed either in terms of instantaneous measurement of the efficiency of carbon gain per water loss by plants or as the integral of such an efficiency over time (expressed as the ratio of biomass accumulation or harvested

Received 2 Dec. 2006 Accepted 25 May 2007

MF Ortuño was granted a Postdoctoral research fellowship from the Spanish Ministry of Education and JM Costa was supported by a postdoc fellowship granted by Fundação para a Ciência e Tecnologia (FCT) (ref. POCI2010/SFRH/BPD/14498/2003). The WATERWEB project provided funds for research in grapevine.

*Author for correspondence.

Tel: + 351 2 1365 3415;

Fax: + 351 2 1365 3238;

E-mail: <mchaves@isa.utl.pt>.

© 2007 Institute of Botany, the Chinese Academy of Sciences

doi: 10.1111/j.1672-9072.2007.00556.x

yield to water use) (Bacon 2004). The WUE in the agricultural sector has been slowly improving due to the use of genotypes with increased WUE (Condon et al. 2004) and due to adoption of innovative cultivation and irrigation practices (e.g. drip irrigation, use of irrigation calendars based on the depth of water table and soil salinity, reuse of wastewater) (Chaves et al. 2003; Pereira et al. 2006). Drip irrigation, mulching and protected cultivation have contributed to improve WUE in agriculture by significantly reducing runoff and evapotranspiration losses (Stanghellini et al. 2003; Jones 2004; Kirnak and Demirtas 2006). Mediterranean countries like Israel or Spain led developments in drip irrigation and cultivation under plastic in the past decades, but China has been strongly investing in these techniques. China has recently emerged as the world's largest producer of greenhouse vegetables and ornamentals (close to 2 million ha) and has about 15 million ha using plastic mulches (Costa and Heuvelink 2004). However, the use of drip irrigation remains too restricted (Blanke et al. 2007) suggesting that WUE can still be optimized by adoption of more efficient irrigation practices.

Deficit irrigation strategies have the potential to optimize water productivity in horticulture. Nevertheless, the effects of deficit irrigation on yield or harvest quality are crop-specific. Knowledge of how different crops cope with mild water deficits is the basis for a successful application of deficit irrigation into practice. Our aim is to provide an overview of the physiological basis of deficit irrigation strategies and their potential application to some of the most important horticultural crops.

The Concept of Deficit Irrigation and its Physiological Background

Deficit irrigation strategies deliberately allow crops to sustain some degree of water deficit and sometimes, some yield reduction with a significant reduction of irrigation water. The classic deficit irrigation strategy (DI) implies that water is supplied at levels below full evapotranspiration (ET_c) throughout the season. The other two main deficit irrigation strategies based on the physiological knowledge of crops response to water stress, are regulated deficit irrigation (RDI) and partial rootzone drying (PRD). The foremost principle of the RDI technique is that plant sensitivity to water stress is not constant during the growth season (cycle) and that intermittent water deficit during specific periods may benefit WUE, increase water savings and even improve harvest quality (Chalmers et al. 1981; McCarthy et al. 2002; Loveys et al. 2004; Cameron et al. 2006). In the RDI strategy, irrigation is used to maintain plant water status within certain limits of deficit (with respect to maximum water potential) during certain phases of the crop cycle, normally when fruit growth is least sensitive to water reductions (Marsal et al. 2002; Kang and Zhang 2004). The major disadvantage of the RDI is that it is required to maintain a plant's water status within narrow limits, which is difficult to achieve in practice. In this way,

an excessive application of water suppresses the advantage of using RDI and results in higher costs of water, while a lower water application may result in severe losses of yield and quality, mainly if a sudden increase in temperature occurs (Jones 2004).

An alternative strategy to RDI is partial root drying (PRD). PRD involves exposure of roots to alternate drying and wetting cycles and enables plants to grow with reduced stomatal conductance but without signs of water stress (Zhang et al. 1987; Davies et al. 1994; Santos et al. 2003; Kang and Zhang 2004). This technique is based on plant root to shoot chemical signaling that influences shoot physiology and it can be operated in drip- or furrow-irrigated crops. Theoretically, roots of the watered side of the soil will keep a favorable plant water status, while dehydration on the other side will promote the synthesis of hormonal signals, which will reach leaves via the transpiration stream and further reduce stomatal conductance. This will decrease water loss and vegetative growth and increase WUE (Dry et al. 1996; Davies et al. 2000). The plant hormone abscisic acid (ABA) is a compound that plays a role in stomatal closure as soil dries (See Davies and Zhang 1991 or Dodd 2005 for a review). The PRD strategy may also increase root growth at deeper layers of the soil as it has been described for grapevine (Dry et al. 2000b; Santos et al. 2005) or in overall root system, as shown for tomato (Mingo et al. 2003). PRD strategies have also resulted in higher xylem pH (Davies and Zhang 1991; Dry et al. 1996; Dry and Loveys 1999; Stoll et al. 2000) and lower cytokinins levels (Stoll et al. 2000; Davies et al. 2005) which restricts stomatal opening. The PRD may also bring about other benefits to the crop besides higher WUE. It can influence carbohydrates partitioning between the different plant organs and affect the quantity and quality of the harvest (Kang and Zhang 2004). A practical inconvenience of PRD is that it is obliged to use double the amount of tubes than RDI or DI, increasing installation costs. Nevertheless, the underlying causes of PRD functioning are still a matter of discussion. Bravdo (2005) stated that it is not possible to have absolute control of root drying under field conditions and that hydraulic redistribution from deeper to shallower roots may prevent the clear results that can be obtained in potted plants. Other authors such as Gu et al. (2004) argued that the amount of water used rather than the application system can explain the effects of PRD.

Stomatal Regulation and Water Use Efficiency

The regulation of stomatal aperture is a central process to determine WUE of plants. Given the linear relationship between stomatal conductance and transpiration under a constant vapor pressure deficit of the air (VPD), and the non-linear relationship between stomatal conductance and the photosynthetic rate, lower stomatal aperture may improve water use efficiency (Chaves et al. 2002).

Table 1. Summary of the major factors influencing leaf stomatal conductance to water vapour and CO₂ with a non-exhaustive list of references

Factors	References
Genotype	
- Species	Jones 1992; Bunce 1996; Bernacchi et al. 2002; Chaves et al. 2002; Herrick et al. 2004.
- Leaf morphology (stomata density and size, sun/shade leaves)	
- Leaf age	
Environmental	
- Irradiance	Stalfet 1962; Zeiger 1983; Morison and Gifford 1983; Morison 1987; Zeiger et al. 1987; Honor et al. 1995; Maroco et al. 1997; Assmann 1999; Correia et al. 1999; Lascève et al. 1999; McAinsh et al. 2002; Maherali et al. 2003; Talbot et al. 2003; Ainsworth and Rogers 2007.
- Light quality (blue/red)	
- Air temperature	
- CO ₂	
- Relative humidity, VPD	
- Wind speed	
- Gaseous pollutants	
Physiological	
- Leaf turgor, plant water status	Cummins et al. 1971; Davies and Mansfield 1987; Gollan et al. 1992; Irving et al. 1992; Jones 1992; Talbot and Zeiger 1996; Schroeder et al. 2001; Merlot et al. 2002, 2007; Klein et al. 2003.
- Hormones (ABA, cytokinins, auxin)	
- Sugar accumulation	
- Ions (Ca ²⁺ , K ⁺)	

ABA, abscisic acid; VPD, vapor pressure deficit of the air.

Stomata are bound by two guard cells that are sensitive to different types of signals either environmental (light, humidity, temperature, CO₂) or physiological (phytohormones, calcium) (Table 1). The environmental factors will act directly or indirectly on stomatal aperture, together with circadian rhythms, leaf water status and xylem-born signals (e.g. cytokinins, ABA) and at any moment all of these factors are integrated to deliver a particular stomatal aperture (Webb and Hetherington 1997; Bacon 2004). Maximum stomata aperture is known to occur under irradiances larger than 400 $\mu\text{mol}/\text{m}^2$ per s (PAR) (Jones 1992). Part of the stomatal response to light results from a decrease of the intercellular CO₂ concentration but guard cells are known to respond to blue (436 nm) and red light (681 nm) (Zeiger 1983).

The effects of temperature on stomatal behavior are closely related to metabolism, enzymatic activity and hormones but also to external plant factors such as air vapor pressure. In general, maximal stomata conductance can be achieved at 20–40 °C and is restricted by very low (5 °C) or extremely high temperatures (45 °C) (Stalfet 1962; Jarvis 1976). These limits are species-dependent.

The difference of water vapor pressure between the leaf interior (100% vapor pressure) and the air vapor pressure (variable) (leaf-to-air vapor pressure deficit – LVPD) is another factor influencing stomatal opening and closure. Stomata respond directly to changes in the evaporative demand rather than to changes in the relative humidity (Monteith 1995; Maroco et al. 1997). Stomatal conductance of several plant species decreases as

the VPD increases. Franks et al. (1997) found a decrease in the steady state leaf transpiration rate with increased VPD, which was reversible and independent of leaf water status. There are also reports indicating a direct effect of VPD on stomatal regulation for woody plants (Franks and Farquhar 1999; Maherali et al. 2003). High CO₂ concentrations reduce stomatal sensitivity to VPD (Bunce 1996), whereas water stress tends to increase it (Eamus and Shanahan 2002). Stomatal response to VPD depends on the species as well (Bunce 1996; Chaves et al. 2002).

Soil Versus Leaf Water Status and Stomatal Closure

Stomatal closure and leaf growth inhibition are among the earliest plant responses to drought leading to diminished water losses (Shulze 1986; Chaves 1991; Chaves et al. 2002). In general stomata are not sensitive to changes of leaf water potential (Ψ) until a certain threshold is exceeded. Moreover, there is strong evidence that leaf conductance responds earlier to soil water content than to leaf turgor (Davies and Zhang 1991; Jones 1992). This is because stomata close in response to drying soil even when shoot water status is maintained at high turgor. This was shown via split root experiments where plants were grown with part of their roots in drying soil (Gowing et al. 1990). Further evidence showed that stomatal closure is

mediated by hormonal signals (ABA) traveling from dehydrating roots to shoots (Davies and Zhang 1991; Bacon et al. 1998; Sobeih et al. 2004; Dodd 2005). The signaling pathway triggered by ABA in guard cells is one of the better understood pathways in plants (Schroeder et al. 2001). Substantial progress has been made in the understanding of signal transduction pathways of ABA by screening and characterization of ABA mutants with altered stomatal response to drought (Merlot et al. 2002).

Other hormones are likely to act together with ABA or alone on stomatal regulation. For example, under soil water deficit, the increase in cytokinin concentration in the xylem decreased stomatal sensitivity to ABA and promoted stomatal opening (Wilkinson and Davies 2002), whereas a decrease in cytokinin levels increased stomatal closure (Stoll et al. 2000; Davies et al. 2005). Other hormones belonging to the group of auxins were found to stimulate stomatal opening (Davies and Mansfield 1987).

Xylem sap pH may also influence stomatal conductance under soil water deficit (Schurr et al. 1992; Wilkinson and Davies 1997, 2002; Netting 2000). The pH of the xylem sap, and thereby of the leaf apoplast, becomes more alkaline in response to soil drying. The net result is an accumulation of ABA to physiologically active concentrations in the leaf apoplast adjacent to guard cells, which will induce stomata closure (Wilkinson and Davies 1997; Bacon et al. 1998; Loveys et al. 2004).

Deficit Irrigation: Water Use Efficiency, Crop Growth, Yield and Quality

Major horticultural production areas are located in hot and dry climates (e.g. Mediterranean) where high light, high temperatures and high VPD often co-occur with low soil water content. Deficit irrigation strategies may help to save more water and optimize or stabilize yields and quality in these areas and they

have been investigated for several horticultural crops, namely grapevines, orchard fruit trees and vegetables (Goodwin and Boland 2002; Kang and Zhang 2004; Bravdo 2005; Fereres and Soriano, 2007). The advantages of deficit irrigation practices for production of leaf vegetables are less clear than for fruit crops (Jones 2004). However, deficit irrigation practices can be increasingly justified in order to save water, improve nitrate use efficiency, minimize leaching of nutrients and biocide or in view of higher water prices.

Grapevine

Grapevine (*Vitis vinifera* L.) is grown worldwide and about 55% of its total area is located in Europe (Table 2). Grapevine is one of the well-adapted crops to the South European Mediterranean climate. However, the combined effect of drought, high air temperature and evaporative demand during summer, has often limited grapevine growth yield and quality of wine production in the region (Escalona et al. 1999; Chaves et al. 2002). Irrigation has been adopted as a practice to minimize the problem and it has become common in modern Mediterranean viticulture under certain restrictions.

The use of irrigation in wine production has been always an object of large debate. On one hand, small water supplements may increase yields and maintain or even improve berry quality (Matthews and Anderson 1989; Reynolds and Naylor 1994; Santos et al. 2003, 2005). On the other hand, irrigation may promote excessively vegetative growth, decrease berry's pigments (color), decrease sugar content (if applied later in the season), and further decrease wine quality (Bravdo et al. 1985; Matthews et al. 1990; Dokoozlian and Kliewer 1996; McCarthy 1997; Esteban et al. 2001). Moreover, a larger canopy leaf area increases transpiration losses and disease problems, mainly fungal disorders (Dry et al. 1996; Dry and Loveys 1998; Behboudian and Singh 2001).

Table 2. Cultivated area (million hm²) and production (million ton) of grapes in the different continents relative to 2005 (FAO 2006)

Continent/Country	Area (million hm ²)	Production (million tons)
Europe	4.06	29.8
Italy	0.84	8.6
France	0.85	6.8
Spain	0.95	5.9
Portugal	0.21	1.0
Asia	1.87	16.8
China	0.45	5.7
America	0.91	13.0
USA	0.38	6.3
Africa	0.34	3.7
South Africa	0.12	1.3
Oceania	0.17	2.2
Australia	0.15	2.0
World	7.35	65.6

In order to minimize the inconvenience of irrigation and maximize WUE in wine production, the response of grapevines to deficit irrigation strategies such as RDI and PRD has been investigated (Stone et al. 2001; McCarthy et al. 2002; Santos et al. 2003; Cifre et al. 2005; Souza et al. 2005). A major effect of controlled mild soil water deficits is a decrease in stomatal closure with a slight decrease of net assimilation (Chaves and Oliveira 2004). As a consequence, a higher intrinsic WUE is often found under deficit irrigation conditions as previously described. Our own field studies using the cultivars 'Moscatel', 'Castelão' and 'Aragonez' showed that PRD (irrigation at 50% ET_c alternatively in each side of the root system) and the conventional DI (irrigation at 50% ET_c divided by the two sides of the root system) as compared to full irrigated grapevines (FI, 100% ET_c) promoted WUE, either in the short-term (as expressed by the A/g_s ratio) (Figure 1A) but also in the long-term, as shown by the increase in ¹³C in plant tissues, especially in berries (Souza et al. 2003, 2005). Crop water use efficiency was also significantly higher in PRD and DI as compared to FI (Figure 1B). Such increments in WUE and water savings are in line with studies from other groups for other grapevine cultivars and/or locations (Davies and Zhang 1991; Dodd et al. 1996; Davies et al. 2000; Dry et al. 2000a,b; Stoll et al. 2000; Loveys et al. 2004). Although the differences on stomatal closure and WUE are subtle between PRD and DI (Souza et al. 2003; Santos et al. 2003), we found that PRD tends to induce a reduction of vigor translated in smaller canopy leaf areas and less pruning weight (Souza et al. 2003; Santos et al. 2005) which agrees with previous findings (Loveys 1984; Davies and Zhang 1991; Dodd et al. 1996; Dry et al. 1996; Davies et al. 2000; Loveys et al. 2000). The decrease in vegetative growth caused by PRD leads to better exposure of berry clusters to solar radiation and may improve fruit quality (Santos et al. 2005, 2007). In addition, growth inhibition occurs in spite of similar or even improved water status in PRD as compared to DI, which suggests that vegetative growth is being regulated by non-hydraulic mechanisms (Chaves and Oliveira 2004).

The RDI strategy has also been shown to be a viable practice to control excessive vigor and improve berry quality (Bravdo et al. 1985; Matthews and Anderson 1988). The effect of the RDI depends however, on the phenological stage and on the severity of the stress imposed (Hardie and Considine 1976). The way the RDI strategy is applied in commercial vineyards is not uniform. In Mediterranean conditions it is common to apply water deficit during the final phases of grape development (William and Matthews 1990), whereas in Australia the common practice is to apply less water early in the season (McCarthy et al. 2002). The aim in the first case is to avoid water stress during the ripening stage whereas in the second case the aim is to control berry size.

Regulated deficit irrigation strategies have the potential to reduce yields, although this depends on the timing of application (McCarthy et al. 2002). Yields were reduced by water deficits

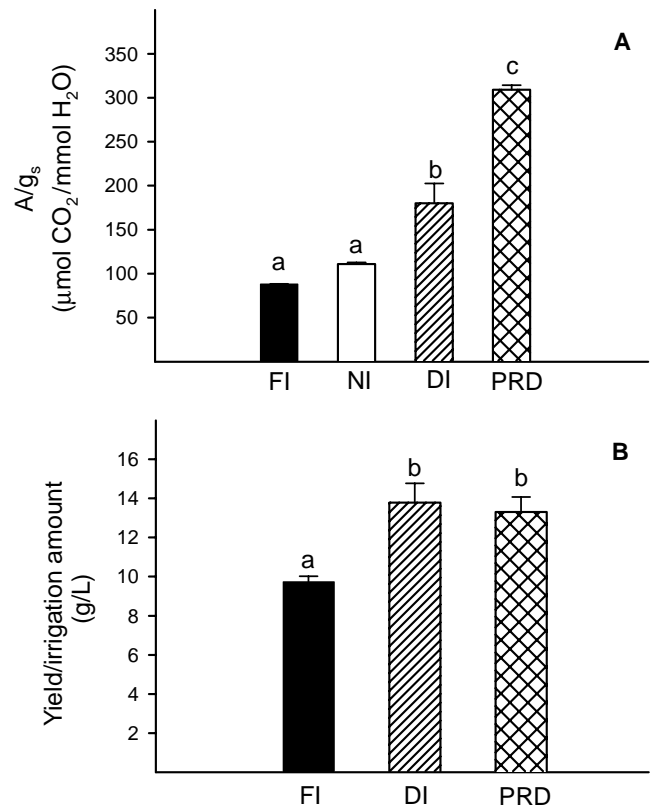


Figure 1. (A) Intrinsic water use efficiency (A/g_s) and (B) crop water use efficiency (Yield berry/liter of irrigation water) for 5-year-old grapevines (*Vitis vinifera* L.) cv 'Aragonez' (syn. 'Tempranillo') grafted on the 1103 Paulsen rootstock and subjected to four irrigation treatments: (1) partial-root drying (PRD), 50% of the ET_c periodically supplied to only one side of the root system with the other allowed to dry, and sides alternated every 15 days; (2) deficit irrigation (DI), 50% of the ET_c supplied simultaneously to both sides of the row (25% to each side); (3) non-irrigated (NI), non irrigated but rain-fed; and (4) full irrigated (FI), 100% of the ET_c supplied to both sides of the row, half to each side. Values are means ± SE (n = 3). Different letters denote significant differences (P < 0.05) by the Duncan's test. Gas exchange measurements were carried out at 360 ppm CO₂, 1200 μmol quanta/m² per s (10% blue light), with temperature set at 25 °C, using a LiCor-6400 portable photosynthesis system. Measurements were carried out in summer (24 August 2005) on mature leaves from the intermediate part of the canopy and at the sunlit side.

imposed either before or after veraison, but mainly when the deficit was imposed before veraison (Matthews and Anderson 1989). Fewer berries per cluster, fewer clusters per vine and decreased berry weight explain the lower yields under such conditions (Matthews and Anderson 1989). In turn, PRD irrigation has been shown to consistently cause no significant yield reduction, even though the amount of irrigation water is significantly reduced (McCarthy et al. 2002; Kang and Zhang

2004; Bravdo 2005). Mild stress imposed by PRD (at 50% ETc) treatments had no negative effect on the yield of the cultivar 'Castelão' (Santos et al. 2005).

Deficit irrigation as compared to FI may also improve berry quality due to an increment in the contents of anthocyanins and total phenols (Dokoozlian and Kliewer 1996; Santos et al. 2005). This is related to less dense canopies and better exposure to light. Nevertheless, Keller and Hrazdina (1998) found no difference in the anthocyanin concentration at 20% or 100% sunlight interception for the cultivar 'Cabernet Sauvignon', suggesting that above a given threshold, light is not the major factor limiting the synthesis of anthocyanins.

Fruit trees

Deciduous

Irrigation in fruit trees provides protection against drought and contributes to increase or stabilize production (Feres and Evans 2006). DI strategies have been developed for high density orchards of tree crops such as apple, pear and peach mainly to balance vegetative and reproductive growth (Goodwin and Boland 2002; Loveys et al. 2004). For these crops the major effect of deficit irrigation is to reduce vegetative growth with minor changes on fruit development (Goodwin and Boland 2002; Loveys et al. 2004). Deficit irrigation strategies can be also a cheaper and equally efficient alternative to branch manipulation, shoot and root pruning or hormonal treatments to control vegetative growth and diminished shading (Goodwin and Boland 2002). Additionally, it reduces water use as well as the risks of nutrient or biocide leaching.

Published reports on the effects of deficit irrigation strategies on yield and quality of fruit crops is however, not conclusive. In apple (*Malus domestica* L.) for example, RDI was shown to decrease yield and fruit size irrespective of the timing of application (Landsberg and Jones 1981; Ebel et al. 2001; Mpelasoka et al. 2001). More recent results with the cultivars 'Fuji' and 'Gala' showed that DI and PRD that permitted water savings of about 45–50% and 25–75% respectively, had no effect on yield nor on fruit size as compared to the FI (100% ETc) plants (Einhorn and Caspari 2004; Leib et al. 2006). Studies with the cultivar 'Braeburn' showed that the classic DI (50% of the control irrigation frequency) reduced water use by 60% as compared to the control and had no significant effects on gross yield (Mpelasoka et al. 2001). DI advanced fruit ripening, increased flesh firmness and increased total soluble solids (TSS) and aroma volatiles both at the ripening phase and after storage (Mpelasoka et al. 2001; Mpelasoka and Behboudian 2002).

In pear (*Pyrus communis* L.), field experiments using trees grown under flood irrigation and a shallow water table, showed that PRD can save 23 to 52% of the irrigation water as compared to fully irrigated trees, without any or only marginal reduction in

yield or fruit size (Kang et al. 2002). The RDI strategy in turn was successfully applied to field-grown plants of the cultivar 'Barlett' especially if water deficits were imposed during stage I of fruit development when cell division occurs (Mitchell et al. 1989). The RDI strategy permitted to save water, limit vegetative growth without affecting fruit growth. RDI was also tested on plants of the same pear cultivar, but grown in containers and decreased shoot growth and to a lesser extent fruit growth (Marsal et al. 2000). The authors suggested that the effect of RDI on canopy growth can be more positive when vigorous rootstocks are used, when soils are fertile or plantation density is very high. On the other hand, O'Connell and Goodwin (2004) found for the cultivar 'Williams Bon Chretien' that PRD strategies (at 50% of ETc) resulted in water-stressed plants.

Regulated deficit irrigation was also tested in peach (*Prunus persica* L.) by various authors (Chalmers et al. 1981; Mitchell and Chalmers 1982; Li et al. 1989; Boland et al. 1993; Girona et al. 2005) who showed in general an increase in WUE and a reduction in vegetative growth, without a negative effect on yield. Similar effects of deficit irrigation strategies on WUE and vegetative growth were described for other crops like the Asian pear (*Pyrus serotina* L.) and prunes (*Prunus domestica* L.) (Goodwin and Boland 2002).

In nut crops like almond (*Prunus dulcis* Mill.), RDI decreased kern yields by about 10 to 20% but improved WUE and water savings up to 50% as compared to FI (Romero et al. 2004). Irrigation regimes influence the incidence of diseases in nut crops and the principle of reducing irrigation before harvest to control hull rot caused by *Monilinia fructicola* and *Rhizopus spp.* is well established (Ogawa and English 1991). Studies with almond showed that DI irrigation (at 70–80% ETc) decreased yields but lessened the incidence of hull rot as compared to FI plants (100% ETc) (Teviotdale et al. 2001). The yield reductions observed under DI conditions were attributed to smaller kernel size but were considered marginal if compared to the benefits due to reduced hull rot incidence (Teviotdale et al. 2001).

Evergreen

Deficit irrigation strategies have been progressively applied to olive trees (*Olea europea* L.) in particular in the Mediterranean Basin where there is an ongoing shift from traditional rain-fed cultivation to irrigated plantations (Testi et al. 2006). RDI strategies successfully reduced water use in different cultivars and growing locations (Alegre et al. 1997; Goldhamer 1999; Wahbi et al. 2005). PRD (50% ETc) resulted in higher WUE in plants of the cultivar 'Picholine marocaine' due to lower stomatal conductance and a non-significant reduction in photosynthesis (Centritto et al. 2005). Trials with adult trees of the same cultivar showed that the PRD (50% ETc) induced a slight decrease in vegetative growth and yield as compared to the FI treatment (Wahbi et al. 2005) but yield was higher than the one obtained for non-irrigated (NI) plants. Identical results were reported for the

cultivar 'Cornicabra' subjected to the RDI regime (Gómez-Rico et al. 2007). RDI resulted in about 35% higher yields than rain-fed trees and improved quality of fruits and derived olive oil. This was explained by the lower total phenol content, which affects sensory bitterness in oils, under irrigated condition (Gómez-Rico et al. 2007).

Citrus are one of the most important fruit crops cultivated in hot and dry regions. Besides water saving, the major objective of using deficit irrigation in citrus production is to improve fruit quality (Verreynne et al. 2001). Conventional DI (60–66% of the control) increased TSS and titrable acidity (TA) in fruits from 'Marisol Clementines'. DI had no effect on external fruit color or on juice content but reduced fruit diameter by about 10% as compared to the control (Verreynne et al. 2001). TSS increased more pronouncedly when deficit irrigation was combined with trunk girdling.

Regulated deficit irrigation strategy has been also tested in a drip-irrigated orchard of 'Clementina de Nules' grafted on Carrizo Citrange (*Citrus sinensis* Osb x *Poncirus trifoliata*). The initial stages of fruit growth were less negatively affected by moderate water deficit than the later stages as fruits might have compensatory growth afterwards (González-Altozano and Castel 2000a; 2000b). RDI applied during the months of July and August, saved about 6 to 22% of the water used for FI (125% ETc) and had no effect on yield nor on fruit quality, provided that a certain water potential was maintained (González-Altozano and Castel 2000b). However, when the RDI was applied at a later stage (September-October) it reduced fruit size and induced external peel disorders (González-Altozano and Castel 2000a). Deficit irrigation treatments did not negatively affect yields of lemon (*Citrus limonium* L.) cv 'Verna' and increased fruit acidity (Sánchez-Blanco et al. 1989).

In mango (*Mangifera indica* L.) cv 'Kent', RDI treatments using about 20 to 25% less water than the well-watered control reduced vegetative growth, saved water and had no effect on yield as compared to the control trees (Pavel and Villiers 2004). Differences in yield, when existing, were related to fruit number and to the fact that RDI negatively affects fruit growth mainly before flowering or during early stages of growth.

Deficit irrigation practices have been also tested in soft fruits. Trials with raspberries (*Rubus idaeus* L.) plants from the cultivars 'Glen Ample' and 'Glen Prosen', were grown in pots, with split-roots, or in the field with manipulated soil water content and subjected to PRD irrigation (50% and 25% of the amount applied to the control at both sides of the plants) (Grant et al. 2004). PRD treatments did not reduce yields compared to the control and plants showed higher WUE, mostly due to reduced stomatal conductance.

Experiments with strawberry (*Fragaria* × *ananassa* Duch.) cv 'Honeyoye' showed that DI and PRD (at 60% of the ETc) decreased plants' leaf area, fresh berry yield and individual berry fresh and dry weight as compared to FI (Liu et al. 2007). Both deficit irrigation strategies increased WUE and saved about 40%

of the irrigation water applied to the FI. The PRD presented no advantage relatively to DI in terms of yield and WUE (Liu et al. 2007).

Vegetables

Tomato

Lycopersicon esculentum Mill is one of the most important vegetable crops worldwide and also one of the most demanding in water (Peet 2005). Therefore, adoption of deficit irrigation strategies may result in significant savings of irrigation water. The available published reports on the effects of deficit irrigation on tomato production presents some discrepancies, which may be linked to the cultivars used and/or to the phenological period of application of deficit irrigation treatments. Greenhouse trials using the cultivar 'Virosa' showed that plants under deficit irrigation (irrigated only at leaf water potentials of -1.0 to -1.2 MPa), would produce about 60% less than the control plants irrigated when water potential was -0.5 MPa (Pulupol et al. 1996). The yield reduction was attributed to flower abortion. Fruit quality was improved under the DI regime mostly due to higher concentrations of soluble sugars and higher color intensity (Pulupol et al. 1996). However, the increment in quality was not enough to compensate the pronounced yield loss.

More recent greenhouse experiments with the cultivar 'Fantastic' showed that the PRD (50% ETc) strategy reduced yields by 20% as compared to FI and water savings reached about 50% (Topcu et al. 2007). The conventional DI resulted also in lower marketable and total yields as compared to the PRD, which is in line with previous findings for the tomato crop (Ramalan and Nwokeocha 2000; Kirda et al. 2004). Fruit size was in general less negatively affected by PRD than by the conventional DI (Davies et al. 2000; Mingo et al. 2003; Topcu et al. 2007).

Experiments with the glasshouse cultivar 'Solairo' showed that PRD (50% ETc) sustained cell turgor and prevented cracking due to turgor fluctuations during the development of fruits (Mingo et al. 2003). PRD also increased pH of sub-epidermal apoplastic compartment in both leaves and fruits (Mingo et al. 2003), as well as ABA concentration in the xylem and ethylene evolution in leaves (Mingo et al. 2004). PRD promoted dry matter partitioning to roots, as root biomass of PRD treated plants was 55% larger than uniformly watered plants (Mingo et al. 2004).

Regarding processing tomato, Mitchell et al. (1991) reported no depression of the marketable yields for the cultivar 'UC82B' subjected to water deficits by arresting irrigation 50–75 days before harvest. Fruit set and soluble solids were generally unaffected by the treatments. Experiments with the cultivar 'Petopride' showed that the effects of PRD on yield and quality varied as a function of the phenological phase. When PRD was applied during the vegetative stage until the first truss the yield

and the amount of marketable fruits were identical to the control with only a 6% reduction in water use. However, when applying the PRD from appearance of the first truss to fruit set or from fruit set to harvest, yield losses reached 1.8 kg of fresh weight per plant as compared to FI (Zegbe et al. 2006). The incidence of blossom-end-rot was significantly higher in PRD plants treated between fruit truss and fruit set (Zegbe et al. 2006). Fruits from plants subjected to PRD since fruit set until harvest, had significantly higher TSS than the other treatments and saved more water (up to 25%). It is possible that water savings and gains in quality may compensate the eventual losses in fresh and dry weight of fruits especially in regions where water is an expensive input (Zegbe et al. 2006).

Potato

According to Shock and Feibert (2002) the economic opportunities for using deficit irrigation in potato (*Solanum tuberosum* L.) are more limited than for other crops because potatoes have a shallow root system and are very sensitive to water stress. Research has shown those yield and tuber grades are considerably reduced by soil water deficits even when briefly applied (Lynch et al. 1995; Shock and Feibert 2002; Liu et al. 2006). The negative effect depends not only on the cultivar (Jefferies and MacKerron 1993) but also on the phenological phase. Severe reductions in tuber yield and quality occurred when brief periods of water stress were imposed following tuber set (Lynch et al. 1995).

Fabeiro et al. (2001) in turn, showed for the cultivar 'Agria' that applying moderate water deficit during growth and tuber bulking resulted in similar yields to fully irrigated plants and that the smallest yields were obtained when deficit was applied in the last part of the growth cycle. Liu et al. (2006) showed no advantage in using PRD (at 50% ETc) relatively to the conventional DI regarding biomass accumulation and WUE when it was applied at the tuber initiation stage.

Nevertheless, Nimah et al. (2000) emphasize the positive effect of deficit irrigation on potato production, regarding water and nitrogen savings, which could reach about 30%. Field studies with the cultivar 'Folva' showed that PRD (50–70% ETc) maintained tuber yields and increased irrigation water use efficiency (IWUE) by 60% as compared to FI plants kept at field capacity (Shahnazari et al. 2007). PRD significantly reduced leaf area index as compared to FI plants in line with findings for crops like grapevine (Stoll et al. 2000; Santos et al. 2003) or tomato (Topcu et al. 2007). According to Shahnazari et al. (2007) the advantage of PRD to FI resides in a better balance of photosynthesis versus transpiration and in a better use of soil water reserves due to a larger root system.

Other vegetables

Vegetable crops such as hot pepper (*Capsicum annum* L.) (Kang et al. 2001), egg plant (*Solanum melongena* L.) (Kirnak

and Demirtas 2006) or cucumber (*Cucumis sativus* L.) (Mao et al. 2003) showed higher WUE when subjected to very moderate water deficits (80–90% ETc) in parallel with losses in yield and fruit weight. Combination of deficit irrigation strategies with mulching was suggested to be a possible way to improve WUE and minimize the negative effects of deficit irrigation on the yield of cucumber grown in open fields (Kirnak and Demirtas 2006).

Glasshouse trials with hot pepper (*Capsicum annum* L.) cv 'Ancho St. Luis' have shown that PRD and DI (irrigated with 50% of the volume of commercial irrigation used as a control) reduced total fresh weight of fruits by about 19% and 35%, respectively as compared to the control FI (Dorji et al. 2005). Fruit number was also reduced by 20% for plants subjected to deficit irrigation, which was attributed to flower abortion just like was suggested for tomatoes (Pulupol et al. 1996; Zegbe-Dominguez et al. 2003). Lower fruit load in DI plants might have favored carbon partitioning to fruits and increased the content in soluble solids by about 20%.

Field studies with two cultivars of watermelon (*Citrullus lanatus* L.), 'Summer sweet 5244' and 'Super seedless 7187', showed that deficit irrigation practices reduced total marketable yield by 15 to 36% and increased yield of small fruits (<5 kg) but had no effect on fruit quality (lycopene content) (Bang et al. 2004). The effects of deficit irrigation on melon (*Cucumis melo* L.) seem to also be dependent on the timing of the treatment. In fact, trials with the cultivar 'Piel de Sapo' showed that yield was particularly reduced when deficits were applied during blooming (Fabeiro et al. 2002). In garlic (*Allium sativum* L.) deficit irrigation had its most detrimental effect on yield when applied during the ripening stage but when applied at the bulbification stage it decreased both yield and quality (bulb size) (Cortés et al. 2003).

Ornamentals

Cameron et al. (2004, 2006) found that deficit irrigation (>50% ETc) has commercial potential to reduce excessive growth of several woody ornamentals belonging to the genus *Cotinus* and *Forsythia* and to reduce water consumption by 50% to 90% relatively to the irrigation used commercially. Moderate water deficits imposed by RDI (at 50% of the ETc) improved commercial crop quality. Shorter internodes and shoots, and identical number of primary shoots gave more compact plants and suppressed the need for mid-season pruning (Cameron et al. 2006). More severe water deficits (at ≤25% of the ETc) resulted in leaf injury and consequently lower quality (Cameron et al. 2006).

The effects of RDI (40% of the fully irrigated control) were tested on *Leucodendron* cv 'Safari Sunset', a commercially relevant protea cultivar (Silber et al. 2007). Short events of water deficits had no negative effect on the flower head dimensions

nor on the number of marketable stems but resulted in too small leaves, and thus on quality loss. Plants under continuous water deficit had the lowest total dry weights and the lowest proportion of marketable heads (Silber et al. 2007).

Different deficit irrigation regimes were tested on seedlings of several ornamental species such as *Silene vulgaris* L., *Rosmarinus officinalis* L. and *Nerium Oleander* L. (Sánchez-Blanco et al. 2004; Arreola et al. 2006; Bañon et al. 2006). Moderate stress during the nursery phase reduced shoot length, stem diameter and leaf area by the time of transplantation and roots were shorter, thicker and less ramified (Sánchez-Blanco et al. 2004). These morphological changes together with a more efficient stomatal regulation resulted in higher survival rates and better adaptation to transplantation under dry environments due to improved water relations (Sánchez-Blanco et al. 2004).

Conclusions and Future Developments

Water scarcity (in quantity and quality) and the increasing competition for water resources between agriculture and other sectors are forcing growers to consider more seriously the adoption of water saving strategies especially in areas of intensive horticulture production and limited water resources. This will be even more relevant if we consider the progressive increase of water prices.

Published reports show that deficit irrigation strategies can be successfully applied to several important horticultural crops, in particular to those that are typically resistant to water stress in order to improve WUE and save water. However, contrasting results described for the same species suggest that a better understanding is needed on how the cultivar, rootstocks or soil characteristics influence plant responses to water deficit. Better knowledge on the vulnerability of each developmental phase of plants to water deficits is also necessary in order to set the most adequate RDI, DI or PRD irrigation scheduling. Studies on the long-term effects of deficit irrigation on plant performance are also important for crops with long commercial life like fruit trees or grapevines. Identically the possibility of extending deficit irrigation strategies to a wider range of horticultural crops, including those more prone to water stress, should be the objects of further investigation.

Combination of deficit irrigation strategies with other practices like mulching, or protected cultivation may also help to improve WUE and minimize losses in yield or quality in vegetable crops (Kirnak and Demirtas 2006). Grafting on specific rootstocks more adapted to water stress conditions may be another tool to improve crop growth response under artificially imposed mild water stress. Finally, developments in monitoring systems to precisely assess plant water status in the field or in greenhouse conditions will facilitate crop management under deficit irrigation conditions.

References

- Ainsworth EA, Rogers A** (2007). The response of photosynthesis and stomatal conductance to rising [CO₂]: Mechanisms and environmental interactions. *Plant Cell Environ.* **30**, 258–270.
- Alegre S, Girona J, Marsal J, Arbones A, Motilva MJ, Romero MP** (1997). Regulated deficit irrigation in olive trees. *Acta Hort.* **474**, 373–376.
- Arreola J, Franco JA, Vicente MJ, Martínez-Sánchez JJ** (2006). Effect of nursery irrigation regimes on vegetative growth and root development of *Silene vulgaris* after transplantation into semi-arid conditions. *J. Hortic. Sci. Biotech.* **81**, 583–592.
- Assmann SM** (1999). The cellular basis of guard cell. sensing of rising CO₂. *Plant Cell. Environ.* **22**, 629–637.
- Bacon M** (2004). Water Use Efficiency in Plant Biology. In: Bacon MA, ed. *Water Use Efficiency in Plant Biology*. Blackwell Publishing, UK. pp. 1–26.
- Bacon MA, Wilkinson S, Davies WJ** (1998). pH-regulated leaf cell expansion in drought plants is abscissic acid dependent. *Plant Physiol.* **114**, 1507–1515.
- Bang H, Sleskovar DI, Bender DA, Crosby K** (2004). Deficit irrigation impact on lycopene, soluble solids, firmness and yield of diploid and triploid watermelon in three distinct environments. *J. Hortic. Sci. Biotech.* **79**, 885–890.
- Bañon S, Ochoa J, Franco JA, Alarcón JJ, Sanchez-Blanco MJ** (2006). Hardening of oleander seedlings by deficit irrigation and low air humidity. *Environ. Exp. Bot.* **56**, 36–43.
- Behboudian MH, Singh Z** (2001). Water relations and irrigation scheduling in grapevine. *Hortic. Rev.* **27**, 189–225.
- Bernacchi CJ, Portis AR, Nakano H, von Caemmerer S, Long SP** (2002). Temperature response of mesophyll conductance; implications for the determination of Rubisco enzyme kinetics and for limitations to photosynthesis *in vivo*. *Plant Physiol.* **130**, 1992–1998.
- Blanke A, Rozelle S, Lohmar B, Wang J, Huang J** (2007). Water saving technology and saving water in China. *Agric. Water Manage.* **87**, 139–150.
- Boland AM, Mitchell PD, Jerie PH, Goodwin I** (1993). The effect of regulated deficit irrigation on tree water use and growth of peach. *J. Hortic. Sci.* **68**, 261–274.
- Bravdo BA** (2005). Physiological mechanisms involved in the production of non-hydraulic root signals by partial rootzone drying – a review. *Acta Hort.* **689**, 267–276.
- Bravdo BA, Hepner Y, Loinger C, Cohen S, Tabacmen H** (1985). Effect of irrigation and crop level on growth, yield and wine quality of Cabernet Sauvignon. *Am. J. Enol. Viticult.* **36**, 132–139.
- Bunce JA** (1996). Does transpiration controls stomata responses to water vapour pressure deficit? *Plant Cell Environ.* **19**, 131–135.
- Cameron RWF, Wilkinson S, Davies WJ** (2004). Regulation of plant growth in container-grown ornamentals through the use of controlled irrigation. *Acta Hort.* **630**, 305–312.
- Cameron RWF, Harrison-Murray RS, Atkinson CJ, Judd HL** (2006). Regulated deficit irrigation – a means to control growth in woody ornamentals. *J. Hortic. Sci. Biotech.* **81**, 435–443.

- Carvalho SMP** (2000). Water availability in Almeria. In: Costa JM, Heuvelink E, eds. *Greenhouse Horticulture in Almeria – Report on a study tour*. Horticultural Production Chains, Wageningen University, The Netherlands. pp. 39–47.
- Centritto M, Wahbi S, Serraj R, Chaves MM** (2005). Effects of partial rootzone drying (PRD) on adult olive tree (*Olea europaea* L.) in field conditions under arid climate: I. Photosynthetic responses. *Agr. Ecosyst. Environ.* **106**, 303–311.
- Chalmers DJ, Mitchell PD, van Heek L** (1981). Control of peach tree growth and productivity by regulated water supply, tree density and summer pruning. *J. Am. Soc. Hortic. Sci.* **106**, 307–312.
- Chaves MM** (1991). Effects of water deficits on carbon assimilation. *J. Exp. Bot.* **42**, 1–16.
- Chaves MM, Oliveira MM** (2004). Mechanisms underlying plant resilience to water deficits: Prospects for water-saving agriculture. *J. Exp. Bot.* **55**, 2365–2384.
- Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML et al.** (2002). How plants cope with water stress in the field. Photosynthesis and growth. *Ann. Bot.* **89**, 907–916.
- Chaves MM, Maroco JP, Pereira JS** (2003). Understanding plant responses to drought – from genes to the whole plant. *Funct. Plant Biol.* **30**, 239–264.
- Cifre J, Bota J, Escalona JM, Medrano H, Flexas J** (2005). Physiological tools for irrigation scheduling in grapevine (*Vitis vinifera* L.). An open gate to improve water-use efficiency? *Agr. Ecosyst. Environ.* **106**, 159–170.
- Cohen Y, Alchanatis V, Meron M, Saranga Y, Tsipris J** (2005). Estimation of leaf water potential by thermal imagery and spatial analysis. *J. Exp. Bot.* **56**, 1843–1852.
- Condon AG, Richards RA, Rebetzke GJ, Farquhar GD** (2004). Breeding for high water-use efficiency. *J. Exp. Bot.* **407**, 2447–2460.
- Correia MJ, Rodrigues ML, Osorio ML, Chaves MM** (1999). Effects of growth temperature on the response of lupin stomata to drought and abscisic acid. *Aust. J. Plant Physiol.* **26**, 549–559.
- Cortés CF, Martín de Santa Olalla F, Urrea RL** (2003). Production of garlic (*Allium sativum* L.) under controlled deficit irrigation in a semi-arid climate. *Agric. Water Manage.* **59**, 155–167.
- Costa JM, Heuvelink E** (2004). China's greenhouse horticulture: An overview. In: Costa JM, Heuvelink E, Botden N, eds. *Greenhouse Horticulture in China: Situation and prospects*. Horticultural Production Chains Group, The Netherlands. pp. 7–41.
- Cummins WR, Kende H, Raschke K** (1971). Specificity and reversibility of the rapid stomatal response to abscisic acid. *Planta* **99**, 347–351.
- Davies WJ, Mansfield TA** (1987). Auxins and stomata. In: Zeiger E, Farquhar GD, Cowan IR, eds. *Auxins and Stomata, Stomatal Function*. Stanford University Press, UK. pp. 293–309.
- Davies WJ, Zhang JH** (1991). Root signals and the regulation of growth and development of plants in drying soil. *Annu. Rev. Plant Phys.* **42**, 55–76.
- Davies WJ, Tardieu F, Trejo CL** (1994). How do chemical signals work in plants that grow in drying soil? *Plant Physiol.* **104**, 309–314.
- Davies WJ, Bacon MA, Thompson DS, Sobeih W, Rodriguez LG** (2000). Regulation of leaf and fruit growth in plants growing in drying soil: Exploitation of the plant's chemical signalling system and hydraulic architecture to increase the efficiency of water use in agriculture. *J. Exp. Bot.* **51**, 1617–1626.
- Davies WJ, Kudoyarova G, Hartung W** (2005). Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought. *J. Plant Growth Regul.* **24**, 285–295.
- Dodd IC** (2005). Root-to-shoot signalling: Assessing the roles of 'up' in the up and down world of long-distance signalling. *Plant Soil* **274**, 251–270.
- Dodd IC, Stikic R, Davies WJ** (1996). Chemical regulations of gas exchange and growth of plants in drying soil in the field. *J. Exp. Bot.* **47**, 1475–1490.
- Dokoozlian NK, Kliewer WM** (1996). Influence of light on grape berry growth and composition varies during fruit development. *J. Am. Soc. Hort. Sci.* **121**, 869–874.
- Dorji K, Behboudian MH, Zegbe-Dominguez JA** (2005). Water relations, yield, and fruit quality of hot pepper under deficit irrigation and partial rootzone drying. *Sci. Hortic.* **104**, 137–149.
- Downward SR, Taylor R** (2007). An assessment of Spains Programa AGUA and its implications for sustainable water management in the province of Almeria southeast Spain. *J. Environ. Manage.* **82**, 272–289.
- Dry PR, Loveys BR** (1998). Factors influencing grapevine vigour and the potential for control with partial rootzone drying. *Aust. J. Grape Wine Res.* **4**, 140–148.
- Dry PR, Loveys BR** (1999). Grapevine shoot growth and stomatal conductance are reduced when part of the root system is dried. *Vitis* **38**, 151–156.
- Dry PR, Loveys BR, Botting D, Düring H** (1996). Effect of partial root-zone drying on grapevine vigour yield composition of fruit and use of water. In: Stockeley C, Sas A, Johnstone R, Lee T, eds. *Proceedings of the Ninth Australian Wine Industry Technical Conference*. Adelaide. pp. 128–131.
- Dry PR, Loveys BR, Düring H** (2000a). Partial drying of the rootzone of grape. I. Transient changes in shoot growth and gas exchange. *Vitis* **39**, 3–7.
- Dry PR, Loveys BR, Düring H** (2000b). Partial drying of the rootzone of grape. II. Changes in the pattern of root development. *Vitis* **39**, 9–12.
- Eamus D, Shanahan ST** (2002). A rate equation model of stomatal responses to vapour pressure deficit and drought. *BMC Ecol.* **2**, 1–14.
- Ebel RC, Proebsting EL, Evans RG** (2001). Apple tree and fruit responses to early termination of irrigation in a semi-arid environment. *Hort. Sci.* **36**, 1197–1201.
- Einhorn T, Caspari HW** (2004). Partial rootzone drying and deficit irrigation of 'Gala' apples in a semi-arid climate. *Acta Hort.* **664**, 197–204.
- Escalona JM, Flexas J, Medrano H** (1999). Stomatal and non-stomatal limitations of photosynthesis under water stress in field-grown grapevines. *Aust. J. Plant Physiol.* **26**, 421–433.
- Esteban MA, Villanueva MJ, Lissarrague JR** (2001). Effect of irrigation on changes in the anthocyanin composition of the skin of cv

- Tempranillo (*Vitis vinifera* L.) grape berries during ripening. *J. Sci. Food Agric.* **81**, 409–420.
- Fabeiro C, Martín de Santa Olalla F, de Juan JA** (2001). Yield and size of deficit irrigated potatoes. *Agric. Water Manage.* **48**, 255–266.
- Fabeiro C, Martín de Santa Olalla F, de Juan JA** (2002). Production of muskmelon (*Cucumis melon* L.) under controlled deficit irrigation in a semi-arid climate. *Agric. Water Manage.* **54**, 93–105.
- FAO** (2006). FAO statistical databases. Agriculture Data Collection <http://faostat.fao.org/>. FAO, Rome, Italy.
- Fereres E, Evans RG** (2006). Irrigation of fruit trees and vines. *Irrigation Sci.* **24**, 55–57.
- Fereres E, Soriano MA** (2007) Deficit irrigation for reducing agricultural water use. *J. Exp. Bot.* **58**, 147–159.
- Franks PJ, Farquhar GD** (1999). A relationship between humidity response, growth form and photosynthetic operating point in C₃ plants. *Plant Cell Environ.* **22**, 1337–1349.
- Franks PJ, Cowan IR, Farquhar GD** (1997). The apparent feedforward response of stomata to air vapour pressure deficit: Information revealed by different experimental procedures with two rainforest trees. *Plant Cell Environ.* **20**, 142–145.
- Girona J, Gelly M, Mata M, Arbonès A, Rufat J, Marsal J** (2005). Peach tree response to single and combined deficit irrigation regimes in deep soils. *Agric. Water Manage.* **72**, 97–108.
- Goldhamer DA** (1999). Regulated deficit irrigation for California canning olives. *Acta Hort.* **474**, 373–375.
- Gollan T, Schurr U, Schulze ED** (1992). Stomatal response to drying soil in relation to changes in the xylem sap composition of *Helianthus annuus*. I. The concentration of cations anions, amino-acids in, and pH of the xylem sap. *Plant Cell Environ.* **15**, 551–559.
- Gómez-Rico A, Salvador MD, Moriana A, Pérez D, Olmedilla N, Ribas F et al.** (2007). Influence of different irrigation strategies in a traditional Cornicabra cv. Olive orchard on virgin olive oil compositions and quality. *Food Chem.* **100**, 568–578.
- González-Altozano P, Castel JR** (2000a). Effects of regulated deficit irrigation on 'Clementina de nules' citrus trees growth, yield and fruit quality. *Acta Hort.* **537**, 749–758.
- González-Altozano P, Castel JR** (2000b). Regulated deficit irrigation in 'Clementina de Nules' citrus trees. II: Vegetative growth. *J. Am. Soc. Hortic. Sci.* **75**, 388–392.
- Goodwin I, Boland AM** (2002). Scheduling deficit irrigation of fruit trees for optimizing water use efficiency. *Deficit Irrigation Practices*. Water Reports Publication n. 22, FAO, Rome. pp. 67–79.
- Gowing DJG, Davies WJ, Jones HG** (1990). A positive root-source signal as an indicator of soil drying in apple *Malus x domestica* Borkh. *J. Exp. Bot.* **41**, 1535–1540.
- Grant OM, Stoll M, Jones HG** (2004). Partial rootzone drying does not affect fruit yield of raspberries. *J. Hortic. Sci. Biotech.* **79**, 125–130.
- Gu S, Gu G, Zoldoske D, Hakim A, Cochran R, Fugelsang K et al.** (2004). Effect of irrigation amount on water relations, vegetative growth, yield and fruit composition of Sauvignon blanc grapevines under partial rootzone drying and conventional irrigation in the San Joaquin Valley of California. *J. Hortic. Sci. Biotech.* **79**, 26–33.
- Hardie WJ, Considine JA** (1976). Response of grapes to water-deficit stress in particular stages of development. *Am. J. Enol. Viticult.* **27**, 55–61.
- Hedrich R, Marten I** (1993). Malate induced feedback-regulation of plasma-membrane anion channels could provide a CO₂ sensor to guard-cells. *EMBO J.* **12**, 897–901.
- Herrick JD, Maherali H, Thomas RB** (2004). Reduced stomatal conductance in sweetgum (*Liquidambar styraciflua*) sustained over long-term CO₂ enrichment. *New Phytol.* **162**, 387–396.
- Honor SJ, Webb AAR, Mansfield TA** (1995). The response of stomata to abscisic acid and temperature are interrelated. *Phil. Trans. R. Soc. London.* **259**, 301–306.
- IPPC** (2001). *Climate Change 2001: Synthesis Report. A contribution of working groups I, II, III to the third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Irving HR, Gehring CA, Parish RW** (1992). Changes in cytosolic pH and calcium of guard cells precede stomatal movements. *Prog. Natl Acad. Sci. USA* **89**, 790–794.
- Jarvis PG** (1976). Interpretation of variations in leaf water potential and stomatal conductance found in canopies in field. *Proc. R. Soc. Lond. Biol. Sci.* **273**, 593–610.
- Jefferies RA, MacKerron DKL** (1993). Responses of potato genotypes to drought. II. Leaf area index, growth and yield. *Ann. Appl. Biol.* **122**, 105–112.
- Jones HG** (1992). *Plants and Microclimate. A Quantitative Approach to Environmental Plant Physiology*, 2nd edn. Cambridge University Press, Cambridge.
- Jones HG** (2004). Irrigation Scheduling: advantages and pitfalls of plant-based methods. *J. Exp. Bot.* **55**, 2427–2436.
- Jones HG, Stoll M, Santos T, Sousa C, Chaves MM, Grant OM** (2002). Use of infra-red thermography for monitoring stomatal closure in the field: Application to grapevine. *J. Exp. Bot.* **53**, 2249–2260.
- Kang S, Zhang J** (2004). Controlled alternate partial root-zone irrigation: Its physiological consequences and impact on water use efficiency. *J. Exp. Bot.* **55**, 2437–2446.
- Kang S, Zhang L, Xiaotao H, Li Z, Jerie P** (2001). An improved water use efficiency for hot pepper grown under controlled alternate drip irrigation on partial roots. *Sci. Hortic.* **89**, 257–267.
- Kang S, Hu X, Goodwin I, Jerie P** (2002). Soil water distribution, water use and yield response to partial rootzone drying under a shallow groundwater table condition in a pear orchard. *Sci. Hortic.* **92**, 277–291.
- Keller M, Hrazdina G** (1998). Interaction of nitrogen availability during bloom and light intensity during veraison. II. Effects on anthocyanin and phenolic development during grape ripening. *Am. J. Enol. Viticult.* **49**, 341–349.
- Kirda C, Cetin M, Dasgan Y, Topcu S, Kaman H, Ekici B et al.** (2004). Yield reponse of greenhouse grown tomato to partial root drying and conventional deficit irrigation. *Agric. Water Manage.* **69**, 191–202.
- Kirnak H, Demirtas MN** (2006). Effects of different irrigation regimes and mulches on yield and macronutrition levels of drip-irrigated cucumber under open field conditions. *J. Plant Nutr.* **29**, 1675–1690.

- Klein M, Perfus-Barbeoch L, Frelet A, Gaedeke N, Reinhardt D, Mueller-Rober B et al.** (2003). The plant multidrug resistance ABC transporter AtMRP5 is involved in guard cell hormonal signalling and water use. *Plant J.* **33**, 119–129.
- Landsberg JJ, Jones HG** (1981). Apple orchards. In: Koslowski TT, ed. *Water Deficits and Plant Growth*, Vol. 4. Academic Press, New York. pp. 419–469.
- Lascève G, Leymarie J, Olney MA, Liscum E, Christie JM, Vavasseur A et al.** (1999). *Arabidopsis* contains at least four independent blue-light-activated signal transduction pathways. *Plant Physiol.* **120**, 605–614.
- Leib BG, Caspari HW, Redulla CA, Andrews PK, Jabro JJ** (2006). Partial rootzone drying and deficit irrigation of 'Fuji' apples in a semi-arid climate. *Irrigation Sci.* **24**, 85–99.
- Li SH, Huguet JG, Schoch PG, Orlando P** (1989). Response of peach tree growth and cropping to soil water deficit at various phenological stages of fruit development. *J. Hortic. Sci.* **64**, 541–552.
- Liu F, Shahnazari A, Andersen MN, Jacobsen SE, Jensen CR** (2006). Effects of deficit irrigation (DI) and partial root drying (PRD) on gas exchange, biomass partitioning and water use efficiency in potato. *Sci. Hortic.* **109**, 113–119.
- Liu F, Savic S, Jensen CR, Shahnazari A, Jacobsen SE, Stikic et al.** (2007). Water relations and yield of lysimeter-grown strawberries under limited irrigation. *Sci. Hortic.* **111**, 128–132.
- Loveys BR** (1984). Diurnal changes in water relations and abscisic acid in field grown *Vitis vinifera* cultivars. III. The influence of xylem-derived abscisic acid on leaf gas exchange. *New Phytol.* **98**, 563–573.
- Loveys BR, Dry PR, Stoll M, McCarthy MG** (2000). Using plant physiology to improve the water efficiency of horticultural crops. *Acta Hort.* **537**, 187–197.
- Loveys BR, Stoll M, Davies WJ** (2004). Physiological approaches to enhance water use efficiency in agriculture: Exploiting plant signalling in novel irrigation practice. In: Bacon MA, ed. *Water Use Efficiency in Plant Biology*. Blackwell Publishing, UK. pp. 113–141.
- Luterbacher J, Xoplaki E, Casty C, Wanner H, Pauling A, Küttel M et al.** (2006). Mediterranean climate variability over the last centuries: A review. In: Lionello P, Malanotte-Rizzoli P, Boscolo R, eds. *The Mediterranean Climate: An Overview of the Main Characteristics and Issues. Mediterranean Climate Variability*. Elsevier, Amsterdam. pp. 27–148.
- Lynch DR, Foroud N, Kozub GC, Farries BC** (1995). The effect of moisture stress at three growth stages on the yield components of yield and processing quality of eight potato cultivars. *Am. Potato J.* **72**, 375–386.
- Maherali H, Johnson HB, Jackson RB** (2003). Stomatal sensitivity to vapour pressure difference over a subambient to elevated CO₂ gradient in a C-3/C-4 grassland. *Plant Cell Environ.* **26**, 1297–1306.
- Mao X, Liu M, Wang X, Liu C, Hou Z, Shi J** (2003). Effects of deficit irrigation on yield and water use of greenhouse grown cucumber in the North China Plain. *Agr. Water Manage.* **61**, 219–228.
- Maroco JP, Pereira JS, Chaves MM** (1997). Stomatal responses to leaf-to-air vapour pressure deficit in sahelian species. *Aust. J. Plant Physiol.* **24**, 381–387.
- Marsal J, Rapoport HF, Manrique T, Girona J** (2000). Pear fruit growth under regulated deficit irrigation in container-grown plants. *Sci. Hortic.* **85**, 243–259.
- Marsal J, Mata M, Arbonés A, Rufat J, Girona J** (2002). Regulated deficit irrigation and rectification of irrigation scheduling in young pear trees: An evaluation based on vegetative and productive response. *Eur. J. Agron.* **17**, 111–122.
- Matthews MA, Anderson MM** (1988). Fruit ripening in grapes (*Vitis vinifera* L.): Responses to seasonal water deficits. *Am. J. Enol. Viticult.* **39**, 313–320.
- Matthews MA, Anderson MM** (1989). Reproductive development in grape (*Vitis vinifera* L.): Responses to seasonal water deficits. *Am. J. Enol. Viticult.* **40**, 52–60.
- Matthews MA, Ishii R, Anderson MM, O'Mahomy M** (1990). Dependence of wine sensory attributes on vine water status. *J. Sci. Food Agr.* **51**, 321–335.
- McAinsh MR, Evans NH, Montgomery LT, North KA** (2002). Calcium signalling responses to pollutants. *New Phytol.* **153**, 441–447.
- McCarthy MG** (1997). The effect of transient water deficit on berry development of cv Shiraz (*Vitis vinifera* L.). *Aust. J. Grape Wine Res.* **3**, 102–108.
- McCarthy MG, Loveys BR, Dry PR** (2002). Regulated deficit irrigation and partial rootzone drying as irrigation management techniques for grapevines. In: *Deficit Irrigation Practices. Water Reports Publication n. 22*, FAO, Rome. pp. 79–87.
- Merlot S, Mustilli AC, Genty B, North H, Lefebvre V, Sotta B et al.** (2002). Use of infrared thermal imaging to isolate *Arabidopsis* mutants defective in stomatal regulation. *Plant J.* **30**, 601–609.
- Merlot S, Leonhardt N, Fenzi F, Valon C, Costa M, Piette L et al.** (2007). Constitutive activation of a plasma membrane H⁺-ATPase prevents abscisic acid-mediated stomatal closure. *EMBO J.* **26**, 3216–3226.
- Mingo DM, Bacon MA, Davies WJ** (2003). Non-hydraulic regulation of fruit growth in tomato plants (*Lycopersicon esculentum* cv Solairo) growing in drying soil. *J. Exp. Bot.* **54**, 1205–1212.
- Mingo DM, Theobald JC, Bacon MA, Davies WJ, Dodd IC** (2004). Biomass allocation in tomato (*Lycopersicon esculentum*) plants grown under partial rootzone drying: Enhancement of root growth. *Funct. Plant Biol.* **31**, 971–978.
- Mitchell PD, Chalmers DJ** (1982). The effect of reduced water supply on peach tree growth and yields. *J. Am. Soc. Hort. Sci.* **107**, 853–856.
- Mitchell PD, van den Ende B, Jerie PH, Chalmers DJ** (1989). Response of 'Bartlett' pear to withholding irrigation, regulated deficit irrigation, and tree spacing. *J. Am. Soc. Hort. Sci.* **114**, 15–19.
- Mitchell JP, Shennen C, Grattan SR, May DM** (1991). Tomato fruit yields and quality under water deficit and salinity. *J. Am. Soc. Hort. Sci.* **116**, 215–221.
- Monteith JL** (1995). A reinterpretation of stomatal responses to humidity. *Plant Cell Environ.* **18**, 357–364.

- Morison JIL** (1987). Intercellular CO₂ concentration and stomatal response to CO₂. In: Zeiger E, Farquhar GD, Cowan IR, eds. *Stomatal Function*. Stanford University Press, Stanford. pp. 229–252.
- Morison JIL, Gifford RM** (1983). Stomatal sensitivity to carbon-dioxide and humidity- a comparison of C₃ and C₄ grass species. *Plant Physiol.* **71**, 789–796.
- Mpelasoka BS, Behboudian MH** (2002). Production of aroma volatiles in response to deficit irrigation and to crop load in relation to fruit maturity for “Braeburn” apple. *Postharvest Biol. Tec.* **24**, 1–11.
- Mpelasoka BS, Behboudian MH, Green SR** (2001). Water use, yield and fruit quality of lysimeter-grown apple trees: Responses to deficit irrigation and to crop load. *Irrigation Sci.* **20**, 107–113.
- Netting AG** (2000). pH, abscisic acid and the integration of metabolism in plants under stressed and non-stressed conditions: Cellular responses to stress and their implication for plant water relations. *J. Exp. Bot.* **51**, 147–158.
- Nimah M, Darwish I, Bashour I** (2000). Potato yield response to deficit irrigation and N fertilization. *Acta Hort.* **537**, 823–830.
- O’Connell MG, Goodwin I** (2004). Pear water relations under partial rootzone drying. *Acta Hort.* **664**, 453–459.
- Ogawa JM, English H** (1991). *Disease of temperature zone tree fruit and nut crops*. University of California, Oakland.
- Pavel EW, Villiers AJ** (2004). Responses of mango trees to reduced irrigation regimes. *Acta Hort.* **646**, 63–68.
- Peet MM** (2005). Irrigation and fertilization. In: Heuvelink E, ed. *Tomatoes, Crop Production Science in Horticulture*. CABI Publishing, UK. pp. 171–198.
- Pereira JS, Chaves MM, Caldeira MC, Correia AV** (2006). Water availability and productivity. In: Morison J, Croft M, eds. *Plant Growth and Climate Change*. Blackwell Publishers, London. pp. 118–145.
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola J-M, Basile I et al.** (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**, 429–436.
- Pulupol LU, Behboudian MH, Fisher KJ** (1996). Growth, yield and postharvest attributes produced under deficit irrigation. *Hort. Sci.* **31**, 926–929.
- Ramalan AA, Nwokeocha CU** (2000). Effects of furrow irrigation methods, mulching and soil water suction on the growth, yield and water use efficiency of tomato in the Nigerian Savanna. *Agr. Water Manage.* **45**, 317–330.
- Reynolds AG, Naylor AP** (1994). ‘Pinot noir’ and ‘Riesling’ grapevines respond to water stress duration and soil water-holding capacity. *Hort. Sci.* **29**, 1505–1510.
- Romero P, Botia P, Garcia F** (2004). Effects of regulated deficit irrigation under subsurface drip irrigation conditions on vegetative development and yield of mature almond trees. *Plant Soil* **260**, 169–181.
- Sánchez-Blanco MJ, Torrecillas A, León A, del Amor F** (1989). The effect of different irrigation treatments on yield and quality of Verna lemon. *Plant Soil* **120**, 299–302.
- Sánchez-Blanco J, Ferrández T, Navarro A, Bañon S, Alarcón JJ** (2004). Effects of irrigation and air humidity preconditioning on water relations, growth and survival of *Rosmarinus officinalis* plants during and after transplanting. *J. Plant Physiol.* **161**, 1133–1142.
- Santos TP, Lopes CM, Rodrigues ML, Souza CR, Maroco JP, Pereira JS et al.** (2003). Partial rootzone drying: Effects on growth, and fruit quality of field-grown grapevines (*Vitis vinifera* L.). *Funct. Plant Biol.* **30**, 663–671.
- Santos TP, Lopes CM, Rodrigues ML, de Souza CR, Ricardo-Da-Silva JM, Maroco JP et al.** (2005). Effects of partial root-zone drying irrigation on cluster microclimate and fruit composition of field-grown Castelão grapevines. *Vitis* **44**, 117–125.
- Santos TP, Lopes CM, Rodrigues ML, de Souza CR, Ricardo-da-Silva JM, Maroco JP et al.** (2007). Effects of deficit irrigation strategies on cluster microclimate for improving fruit composition of ‘Moscatel’ field-grown grapevines. *Sci. Hort.* **112**, 321–330.
- Schroeder JI, Allen GJ, Hugovieux V, Kwak JM, Waner D** (2001). Guard cell signal transduction. *Annu. Rev. Plant Phys.* **52**, 627–658.
- Schurr U, Gollan T, Schulze ED** (1992). Stomatal response to drying soil in relation to changes in the xylem sap composition of *Helianthus annuus* L. Stomatal sensitivity to abscisic acid imported from xylem sap. *Plant Cell Environ.* **15**, 561–567.
- Sepulcre-Cantó G, Zarco-Tejada PJ, Jiménez-Muñoz JC, Sobrino JA, de Miguel, Villalobos FJ** (2006). Detection of water stress in an olive orchard with thermal remote sensing imagery. *Agr. For. Meteorol.* **136**, 31–44.
- Shahnazari A, Liu F, Andersen MN, Jacobsen S, Jensen CR** (2007). Effects of partial root-zone drying (PRD) on yield, tuber size and water use efficiency in potato (*Solanum tuberosum*) under field conditions. *Fields Crops Res.* **100**, 117–124.
- Shock CC, Feibert EBG** (2002). Deficit irrigation in potato. In: *Deficit Irrigation Practices*. Water Reports Publication n. 22, FAO, Rome. pp. 47–56.
- Schulze ED** (1986). Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. *Annu. Rev. Plant Physiol.* **37**, 247–274.
- Silber A, Levi M, Cohen M, Davis N, Shtaynmetz Y, Assouline S** (2007). Response of *Leucadendron* ‘Safari Sunset’ to regulated deficit irrigation: Effects of stress timing on growth and yield quality. *Agr. Water Manage.* **87**, 162–170.
- Sobeih W, Dodd IC, Bacon MA, Grierson DC, Davies WJ** (2004). Long-distance signals regulating stomatal conductance and leaf growth in tomato (*Lycopersicon esculentum*) plants subjected to partial rootzone drying. *J. Exp. Bot.* **55**, 2353–2364.
- Souza CR, Maroco JP, Santos T, Rodrigues ML, Lopes C, Pereira JS et al.** (2003). Partial rootzone-drying: Regulation of stomatal aperture and carbon assimilation in field grown grapevines (*Vitis vinifera* cv. ‘Moscatel’). *Funct. Plant Biol.* **30**, 653–662.
- Souza CR, Maroco J, Santos T, Rodrigues ML, Lopes CM, Pereira JS et al.** (2005). Impact of deficit irrigation on water use efficiency and carbon isotope composition ($\delta^{13}\text{C}$) of field-grown grapevines under Mediterranean climate. *J. Exp. Bot.* **56**, 2163–2172.
- Stafet MG** (1962). The effect of temperature on opening of the stomatal cells. *Plant Physiol.* **15**, 772–779.

- Stanghellini C, Kempkes FLK, Knies P** (2003). Enhancing environmental quality in agricultural systems. *Acta Hort.* **609**, 277–283.
- Stoll M, Loveys BR, Dry P** (2000). Hormonal changes induced by partial root zone drying of irrigated grapevine. *J. Exp. Bot.* **51**, 1627–1634.
- Stone PJ, Wilson DR, Beid JB, Gillespie RN** (2001). Water deficit effects on weet corn I. water use, radiation use efficiency, growth, and yield. *Aust. J. Agr. Res.* **52**, 103–113.
- Talbott LD, Zeiger E** (1996). Central roles for potassium and sucrose in guard-cell osmoregulation. *Plant Physiol.* **111**, 1051–1057.
- Talbott LD, Rahveh E, Zeiger E** (2003). Relative humidity is a key factor in the acclimation of the stomatal response to CO₂. *J. Exp. Bot.* **54**, 2141–2147.
- Testi L, Villalobos FJ, Orgaz F, Fereres E** (2006). Water requirements of olive orchards: I simulation of daily evapotranspiration for scenario analysis. *Irrig. Sci.* **24**, 69–76.
- Teviotdale BL, Goldhammer DA, Viveros M** (2001). Effects of deficit irrigation on hull rot disease of almond trees caused by *Monilinia fructicola* and *Rhizopus stolonifer*. *Plant Dis.* **85**, 399–403.
- Topcu S, Kirda C, Dasgan Y, Kaman H, Cetil M, Yazici A et al.** (2007). Yield response and N-fertilizer recovery of tomato grown under deficit irrigation. *Eur. J. Agron.* **26**: 64–70.
- Verreynne JS, Rabe F, Theron KI** (2001). The effect of combined deficit irrigation and summer trunk girdling on the internal fruit quality of 'Marisol' Clementines. *Sci. Hortic.* **91**, 25–37.
- Wahbi S, Wakrim B, Aganchich B, Tahi H, Serraj R** (2005). Effects of partial rootzone drying (PRD) on adult olive tree (*Olea europea*) in field conditions under arid climate. I. Physiological and agronomic responses. *Agr. Ecosyst. Environ.* **106**, 289–301.
- Webb AAR, Hetherington AM** (1997). Convergence of the abscisic acid, CO₂, and extracellular calcium signal transduction pathways in stomatal guard cells. *Plant Physiol.* **114**, 1557–1560.
- Wilkinson S, Davies WJ** (1997). Xylem sap pH increase: A drought signal received at the apoplastic face of the guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. *Plant Physiol.* **113**, 559–573.
- Wilkinson S, Davies WJ** (2002). ABA-based chemical signalling: The co-ordination of responses to stress in plants. *Plant Cell Environ.* **25**, 195–210.
- Williams LE, Matthews MA** (1990). Grapevine. In: Stewart BA, Nielsen DR, eds. *Irrigation of Agricultural Crops*. Series of Agronomy n. 30, Madison, Wisconsin. pp. 1019–1055.
- Zegbe JA, Behboudian MH, Clothier BE** (2006). Responses of 'Petopride' processing tomato to partial rootzone drying at different phenological stages. *Irrig. Sci.* **24**, 203–210.
- Zegbe-Dominguez JA, Behboudian MH, Lang A, Clothier BE** (2003). Deficit irrigation and partial rootzone drying maintain fruit dry mass and enhance fruit quality in "Petopride" processing tomato (*Lycopersicon esculentum*, Mill). *Sci. Hortic.* **98**, 505–510.
- Zeiger E** (1983). Biology of stomatal guard cells. *Annu. Rev. Plant Physiol.* **34**, 441–475.
- Zeiger E, Farquhar GD, Cowan LR** (1987). *Stomatal function*. Stanford University Press, California.
- Zhang JH, Schurr U, Davies WJ** (1987). Control of stomatal behavior by abscisic-acid which apparently originates in the roots. *J. Exp. Bot.* **38**, 1174–1181.

(Handling editor: Jianhua Zhang)