

REVIEW PAPER

# Water shortage and quality of fleshy fruits—making the most of the unavoidable

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## Abstract

**Extreme climatic events, including drought, are predicted to increase in intensity, frequency, and geographic extent as a consequence of global climate change. In general, to grow crops successfully in the future, growers will need to adapt to less available water and to take better advantage of the positive effects of drought. Fortunately, there are positive effects associated with drought. Drought stimulates the secondary metabolism, thereby potentially increasing plant defences and the concentrations of compounds involved in plant quality, particularly taste and health benefits. The role of drought on the production of secondary metabolites is of paramount importance for fruit crops. However, to manage crops effectively under conditions of limited water supply, for example by applying deficit irrigation, growers must consider not only the impact of drought on productivity but also on how plants manage the primary and secondary metabolisms. This question is obviously complex because during water deficit, trade-offs among productivity, defence, and quality depend upon the intensity, duration, and repetition of events of water deficit. The stage of plant development during the period of water deficit is also crucial, as are the effects of other stressors. In addition, growers must rely on relevant indicators of water status, i.e. parameters involved in the relevant metabolic processes, including those affecting quality. Although many reports on the effects of drought on plant function and crop productivity have been published, these issues have not been reviewed thus far. Here, we provide an up-to-date review of current knowledge of the effects of different forms of drought on fruit quality relative to the primary and secondary metabolisms and their interactions. We also review conventional and less conventional indicators of water status that could be used for monitoring purposes, such as volatile compounds. We focus on fruit crops owing to the importance of secondary metabolism in fruit quality and the importance of fruits in the human diet. The issue of defence is also briefly discussed.**

**Key words:** Water shortage, fruit quality, irrigation management, adaptation and interaction mechanisms, volatile metabolome.

Abbreviations: ABA, abscisic acid; AGP-ase, ADP-glucose pyrophosphorylase; AO, ascorbate oxidase; APX, ascorbate peroxidase; AsA, ascorbic acid; CA, carbonic anhydrase; DHAR, dehydroascorbate reductase; ET, ethylene; ETC, daily evapotranspiration; GAPDH, glyceraldehyde-3-phosphate dehydrogenase; GDBH, growth differentiation balance hypothesis; JA, jasmonic acid; LOX, lipoxygenase; MDHA, monodehydroascorbate; MDHAR, monodehydroascorbate reductase; NIRS, near infrared spectroscopy; NMR, nuclear magnetic resonance; NO, nitric oxide; PEG, polyethylene glycol; PRI, photochemical reflectance index; QTL, quantitative trait locus; ROS, reactive oxygen species; SA, salicylic acid; SSC, soluble solids concentrations; SUSY, sucrose synthase; TA, titratable acidity; TFs, transcription factors; TSS, total soluble solids; VOC, volatile organic compound; WD, water deficit; WUE, water-use efficiency.

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## Introduction

Agriculture is facing increasingly frequent periods of drought, and in the future water reduction is expected to exert the most adverse impact upon growth and productivity among abiotic stress factors (Shao *et al.*, 2008). This trend is of particular concern in the Mediterranean region, which will experience more frequent periods of intensive drought, leading to the extension of arid areas (Gao and Giorgi, 2008). In many countries where the lack of water is not yet critical, crops are currently irrigated in excess to avoid water shortage and promote plant growth; however, this irrigation may be detrimental to crop quality and water resources around the world. In the Mediterranean area, agriculture consumes approximately  $177.7 \times 10^9 \text{ m}^3 \text{ year}^{-1}$  (an average figure obtained from data collected between 2003 and 2007 from Mediterranean countries with the exception of countries of the African continent), and a marked reduction in irrigation would save a considerable amount of water (<http://www.fao.org/nr/water/aquastat/data/query/results.html>; e.g. 6 September 2013). It is generally accepted that this objective can be achieved by increasing water-use efficiency (WUE). For instance, regulated deficit irrigation or partial root drying have been proposed to reduce water consumption in fruit orchards and to stimulate plant adaptation to stress-prone environments (Stikic *et al.*, 2003). These techniques enable the plants to more effectively explore the soil with their roots and stimulate the production of compounds such as abscisic acid (ABA), a major phytohormone involved in the responses of plants to abiotic stress (Shen *et al.*, 2014). These strategies are promising but they have been only partially 'explored' in order to preserve yield and have overlooked other traits such as crop quality. Based on our knowledge of the mechanisms involved in plant and fruit responses to water deficit (WD), we believe that other irrigation strategies involving a greater reduction in water supply could be developed. Moreover, in this review, we propose a re-examination of commonly held ideas on water requirements for crop performance in light of current knowledge of the effect of drought on quality criteria, such as the content of phytonutrients, and on plant defences. We focus on fruit crops owing to their agronomic and dietary importance. Fleshy fruits are the most important crops in the world after grains, and they represent a key ingredient of a healthy diet (<http://www.fao.org/publications/sofi/en>; e.g. 16 September 2013) owing to their high contents of phytonutrients, vitamins, and antioxidants.

Fruit quality is measured according to several criteria, the relative importance of which differs among producers, consumers, and distributors (Shewfelt, 1999). Fruit size and external attractiveness (colour, form, size...) determine commercial quality, whereas adequate flesh firmness ensures a reasonable shelf-life. The consumer purchases fruit based on appearance and aroma, which are associated with taste and shelf-life. However, flavour promotes fruit consumption, and the characteristics of high-quality fruit include high sugar levels and an appropriate sugar-to-acid ratio. Consumers are also increasingly concerned with the nutritive value of fresh fruits, which is typically related to the antioxidant content (primarily polyphenols and vitamin C). The global demand

for high-quality fruits that taste good, are rich in vitamins and antioxidants, are environmentally friendly, and can endure the demands of worldwide supply chains is growing rapidly and requires continuous effort to improve varieties and respond to environmental constraints.

A wealth of studies have compared the behaviour of different plant species under well-irrigated and deficit irrigation conditions. The molecular response to drought has been intensively investigated in many species and numerous responsive genes have been identified which are involved in many signalling and metabolic pathways (Atkinson and Urwin, 2012). To date, only few candidate genes for stress resistance have been characterized and the links between gene or protein expression, and plant or organ phenotype under field conditions are still poorly understood. At the plant or organ level, many studies have discussed the overall negative impact of WD on yield, which leads to growth limitation or even plant death or organ abortion under extreme conditions. One of the major and most well-documented effects of drought is stomatal closure (Damour *et al.*, 2010). The associated decrease in transpirational water loss is beneficial for plant survival because it helps the plant to maintain water balance; however, this positive effect comes at the price of a reduction in net  $\text{CO}_2$  uptake. A decrease in net photosynthesis not only translates into a decrease in carbohydrate supply to the fruits, it also creates conditions that are conducive to photo-oxidative stress, i.e. the photosynthesis-associated production of reactive oxygen species (ROS), including  $\text{O}_2^-$ ,  $\cdot\text{OH}$  and possibly  $\text{H}_2\text{O}_2$  (Grassmann *et al.*, 2002). Because oxidative stress stimulates the accumulation of antioxidant compounds, a beneficial effect of WD on the health value of fruits may be expected and has been reported in many descriptive studies (Nora *et al.*, 2012). More generally, a recent review (Wang and Frei, 2011) outlined some typical patterns in crop-quality response to several abiotic stressors and indicated a tendency towards a loss in taste but an increase in nutritional value. Thus, trade-offs between crop yield and quality might be achieved under controlled WD conditions provided that growers have access to quantitative information not only related to productivity but also to crop quality. In this perspective, experimental conditions should better cover the range of conditions experienced by plants under natural conditions (West *et al.*, 2004). Indeed, compared with experimental conditions that focus on one or two stress factors applied at a given period, in the field, plants are prone to stresses of varying intensity (from mild to severe stress), the progressive development of stress and soil dehydration and repeated alternating cycles of stress and recovery that occur during different periods of plant development. Moreover, in the field, one single stress factor rarely occurs in isolation; thus, several complex interactions and feedback cycles involved in plant responses must be considered. Finally, cumulative or transient effects are integrated by the plant throughout the crop cycle, which may lead to markedly contrasting responses with respect to plant health, productivity, and quality.

We review in this paper our current state of knowledge about the effects of WD on quality criteria of fleshy fruits

(soluble sugars, organic acids, volatile aromas, and texture), with special emphasis on the underlying physiological mechanisms. Because of the growing importance of the concentration in phytochemicals as a quality criteria of fruits, we examine in detail the roles played by the reduction in supply of precursors and the oxidative stress, which are both associated with WD. During WD, trade-offs among productivity, defence, and quality depend upon the intensity, duration, and repetition of the phases of WD. The stage of plant development during the period of WD is also crucial, as are the effects of genetic factors and other co-occurring stresses. We therefore examine the range of plant/fruit responses to WD depending on genotype, stress intensity, timing, and interactions with other abiotic and biotic stresses. Finally, we review briefly novel non-destructive methods and tools that can be used to assess plant physiological status and fruit quality criteria in response to WD.

To avoid redundancy with several recent reviews on WD or stress (not specifically devoted to fruit), we do not detail the impact of drought on photosynthetic machinery, ROS synthesis, and the damaging effects of ROS on metabolic pathways (Silva *et al.*, 2013), genes responding to water stress (Tardieu *et al.*, 2011), or the regulation of these genes (Atkinson and Urwin, 2012; Claeys and Inze, 2013; Sujata and Kshitija, 2013), or hormonal pathways (Albacete *et al.*, 2014; Perez-Alfocea *et al.*, 2011; Wilkinson and Davies, 2002). Similarly, we do not discuss the impact of WD on post-harvest quality (Nora *et al.*, 2012). Because the notion of physiological stress is a subject of debate, the term water deficit (WD) is used throughout this review.

## The impact of water deficit on processes underlying fruit organoleptic quality

Important characteristics of fruit organoleptic quality include a fruit's external appearance, size, texture, and taste. Fruit's taste and texture are primarily determined by the amount of dry matter and its sugar, acid, cellulose, and protein composition in addition to the ratio between sugars and acids. Fruit size results from cell division and cell expansion, which are relative to carbohydrate and water fluxes, and carbon metabolism within the fruit. All of these processes are regulated based on the fruit ontogenetic programme and in response to environmental conditions (Génard *et al.*, 2007). Many studies have reported that in several species WD typically results in depressed plant growth, enhanced fruit quality (e.g. increased sugar and acid levels), and an acceleration in fruit maturation but low marketable fruit yield (Guichard *et al.*, 2005; Ho, 1996b; Mirás-Avalos *et al.*, 2013). However, the reported effects of WD on fruit quality are highly variable and occasionally conflicting owing to the large number of underlying processes that interact during fruit development and the timing and intensity of WD and because different species show different sensitivities. Therefore, an analysis of the effects of WD at the level of the processes involved should contribute to an understanding of global effects observed at the fruit level.

## The effect of water deficit on fruit development and growth processes

Independent of the species, fruit growth may be divided into distinct developmental phases, including a period of intense cell division followed by a period of cell expansion and ending with the ripening period.

Cell division, which is typically restricted to a short period of fruit development and does not lead to a large increase in tissue volume, strongly influences the final fruit size in many species (e.g. in tomato (Bertin *et al.*, 2003; Bohner and Bangerth, 1988; Prudent *et al.*, 2010); pear *Pyrus* L. (Zhang *et al.*, 2006); and melon *Cucumis melo* L. (Higashi *et al.*, 1999)). Only a few studies have addressed the effects of WD on cell division in fruit tissues. In grape (*Vitis vinifera* L.) berries, negative or no effects were reported depending on the timing of treatment (McCarthy *et al.*, 2002; Ojeda *et al.*, 2001). An absence of effects was also observed in olives (*Olea europaea* L.; Gucci *et al.*, 2009) and pear fruit (Marsal *et al.*, 2000), with the exception of severe stress (Gucci *et al.*, 2009). Under intensive WD, the induced carbon starvation may negatively regulate cell division, as has been observed in tomato fruit at the tissue (Bertin, 2005; Prudent *et al.*, 2010) and at the gene (Baldet *et al.*, 2006) level.

When cell division ceases, an increase in tissue volume is induced owing to cell growth through an increase in cytoplasmic volume and an expansion of the vacuoles. Cells are smaller in fruits grown under WD, as has been observed in olives (Gucci *et al.*, 2009), pears (Marsal *et al.*, 2000), grapes (Ojeda *et al.*, 2001), and tomatoes (our experimental observations). Cell expansion is supported by the pressure of cell contents and constrained by cell wall properties (Cosgrove, 1997). The decrease in cell turgor and water potential resulting from cell-wall relaxation and loosening enables water to enter the cell and stimulate expansion (Lockhart, 1965). Water enters the fruit via xylem and phloem tissues and follows the stem-to-fruit gradient of water potential, which is generated by a gradient of osmotic potential between sources and sink tissues and that links cell expansion to sugar metabolism and sub-cellular compartmentalization. Thus, WD may affect tissue expansion through its effects on the biophysical, metabolic, and hormonal factors involved in the regulation of cell turgor and osmotic pressures and cell-wall extension. Although the fruit-water balance and osmotic regulation under WD are likely to have major impacts on tissue expansion, other hypotheses have been proposed. Mingo *et al.* (2003) demonstrated that fruit growth is affected by WD without changing fruit cellular turgor and proposed that cell expansion is regulated by sub-epidermal pH, which is consistent with previous results (Thompson, 2001). Modifications of the biochemical and physical properties of the cell wall under WD have also been suggested (Boyer, 1988). Several cell wall-loosening factors have been identified in plant cells, including numerous acid-induced or hormone-induced proteins (for example, expansins hydrolases) and hydroxyl radicals (OH), the production of which can be catalysed by peroxidase (Schopfer, 2001). Other studies have supported the hypothesis that ROS participate in cell-wall softening, for example, during pear

fruit maturation (Fry *et al.*, 2001). Thus, the potential effect of WD on cell-wall loosening and water balance is complex and involves many factors that may have opposing effects on the final cell size.

The onset of fruit ripening coincides with a rapid slowdown in cell expansion. Under WD, the onset of fruit ripening is hastened in peach *Prunus persica* L. (Mercier *et al.*, 2009), apple *Malus domestica* B. (El-Soda *et al.*, 2014), and detached avocado *Persea americana* M. (Adato and Gazit, 1974). These effects have been attributed to a stress-induced increase in endogenous ethylene, which plays an important role in the coordination of fruit-ripening processes in many fruit crop species, including climacteric (e.g. tomato, apple, or banana *Musa x paradisiaca* L.) and non-climacteric (e.g. strawberry *Fragaria x ananassa* D., *Citrus spp.* L., or grape berries) fruits (Barry and Giovannoni, 2007). The biochemical features of the ethylene biosynthesis pathway under both normal and water-stress conditions and associated genes are well defined and have been reviewed previously (Apelbaum and Yang, 1981; Barry and Giovannoni, 2007; Fray *et al.*, 1994).

#### *The effect of water deficit on fruit texture*

The overall structure and spatial organization, the cellular morphology of primary tissues (Aurand *et al.*, 2012), the cell turgor and fruit-water status (Jackman *et al.*, 1992; Shackel *et al.*, 1991), the accumulation and distribution of osmotically active solutes (Saladie *et al.*, 2007), the chemical and mechanical properties of cell walls (Rosales *et al.*, 2009; Toivonen and Brummell, 2008), and the cuticle properties and loss of water by transpiration (Saladie *et al.*, 2007) predominate in the determination of texture. Although many of these processes and traits are regulated by various environmental factors (Sams, 1999), of which water is of primary importance, very few studies have investigated the mechanisms involved in the environmental control of texture/firmness, and little information is available on the mechanisms affected (Harker *et al.*, 1997). Fruit texture is a primary determinant of consumer acceptance, and it greatly impacts organoleptic quality, flavour and aroma perception, and shelf-life and transportability (Causse *et al.*, 2003; Seymour *et al.*, 2002). Several descriptive studies have reported significant but contrasting variations in fruit firmness (physical component of texture) under WD. For example, WD increases the firmness of pears (Lopez *et al.*, 2011); however, an absence of effect was reported for apricots *Prunus armeniaca* L. (compression test; Perez-Pastor *et al.*, 2007), kiwi fruit *Actinidia deliciosa* (puncture test; Miller *et al.*, 1998), and apples (puncture test, Hooijdonk *et al.*, 2007). A recent study on tomatoes revealed that a moderate WD protocol decreased firmness when measured using the compression test but increased firmness when measured using the puncture test, with strong interactions between WD and genotypes (Bertin N, personal communication). These conflicting results may arise from different methods of texture evaluation, different stress intensities, strong genotype interactions with the environment, and complex interactions among the numerous mechanisms involved in final fruit texture.

The most likely hypotheses are that WD impacts texture through its effect on cell size, cell turgor, solute transport, and the accumulation of osmotically active solutes at the cell level. Indeed, a positive link between dry matter or total soluble solids (TSS) and firmness was reported for the tomato (Aurand *et al.*, 2012; Saha *et al.*, 2009) and kiwi fruit (Nardoza *et al.*, 2011). In addition, drought stress has been shown to cause alterations in the chemical composition and physical properties of the cell wall (Peleman *et al.*, 1989). Similarly, in cherry tomato fruit, environmental stressors promote the solubilization of cell wall pectin and reduce the concentration of calcium (Rosales *et al.*, 2009), which is involved in the maintenance of cell-wall structure and fruit firmness (Poovaiah *et al.*, 1988). In addition, the pectin matrix has many critical functions in the development of plant organs, such as the determination of apoplast porosity (Baron-Epel *et al.*, 1988), ionic-exchange capacity (Gillet *et al.*, 1998), and cell adherence (Knee, 1978). The oxidative stress-induced accumulation of antioxidant compounds, which prevent oxidative damage, may also impact texture. For example, ascorbate has been shown *in vitro* to solubilize tomato pectins (Dumville and Fry, 2003), which may explain the positive correlation between fruit firmness and reduced ascorbate content observed in tomato in response to post-harvest chilling injury (Stevens *et al.*, 2008).

The effect of water supply during fruit growth on post-harvest texture is an additional important issue. Kiwi (Reid *et al.*, 1996), apple (Hooijdonk *et al.*, 2007), and pear (Lopez *et al.*, 2011) fruits grown under WD have been shown to have a better shelf life after harvest. In contrast, no effect of growth conditions on post-harvest firmness has been reported for apricot (Perez-Pastor *et al.*, 2007) or kiwi (Miller *et al.*, 1998) fruits. This phenomenon requires further investigation.

#### *The effect of water deficit on fruit taste relative to sugar and acid content*

Soluble sugars and organic acids (primarily malic and citric acids) are major osmotic compounds that accumulate in fleshy fruits. These compounds determine taste and represent more than half of the total dry matter in tomatoes. The metabolic pathways underlying acid and sugar syntheses and the links between enzymatic activities and product accumulation in fruits have been well documented (reviewed by Etienne *et al.* (2013) for acids and by Beckles *et al.* (2012) for sugars). Under WD, fruit sugar content increases in tomato fruit depending upon the cultivar and timing of stress (Bertin *et al.*, 2000; Veit-Köhler *et al.*, 1999). WD applied near ripening shows the greatest positive impact on soluble sugar accumulation in various fleshy fruits (i.e. sucrose, glucose, and fructose in Satsuma Mandarin fruit (Yakushiji *et al.*, 1996); glucose and fructose in grape berries (Castellarin *et al.*, 2007); and glucose and fructose in tomato fruit (Ho, 1996a)). In contrast, the effects of WD on fruit acidity are more conflicting. In many species (peach, clementine, mandarin, pear, tomato), water supply has been shown to correlate negatively with organic acid content in ripe fruits, but in grapes, nectarines (Etienne *et al.*, 2013), and tomatoes (Bertin *et al.*, 2000; Mitchell *et al.*,

1991; Veit-Köhler *et al.*, 1999), this correlation has been shown to be positive. The variations in soluble sugar and acid accumulation in response to WD, often reported on the basis of fresh weight, may result either from dilution/dehydration effects (Etienne *et al.*, 2013; Guichard *et al.*, 2001), from active solute accumulation (Lo Bianco *et al.*, 2000; Hummel *et al.*, 2010), or from starch breakdown, as observed on tomatoes under salinity-induced WD (Balibrea *et al.*, 2003). For example, in strawberries, water stress increases sugar content and does not affect acid content relative to fresh weight; however, it does not affect sugar content and reduces acid content relative to dry weight (Terry *et al.*, 2007). In addition, water stress-induced carbon starvation is thought to decrease fruit sugar content, as has been observed in grape berries, peaches, tomatoes, mangoes (*Mangifera* L.), and clementines (Poiroux-Gonord *et al.*, 2012; Poiroux-Gonord *et al.*, 2013a), whereas organic acids typically show the opposite trend (Poiroux-Gonord *et al.*, 2012).

In the tomato, sucrose-metabolizing enzymes (acid invertases and sucrose synthase, SUSY) and the starch-synthesizing enzyme (ADP-glucose pyrophosphorylase, AGPase) play important roles in sugar import and metabolism (Beckles *et al.*, 2012). Invertases, whether alone or combined with plant hormones, have been recognized as key metabolic enzymes involved in plant responses to environmental stimuli owing to their role in sugar signalling and sensing (Roitsch and Gonzalez, 2004; Ruan *et al.*, 2010). For instance, the reduction in apoplastic invertase activity has been suggested as an early step in the signal transduction cascade induced by water stress that leads to irreversible fruit abortion (Zanor *et al.*, 2009). However, the effects of WD on sugar-metabolizing enzymes in sink organs remain poorly documented. An increase in SUSY activity has been observed in water-stressed fruits in orange (*Citrus sinensis* L.; Hockema and Etxeberria, 2001). In peach fruit, water stress-induced ABA stimulates sugar accumulation by increasing the activity of sorbitol oxidase; however, this effect was observed under moderate water stress but not severe water stress (Kobashi *et al.*, 2001). A recent study of transformed tomato lines (Centeno *et al.*, 2011) revealed a negative link between malate accumulation and levels of transitory starch and final soluble sugar content, and suggested the regulation of AGPase activity by the cellular redox status in developing fruit. Although links between enzyme activities and sugar accumulation have been studied extensively (Steinhauser *et al.*, 2011), the relationships involving hormones, sugar-metabolizing enzymes, and sugar accumulation in fleshy fruits under water-stress conditions merits much more consideration in future research.

For many fleshy fruits, consumer acceptance not only correlates with individual concentrations of sugars and acids but also with the sugar/acid ratio. Based on the above-described effects of water stress on sugar and acid content, it is difficult to anticipate the effect of water stress on this ratio. In strawberries, the ratio increases under WD owing to an increase in sugar content (Terry *et al.*, 2007). In tomato fruit, the sugar/acid ratio was shown to increase under high air-vapour pressure deficit, but the effect was dependent on the plant fruit load and harvest period (Bertin *et al.*, 2000). The sugar/acid

ratio increases from spring to summer; it correlates better with acid content in spring but correlates equally with both components (soluble sugars and organic acids) in summer. These variations are probably influenced by water deficit-induced carbon starvation. In clementine fruit, the ratio is lowered by carbon starvation owing to the decrease in sugar accumulation and increase in acid accumulation (Poiroux-Gonord *et al.*, 2013b).

#### *The effect of water deficit on fruit aromas*

All fleshy fruits contain and release a great variety of volatiles that confer their typical aroma. For example, in tomatoes over 400 volatile compounds have been identified (Buttery *et al.*, 1987), many of which affect consumer taste perception together with sugars and acids (Baldwin *et al.*, 1998). Although fruit aroma represents a fundamental criterion of the organoleptic quality, few studies on its dependence on irrigation strategies were available, except in grapes. Several independent studies on grapevines have shown that water limitation increases aromatic compound content, in particular carotenoid breakdown volatiles (so-called norisoprenoids), which confer berries and wine a more fruity character (Bindon *et al.*, 2007; Chapman *et al.*, 2005; Koundouras *et al.*, 2009; Song *et al.*, 2012). Consistent with these findings, Deluc *et al.* (2009) observed an increased abundance of a carotenoid cleavage enzyme transcript in grapes grown under WD. The increase in norisoprenoids in fruits may be associated with metabolic responses to excess light energy and the build-up of oxidative stress under drought (Deluc *et al.*, 2009; see also the following section on the effect of water deficit on health-promoting phytochemicals). Other irrigation experiments in vineyards reported that aroma and flavour improved with irrigation (Reynolds *et al.*, 2007) or were not affected (Bravdo, 2001). In addition to grapes, some studies on apples reported significant positive effects of WD on the concentration of aroma compounds (Behboudian *et al.*, 1998; Hooijdonk *et al.*, 2007; Mpelasoka and Behboudian, 2002), although one study reported no effect (Mpelasoka *et al.*, 2000). Two studies on tomatoes and strawberries reported significant aroma enrichment in response to WD (Modise *et al.*, 2006; Veit-Köhler *et al.*, 1999).

In summary, across all fruit types, the majority of studies have reported beneficial effects of reduced water availability on fruit aroma, as has been generally acknowledged with respect to the aroma content of spices and medicinal plants (Nowak *et al.*, 2010). However, in many studies, the gain in aroma content was accompanied by a loss in fruit size (e.g. Song *et al.*, 2012). Therefore, it remains unclear whether the reported enhancement in aroma was due to the true stimulation of aroma biosynthesis or, rather, due to a dilution/concentration effect based on changes in fruit size and water content, as has been discussed with respect to soluble sugars and organic acid contents (Koricheva, 1999). Further, the effects of water limitation on fruit aroma may be indirect, in part owing to changes in the fruit microclimate (reduction in canopy density) or the nutrient status of the entire plant. Indeed, fertilization, shading and pruning practices have been

shown to affect fruit aromas (Pelayo-Zaldívar, 2010). Many more studies are required to unravel the multiple mechanisms underlying the effects of WD on fruit aromas. Particular attention should be paid to the timing and intensity of the applied water stress because the majority of aroma compounds and/or their precursors accumulate primarily during fruit growth and subsequently change during ripening and/or senescence. Future studies should also include quantitative measurements of aroma compounds in the headspace of intact fruits and not only their concentrations in fruit tissues. Indeed, the profiles of aromas released by intact fruits may differ greatly from their aroma content because not all volatiles produced and released by fruits accumulate in fruit tissues at detectable amounts, a phenomenon that is well known for many volatiles produced by vegetative plant organs (Staudt and Bertin, 1998).

### The effect of water deficit on health-promoting phytochemicals

Fruits supply a large range of health-promoting phytochemicals, of which secondary metabolites, primarily terpenoids (carotenoids, ABA, and others), and phenolic compounds are the largest groups along with ascorbate. Very little is known, for example, about the effect of ABA, the single most important plant hormone associated with drought, on fruit development and physiology. An increasing body of evidence suggests that ABA produces powerful biological effects. ABA is effective against a large range of diseases, including type II diabetes, obesity, and hypertension associated with atherosclerosis (Guri *et al.*, 2007; Guri *et al.*, 2010). Although the nutritional benefits of fruits and vegetables have been long established, consumption remains insufficient. Fortunately, there is great potential to increase the concentrations of phytochemicals in plant products using genetic approaches either by conventional breeding or breeding assisted by markers or metabolic engineering in addition to using agronomic approaches (Poiroux-Gonord *et al.*, 2010). Of all of the environmental factors that play a stimulating role in the synthesis and accumulation of useful phytochemicals in fruits, moderate stress, and more specifically, controlled drought, seem promising (Poiroux-Gonord *et al.*, 2013b). We now review briefly current knowledge on the effects of WD on the concentrations of the primary health-promoting phytochemicals in fruits and related physiological mechanisms involved in their synthesis and accumulation.

#### *Drought can increase phenolic compounds, carotenoids, and vitamin C content in fruits*

Many observations of the effects of WD on the accumulation of phytochemicals in berry fruits have been made since the 1990s (Lovisol *et al.*, 2010). With respect to phenolic compound content, the response to drought generally seems positive (Anttonen *et al.*, 2006; Deluc *et al.*, 2009; Esteban *et al.*, 2001; Keutgen and Pawelzik, 2007; Krauss *et al.*, 2006; Navarro *et al.*, 2006) and peaks at +40%. The picture is

slightly different for carotenoids, for which the effects range from negative (De Pascale *et al.*, 2007; Riggi *et al.*, 2008) to non-significant (Krumbein *et al.*, 2006) to positive (De Pascale *et al.*, 2001; Favati *et al.*, 2009; Krauss *et al.*, 2006; Marin *et al.*, 2009; Navarro *et al.*, 2006; Wu *et al.*, 2004; Zushi and Matsuzoe, 1998), and in the last case can reach greater than +150%. With respect to vitamin C, the findings are quite similar, with many reports showing positive effects of WD (Favati *et al.*, 2009; Murshed *et al.*, 2013; Veit-Köhler *et al.*, 1999; Zushi and Matsuzoe, 1998). It is important to stress that these studies show variable effects depending on genetic and seasonal factors or the intensity and duration of treatment. Drought may influence the metabolism of these phytochemicals via at least two major mechanisms that are not mutually exclusive and that may even interact (Fanciullino *et al.*, 2014). First, drought typically induces a decrease in leaf stomatal conductance, resulting in a decrease in net photosynthesis. The decrease in net photosynthesis may result in a reduced transport of primary metabolites to the fruits that are the major source of precursors for the biosynthesis of phenolic compounds, carotenoids and ascorbate. Second, drought may exacerbate oxidative stress/oxidative signalling. Oxidative stress is known to directly and indirectly influence the biosynthetic pathways of these compounds. Both mechanisms seem closely linked because the accumulation of carbohydrates may exacerbate photo-oxidative stress in photosynthetic organs, such as leaves (Urban and Alphonsout, 2007), whereas the latter mechanism may influence primary metabolism in nearby fruits (Poiroux-Gonord *et al.*, 2013b). Moreover, WD may influence the metabolism of health-promoting phytochemicals by hastening fruit development.

#### *Are drought-induced variations in phytochemicals due to a reduction in the availability of primary metabolites?*

It has often been reported that the availability and long-distance transport of primary metabolites determines the biogenesis of phytochemicals in fruits, such as ascorbate (Wheeler *et al.*, 1998) or carotenoids (Cunningham, 2002). Consistent with this idea, sucrose limitation was observed to delay and reduce lycopene and phytoene accumulation in green tomato fruit pericarp disks (Telef *et al.*, 2006), whereas sucrose feeding was shown to promote colour break in citrus fruit (Telef *et al.*, 2006). However, in both cases, the reported effects are ethylene dependent, which suggests that the positive effects of sucrose on carotenoid synthesis before maturity are probably indirect, i.e. mediated by the maturation process itself. Other observations on clementines suggest that during the cell division phase, low carbohydrate supply to fruits does not inhibit but, rather, stimulates the accumulation of carotenoids, possibly owing to an indirect effect on plastid formation (Poiroux-Gonord *et al.*, 2012; Poiroux-Gonord *et al.*, 2013a). In tomato fruit, the absence of a correlation between sugars and reduced ascorbic acid (AsA) content also suggests that fruit AsA content is not limited by leaf photosynthesis or sugar availability (Gautier *et al.*, 2009). All of these observations seem to refute the idea that carbohydrate availability determines the synthesis and accumulation of secondary

metabolites or vitamin C, at least in fruits. Historically, the issue of the effect of carbon supply on secondary metabolites was addressed by ecologists who predicted how plants allocated resources between differentiation-related processes (including the production of secondary metabolites involved in defence) and growth-related processes, giving rise to the growth differentiation balance hypothesis (GDBH) (Herms and Mattson, 1992; Loomis, 1932; Wilkens *et al.*, 1996). However, the GDBH is unlikely to apply to storage organs such as fruits. For example, in tomatoes grown under nitrogen deficit conditions, phenolic compounds accumulate in leaves, as predicted by the GDBH (Le Bot *et al.*, 2009), but not in fruits (Benard *et al.*, 2009). Carotenoids accumulate in fruits to advertise the nutritional status of fruits to potential seed disseminators rather than to fulfil defence functions. More recently, sugar signalling (Gibson, 2005; Rolland *et al.*, 2002) has modified our simplistic view of the effect of carbohydrate availability on secondary metabolism. The emerging mechanistic view is instead one of a modulating role of carbohydrates with regard to the biogenesis of secondary metabolites (Cazzonelli and Pogson, 2010; Fraser *et al.*, 2007; Lillo *et al.*, 2008; Telef *et al.*, 2006).

#### *Stimulation of the synthesis of health-promoting phytochemicals by drought-induced oxidative stress*

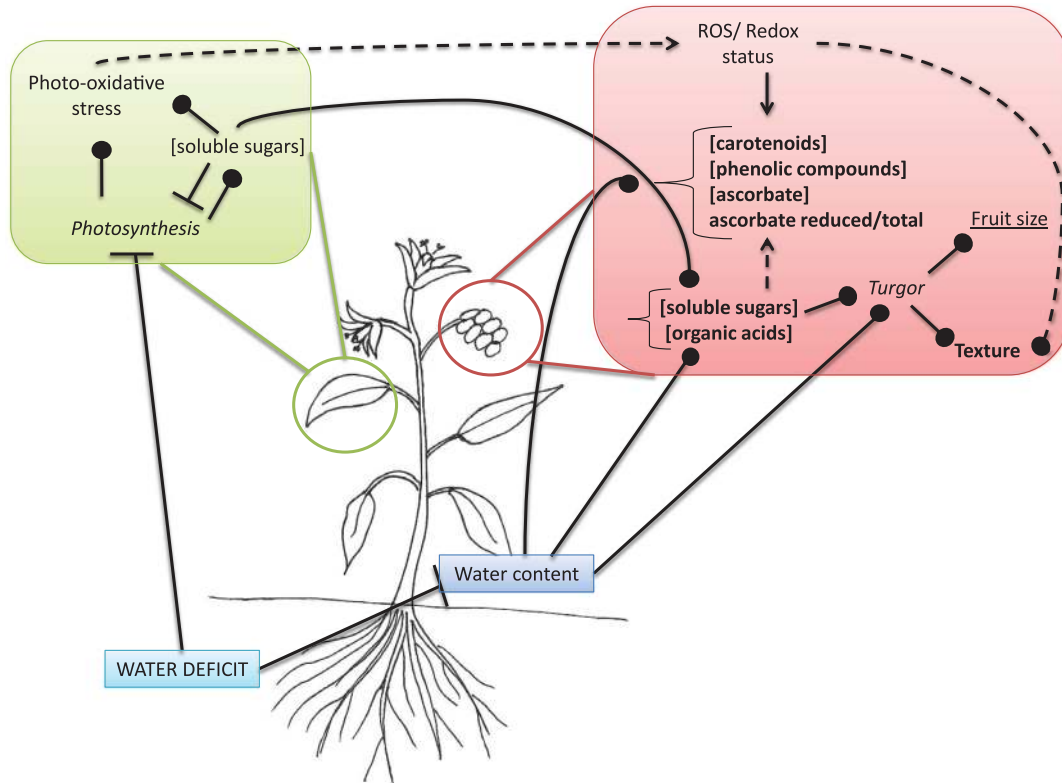
There are ample grounds to consider that the cellular redox state, resulting from the stress-induced production of ROS, ROS regulatory processes, and the accumulation of reducing power, controls tightly the synthesis of carotenoids in leaves and fruits (Fanciullino *et al.*, 2014). Similarly, the entire biosynthetic pathway of phenolic compounds is under ROS/redox control (Lillo *et al.*, 2008; Wingate *et al.*, 1988). The idea that the biosynthetic pathways of carotenoids and phenolic compounds are under ROS/redox control is consistent with knowledge of the gene-controlling role of redox-sensitive systems (Buchanan *et al.*, 2012; Potters *et al.*, 2010). However, the specific molecular mechanisms involved are not well understood, and the genes expressed in various fleshy fruits during drought, for example, in grapes (Castellarin *et al.*, 2007), require further investigation. In addition, recent results suggest that ROS formed during WD, osmotic stress, and salt stress may indirectly orchestrate phenylpropanoid and flavonoid biosynthetic pathways through the initiation of phosphorylation cascades by H<sub>2</sub>O<sub>2</sub> and MAPK that are highly activated during WD (Grassmann *et al.*, 2002; Mateos *et al.*, 2003).

AsA also plays a major role in the antioxidant scavenging of H<sub>2</sub>O<sub>2</sub> via ascorbate peroxidase (APX) or AsA itself. In fruits, AsA content depends upon its biosynthesis, its recycling after APX- or ascorbate oxidase (AO)-mediated oxidation into monodehydroascorbate (MDHA), its eventual travels from the leaf to the fruit and its catabolism. There is evidence that drought tolerance correlates with plant AsA content and/or its regeneration by monodehydroascorbate reductase (MDHAR), which plays a fundamental role in ROS detoxification (Wang *et al.*, 2012). This role of ROS detoxification is supported by the behaviour of AsA mutants

under drought stress. For example, ascorbate-deficient mutants of *Arabidopsis* are more sensitive to WD (Niu *et al.*, 2013). Moreover, tomato plants with reduced expression of AO show 30% greater AsA content than control plants and show improved tolerance to WD resulting in higher stomatal conductance and photosynthesis rate (Garchery *et al.*, 2013; Zhang *et al.*, 2011).

#### *Photo-oxidative stress in leaves impacts secondary metabolism and antioxidant metabolism in fruits*

The role of ROS and redox status in the synthesis of secondary metabolites in the pulp of fruits raises an intriguing question. At the time of maturation, when chloroplasts have been transformed in chromoplasts, ROS cannot originate from photosynthesis because the pulp has lost its photosynthetic machinery. In the pulp of stressed fruits, ROS may originate from NADPH oxidase located in the membranes, from xanthine oxidase in peroxisomes (Luis *et al.*, 2006; Mateos *et al.*, 2003) or from the respiratory electron transport chain of mitochondria. Recently, Poiroux-Gonord *et al.* (2013b) provided evidence that leaves of orange trees undergoing photo-oxidative stress can influence metabolism in the pulp of nearby fruits. Among other findings, they observed modifications of antioxidant metabolism and a 15% increase in the concentration of total carotenoids 99 hours after exposure of the leaves to stressful conditions. The idea that stressed leaves may be the source of oxidative stress or redox signalling in fruit or that ROS may even be exported from stressed leaves to nearby fruits is appealing and deserves attention. This idea is consistent with the concept of systemic acquired resistance (SAR) in cases of biotic stress (Ryals *et al.*, 1996) and systemic acquired acclimation (SAA) in cases of abiotic stress (Karpinski *et al.*, 1999). In *Arabidopsis thaliana* L., it has been observed that in response to wounding a ROS auto-propagating signal may be carried over a long distance at a rate of up to 8.4 cm min<sup>-1</sup> (Miller *et al.*, 2009; Mittler *et al.*, 2011). Eventually, even secondary metabolites, such as phenolic compounds accumulated in leaves in response to stress, may move directly to fruit. Indeed, highly soluble phenolic acids and hydroxycinnamic acids have been found in phloem and xylem saps (Bidel *et al.*, 2010). When applied on *Arabidopsis* roots, flavanones (i.e. naringenin, hydroxykaempferol, and hydroxyquercetin) move from root to shoot using the symplastic pathway, whereas shoot-to-root transfer seems to be limited to the vascular tissues and depends upon ABC-C-type carriers (Buer *et al.*, 2007). The importation of flavanol derivatives to fruits may occur when they are highly abundant, as in the tomato (e.g. naringenin-chalcone) or in *Citrus* species (e.g. naringenin-glycosides). No data exist that assess the participation of these derivatives in flavonoid accumulation in fruits or the role of water stress in long-distance transport. Here, we detail the role of leaf-to-fruit signalling; however, it is quite clear that skin-to-pulp signalling may also exist at least as long as the photosynthetic machinery is effective. Fig. 1 summarizes the effects of water deficit on quality criteria of fleshy fruits associated with photooxidative stress and reduced carbon gain.



**Fig. 1.** A simplified model of the prevailing effects of water deficit (WD) on quality criteria of fleshy fruits, derived from the available literature on peach, tomato, and orange fruits. This model brings forward the way WD influences quality criteria in fruits either directly or indirectly through its effects on leaves. Up- and down-regulations are indicated by arrow endings (circles and bars, respectively), except when no general trend predominates (arrow endings), depending on species, genotypes, plant and fruit stage, and intensity of WD. WD induces a decrease in leaf water status, and also in leaf stomatal conductance and net photosynthesis. The water deficit-associated decrease in photosynthesis increases the risk of photooxidative stress in leaves while decreasing the amount of carbohydrates for export to fruits. The decrease in water supply to fruits is at the origin of a decrease in fruit size but may also increase levels in carbohydrates, secondary metabolites, and ascorbate by exerting a concentration effect or by stimulating the synthesis of these compounds. But then the water deficit-associated decrease in carbohydrate supply to fruits may have the opposite effect by decreasing the amount of carbohydrates. At the fruit level, the effect of carbohydrate availability on the concentrations of secondary metabolites and ascorbate, being a matter of debate, is represented using a broken line. We also used a broken line to represent the potential effect of the water deficit-associated increase in photooxidative stress in leaves on the redox status and the concentrations in secondary metabolites of fruits (Poiroux-Gonord *et al.*, 2013b). Eventually we represented the effects of the redox status and of turgor (as influenced by water supply and the concentrations in carbohydrates) on texture (Pilati *et al.*, 2007). (This figure is available in colour at *JXB* online.)

## How do different types of water deficit affect fruit quality?

The great number of studies on WD highlight highly variable responses of plants and fruits depending on the length and intensity of the deficit, the plant/fruit development stage affected by the WD protocol, the genotype, and the presence or absence of other stress factors (high temperature and light, salinity, pathogens) (Bray, 1997; Tardieu *et al.*, 2006). In this section, we review the variable effects of a few of these primary factors on fruit quality. When available in the original studies, indicators of stress intensity are mentioned.

### *The effect of water deficit applied at different developmental stages and intensities*

Contrasting effects of WD have been observed depending on the plant developmental stage. In germinated tomato seeds, WD applied by the addition of polyethylene glycol was mostly lethal, whereas the rare surviving seeds produced either resistant

or very sensitive plants (Kulkarni and Deshpande, 2007). These responses to PEG are dependent on the concentration and duration of the treatment and might be mediated by epigenetic changes (Parra *et al.*, 2007). The vegetative growth stage is highly sensitive to WD, and a major consequence of WD during this stage is the reduction of plant growth and the subsequent fruit yield owing to numerous fruit abortions (Gladden *et al.*, 2012). In grapes, WD applied during the vegetative stage (no irrigation until veraison) reduces the maximum rate of shoot elongation and node production, accelerates periderm development, decreases fruit growth (Matthews *et al.*, 1987), and increases total phenolic content in contrast to malate (Matthews and Anderson, 1988). Thus, early WD applied during the vegetative phase may affect the entire reproductive period and negatively affect yield and improve fruit quality. In tomatoes, WD applied from flowering to fruit set primarily affects the number of reproductive organs and potentially leads to an increase in fruit size and quality by increasing the availability of assimilates for the remaining fruits (~50% of daily evapotranspiration (ETc), Patané and Cosentino, 2010;



–66% of control, Wang *et al.*, 2011). However, intensive stress (–80% of control irrigation) may lead to abnormal ovule development (Rapoport *et al.*, 2012).

At the level of the fruit, the effects of WD also depend upon the stage of fruit development during treatment. In peaches, moderate WD applied during cell division (stage I) promotes fruit size but does not affect fruit water content (Li *et al.*, 1989). When applied during the phase of rapid endocarp hardening (stage II), WD (–1.8 MPa stem water potential compared with control with –1.0 MPa at maximum) improves sweetness and flavour intensity and increases consumer acceptance, with contrasting effects on yield depending on the year (Vallverdu *et al.*, 2012). WD applied during the main fruit-growth stage (Stage III) results in a negative impact on yield owing to carbon limitation (Girona *et al.*, 2004) but is associated with a marked decrease in fruit water content (Li *et al.*, 1989). Finally, in peaches, the ripening stage is the most sensitive stage to WD, and the stress-induced reduction in yield is proportional to the reduction in water supply up to 25% of ETc (Wang and Gartung, 2010). Similarly, in tomatoes, WD applied during ripening (50% of water capacity) shows the greatest increase on fruit quality (soluble sugars, organics acids, aromas and vitamin C) when applied during the red stage compared with the mature green or orange stages (Veit-Köhler *et al.*, 1999).

WD has also been applied during the entire growing season. This stress leads to a significant decrease in fruit fresh weight and yields in tomatoes (under 65% and 80% reductions of water supply) (Nuruddin *et al.*, 2003) and mangoes (33–75% ETc) and promotes TSS accumulation in mangoes. The response intensities correlate with the intensity of WD (Durán Zuazo *et al.*, 2011).

In addition to the stage of application, the intensity of WD is an important determinant of the plant and fruit responses. To our knowledge, the effects of different stress intensities during targeted periods of fruit development have rarely been investigated. In oranges, different combinations of two stress intensities (55% and 70% of control) were applied during two phases (flowering, and fruit growth or ripening), and the results indicated that the improvement in fruit quality is counterbalanced by the decrease in yield when at least one development phase is exposed to intensive stress (García-Tejero *et al.*, 2010).

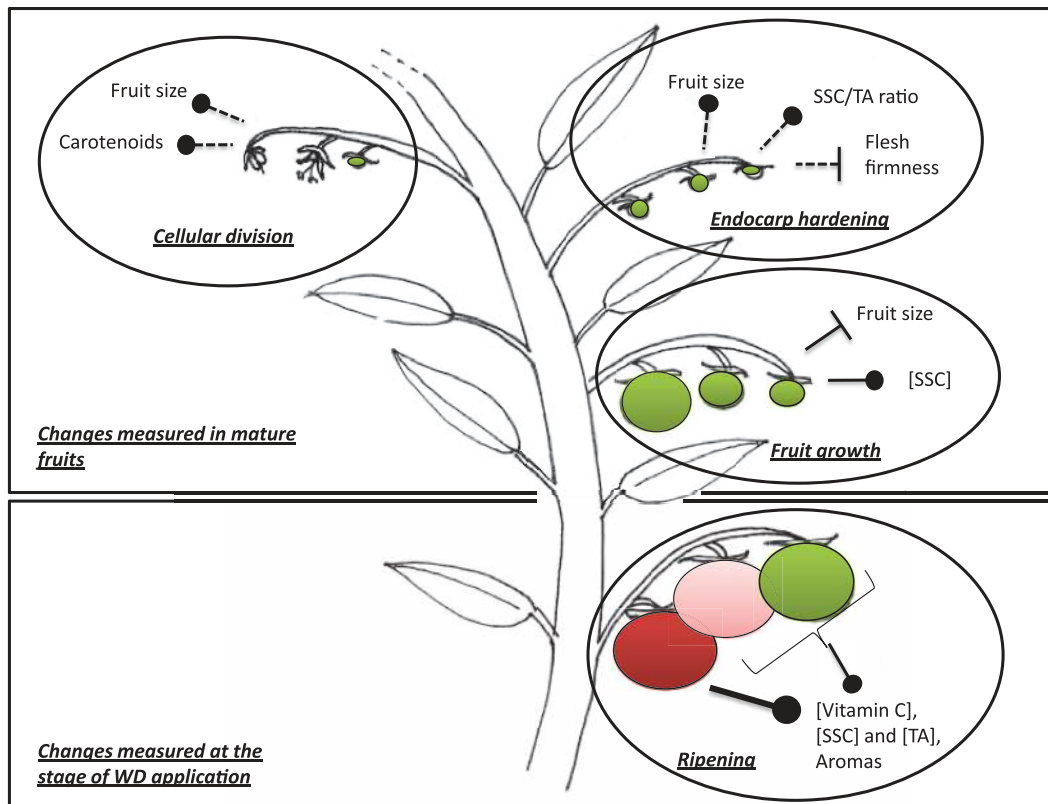
These results suggest that compromise between yield and quality could be achieved if WD occurs at the right intensity and at the right period of plant and fruit development. However, the intensity that optimizes both traits and enables the developmental stages to be preserved from stress remains unclear and is probably species- and season-dependent. Finally, the impact of WD on fruit yield and quality is not as simple as it first seems. Figure 2 summarizes the potential impact of WD on fruit yield and quality depending on fruit development phase, excluding severe stress, which is clearly deleterious.

#### Water deficit and plant priming

The capacity of plants to enhance their tolerance to future biotic or abiotic stresses upon appropriate stimulation by

a prior exposure to stress is called ‘primed acclimation’ or ‘priming’ (see the reviews by: Bruce *et al.*, 2007; Conrath, 2011; Filippou *et al.*, 2013). Therefore, plant acclimation to water stress may lower the sensitivity to more severe drought phases and to other biotic or abiotic stressors often sharing common response pathways. Thus, primed plants are expected to minimize yield losses through adaptation, but also to increase fruit quality through the up-regulation of the synthesis of some health compounds. Alternating cycles of stress have been applied to the entire root system or to part of the root system, i.e. partial root drying, to stimulate plant adaptation to WD and improve fruit quality (Stikic *et al.*, 2003). For example, two short periods (10 days) of WD (40–50% soil humidity) applied to tomato plants were observed to increase the carotenoid content in fruits harvested after the recovery period owing to an increase in antioxidant enzyme activity during the stress period (Stoeva *et al.*, 2010; 2012). Similar results were observed in cucumber (Akinci and Losel, 2009).

In addition to the cascade of responses to priming that cause morphological, physiological and biochemical changes that make the plant more tolerant to subsequent stress, it has been shown that plants have a ‘memory’ of encountered stress conditions that enables them to enhance their adaptation to changing environments. Indeed, primed plants demonstrate a faster activation of defence responses following stress perception. In recent years, the molecular mechanisms involved in priming have been investigated in the field of plant pathology, and the existence of a stress imprint in the primed plant that conserves information from a previous stress to be applied when the next stress occurs has been suggested by Bruce *et al.* (2007). Many mechanisms of response to stress are shared among several abiotic or biotic stresses (so-called cross-tolerance) and could have an analogous effect on the induction of priming. ABA, which is central in regulating the plant response to abiotic stress, seems to be involved in plant priming in addition to jasmonic and salicylic acids (Li and Zhang, 2012). Priming induces the accumulation of signalling proteins and transcription factors (TFs) in their inactive forms and enables their rapid up-regulation after a subsequent exposure to secondary stress. Thereby priming is expected to mitigate the damages and yield reduction associated to stress. The accumulation of dormant MAP kinases (MPK3 and MPK6), which are implicated in signal transduction, also seems to be necessary for the stress imprint (Beckers *et al.*, 2009); moreover, both MPKs are linked to the activation of phenylalanine lyase, which is involved in polyphenol synthesis, thus involving plant defence and fruit quality. It has been also suggested that nitric oxide (NO) induced in response to priming stress could involve *S*-nitrosylation and denitrosylation of proteins (Floryszak-Wieczorek *et al.*, 2012). By using a proteomic approach, Arasimowicz-Jelonek *et al.* (2013) demonstrated that the priming induced by chemical agents ( $\beta$ -amino-butyric acid, GABA, INA, and Lamarin) involved NO and redox-regulated enzymes implicated in primary metabolism and oxidative responses, such as glyceraldehyde-3-phosphate dehydrogenase (GAPDH), carbonic anhydrase (CA), and ascorbate recycling (with the dehydroascorbate reductase



**Fig. 2.** A simplified model of the effects of water deficit (WD) applied during specific fruit developmental stage on fruit size and criteria of quality according to the literature on peach, tomato, and Citrus. This model summarizes the effects of WD applied during specific fruit developmental stages on fruit size, soluble solids concentration (SSC), titratable acidity (TA), firmness, aromas, and the concentration in phytonutrients. A stimulating effect is expressed by lines ending with circles; lines ending with bars express an inhibitory effect, whereas dotted arrows express hypothetical or year-dependent effects of WD. At the stage of cellular division, the effect of WD is believed to be an increase in fruit size as observed in peach (Li *et al.*, 1989) and tomato (Nuruddin *et al.*, 2003) although the behaviour of tomatoes seems to depend on year-to-year variations. Observations on Citrus fruits by Fanciullino *et al.* (2014) led us to represent the hypothetical positive effect of WD during cellular division on carotenoids. WD applied during rapid endocarp hardening can increase the SSC/TA ratio but the effects seem contrasted on flesh firmness and fruit size as a consequence of year-to-year variations (Vallverdu *et al.*, 2012). During fruit growth, WD increases soluble sugars content and reduces fruit size (Girona *et al.*, 2004; Li *et al.*, 1989). At the ripening stage, the increase in vitamin C, soluble sugars, and organic acids is more marked when fruits are red than when they are at the turning point. Finally, aromas are improved by WD during ripening as indicated by increased emissions of hexanal, (Z)-3-hexenal, (E)-2-hexenal, and benzaldehyde (Veit-Köhler *et al.*, 1999). (This figure is available in colour at JXB online.)

DHAR). GAPDH is a key enzyme involved in oxidative and NO signalling pathways that acts as an NO sensor (Kornberg *et al.*, 2010; Morigasaki *et al.*, 2008; Muñoz-Bertomeu *et al.*, 2010), whereas CA exhibits antioxidant activity and SA response (Slaymaker *et al.*, 2002). Positive side-effects on the accumulation of health-promoting compounds are expected, as observed by Stoeva *et al.*, (2010; 2012).

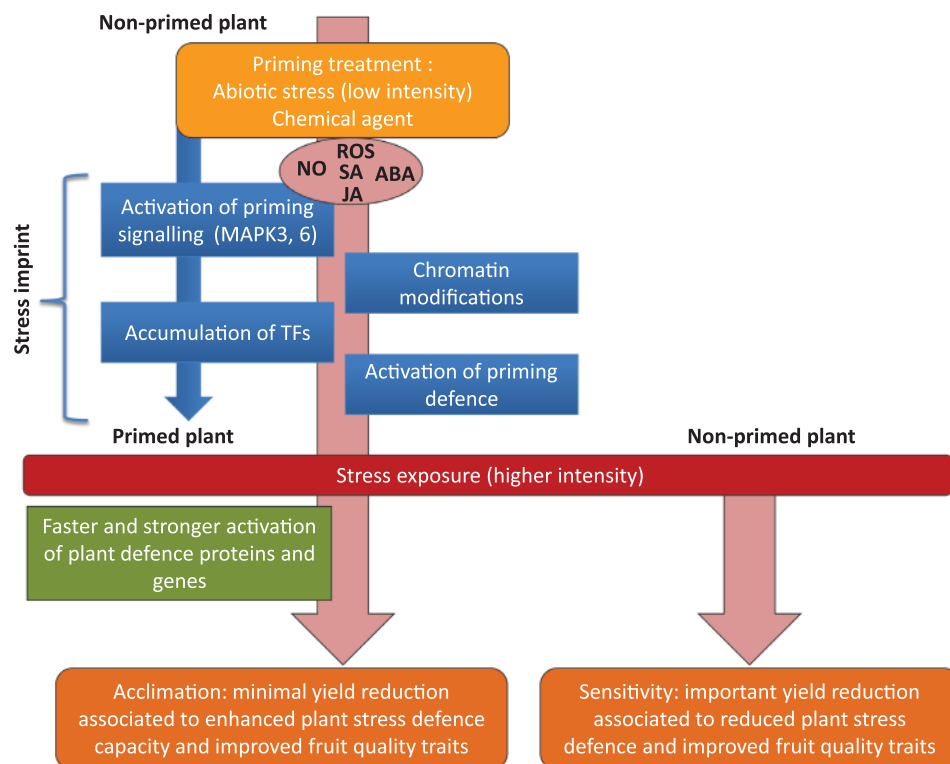
Often, the tolerance due to priming can persist for several days, but the stress imprint is in some cases transmitted to the next generation, suggesting that plants may inherit acclimation capacity (Molinier *et al.*, 2006; Slaughter *et al.*, 2012). Thus, plant priming represents an adaptive and cost-efficient defence strategy that increases the plant's ability to survive in hostile environments, summarized in Fig. 3. Priming may also be applied to improve fruit quality and fruit tolerance to stresses encountered during harvest and post-harvest treatments (Capanoglu, 2010). However, as outlined above in the section 'the effect of water deficit applied at different developmental stages and intensities', it will be crucial to determine when and how much stress should be applied to maintain and even improve quality.

## Factors affecting the fruit response to water deficit

In the field, WD may induce very different effects depending on the genotype and the interactions with other biotic or abiotic stresses. Commercial genotypes have primarily been selected based on plant productivity, fruit size, shelf life, and resistance to specific pathogens. Thus, cultivated genotypes became less tolerant to multiple stress environments, in particular to abiotic stress factors. Indeed, breeding has favoured yield and economic criteria, and natural allelic variations of genes favouring adaptation to environmental stresses have been lost (Gorovits and Czosnek, 2007; Gur and Zamir, 2004; Tanksley and McCouch, 1997).

### Interactions between water deficit and genetic factors

Understanding the genetic variability and the genotype–environment interactions involved in fruit quality and plant tolerance to WD is crucial (Panthee *et al.*, 2012). A great



**Fig. 3.** Plant priming mechanisms for acclimation to abiotic stress and improvement of fruit quality. Abiotic stress or chemical agents applied to plants can induce ‘priming’ to prepare plants to better cope with subsequent and more severe stressing conditions. The priming treatment induces early accumulation of ROS and nitric oxide (NO) that interact with hormonal responses and leads to the ‘primed state’ of plant cells. The resultant ‘stress imprint’ is characterized by epigenetic alterations such as chromatin modifications (histone modifications and DNA methylation), as well as accumulation of transcription factors (TFs) and inactive forms of mitogen-activated protein kinases (MAPKs). Therefore, primed plants are able to respond with increased or faster induction of defence responses upon exposure to subsequent stress. Finally, priming treatment causes a reduction of stress symptoms through enhanced tolerance, whereas non-primed plants exhibit severe damages. Thereby, primed plants are expected to minimize the impact on yield, and at the same time to trigger antioxidant mechanisms that positively affect fruit quality. (This figure is available in colour at JXB online.)

deal of research has been conducted to identify genes that are sensitive to WD. The majority of the molecular mechanisms (involved in plant growth and ABA signalling) have been elucidated, in particular in *Arabidopsis* (Blum, 2011). However, their use and transfer to cultivated genotypes is far from simple. In tomato, only a small proportion of genes involved in adaptation to water stress is known (Fischer *et al.*, 2011; Labate *et al.*, 2007). Genetic sources of variability to abiotic stress adaptation in tomato primarily include a small number of wild species, which made their use for breeding long and intricate (Foolad and Lin, 1999; Labate *et al.*, 2007). Moreover, water stress-responsive genes are involved in a myriad of physiological processes (osmotic regulation, photosynthesis, hormone synthesis, antioxidant activities, etc.), but they do not necessarily confer plant resistance (Gong *et al.*, 2010) or yield stability. Genes and quantitative trait loci (QTLs) for plant stress adaptation should be identified by comparing genotypes with contrasting behaviour under stress conditions (Labate *et al.*, 2007). For example, a transcript study of metabolic pathways affected by WD carried out on two cultivars of grape berries revealed 6000 unigenes which vary with the cultivar and WD treatment and play a role in the phenylpropanoid, the ABA, the isoprenoids, the carotenoids, the amino acids and the fatty acids pathways (Deluc *et al.*, 2009). Furthermore, genome-wide association

mapping could allow the exploration of genome variability and the discovery of new QTLs and candidate genes (Ranc *et al.*, 2012). Moreover, using QTLs for stress adaptation based on physiological underlying processes instead of complex traits, such as yield or quality, would be more efficient for understanding the genetic control and interactions with the environment (Bertin *et al.*, 2010; Martre *et al.*, 2011). Because WD is expected to enhance fruit quality, interesting QTLs that enable adaption to WD should improve plant development, carbon acquisition, and allocation to fruits, thereby maintaining yield under WD. In practice, several genotypes have been identified as tolerant to drought, either in terms of metabolic content and plant survival (for example in cucumber *Cucumis sativus* L. (Akinci and Losel, 2009) and in tomato (Sanchez-Rodriguez *et al.*, 2010; 2011), or in terms of yield stability (Foolad, 2007). Such cultivars represent important genetic resources for breeding.

#### *Interactions between water deficit and other stress factors*

Because plants are exposed simultaneously to multiple abiotic and biotic stresses under natural crop conditions, interactions among stress factors under realistic ranges of variability are important. Endogenous phytohormones act as signals to

combat many stress factors. Some phytohormones, such as ABA, are specific to abiotic factors, in particular WD, whereas others, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are more specific to biotic stresses (Fujita *et al.*, 2006). These phytohormones influence plant growth processes (ET and JA) and plant survival mechanisms (ABA and SA) (Albacete *et al.*, 2014). However, hormonal signalling pathways are interconnected (Atkinson and Urwin, 2012; Fujita *et al.*, 2006); thus, multiple individual stress factors do not show simple additive effects when combined (Mittler, 2006). Interactions between WD and other abiotic stress factors in relation to fruit quality have rarely been studied. Generally, interactions among abiotic stress factors, such as a combination of very high temperatures and WD, induce more deleterious effects for plant health than individual factors (Mittler and Blumwald, 2010). Thus, deficit irrigation should be sufficient to improve fruit quality, but it must be well balanced to avoid weakening the plant's ability to respond to other abiotic stress factors.

In contrast, interactions between biotic and abiotic stresses often show beneficial effects of one or both stressors. For example, molecular studies have shown that *Botrytis cinerea* infection triggers the expression of genes involved in pathogen resistance, like *BOS1* in *A. thaliana* (Mengiste *et al.*, 2003) and *SIAMI* in tomato involved also in adaptation to abiotic stress by modulating responses to ABA (AbuQamar *et al.*, 2008). In these studies, the co-occurrence of *B. cinerea* and abiotic stresses (water stress, osmotic stress and oxidative stress) reduces the susceptibility to the pathogen and induces tolerance to the abiotic stress. Similar positive interactions have been reported between powdery mildew and water stress, saline stress or proton stress (low-pH nutrient solution) in barley (Wiese *et al.*, 2004).

Beneficial interactions between pests and drought have also been reported in *Citrus latifolia* (Quiros-Gonzalez, 2000) and in apple (Gutbrodt *et al.*, 2012), independent of stress intensity. Fruit quality may be impacted by interactions between stressors. For example, in tomato, nematode attacks combined with 3-week WD promoted sugar and flavonoid levels compared with control and stressors alone (Atkinson *et al.*, 2011). However, this stress combination often reduced the above- and below-ground biomass (Grinnan *et al.*, 2013) and thus may induce negative effects on plant yield. In contrast, symbiosis with mycorrhizal fungus was shown to increase fruit production under WD and to improve fruit quality by increasing ascorbic acid concentration and reducing tomato acidity (Subramanian *et al.*, 2006). Indeed biotization, which comprises the inoculation of young plants with beneficial microorganisms such as bacteria or mycorrhizal fungi, may increase antioxidant contents in fleshy fruit and improve tolerance to abiotic stress (Gollotte *et al.*, 2009).

These results indicate that interactions between drought and plant pathogens may advantageously stimulate the accumulation of sugars, secondary metabolites and vitamin C in fruits. In addition, plant acclimation based on crosstalk responses to combined stress factors may be used to boost plant performances under non-optimal conditions including defence and quality.

## New perspectives for monitoring and sensing water deficit and its impact on fruit quality

Setting up innovative irrigation-sparing strategies requires efficient and non-destructive methods enabling the real-time monitoring of relevant indicators of plant physiological status and fruit quality. Although methods for assessing soil humidity, leaf photosynthetic activity, water fluxes, or plant growth, the majority of current measurements of fruit quality are destructive, particularly with respect to biochemical components. Complementary non-destructive methods that could be used to better assess plant and fruit physiological responses to WD or to understand the complex interactions among the numerous factors involved are reviewed here. Moreover fruit quality under different scenario of WD could be predicted.

### *The volatile metabolome as a potential indicator of plant health status*

Plants lose a considerable portion of carbon and biochemical energy gained in photosynthetic processes via the biosynthesis of volatile organic compounds (VOCs). Indeed, more than one thousand plant metabolites are volatile under ambient conditions, including saturated and non-saturated hydrocarbons, oxygen, nitrogen, and sulphur-containing molecules, with carbon skeletons ranging from C1 (e.g. methane, methanol, formaldehyde) to C20 (e.g. diterpenes; Schwartzberg *et al.*, 2004). The release of VOCs by plants is not restricted to flavour-producing flowers, fruits, or vegetative secretory organs such as resin ducts and trichomes. All plant organs produce at least traces of volatiles under certain conditions (Loreto and Schnitzler, 2010). The metabolic origins and biosynthetic pathways of the majority of plant VOCs are well described. The majority of plant VOCs can be assigned to one of the three following biochemical classes: terpenoids, also called isoprenoids, that are synthesized in two distinct pathways in plants; lipoxygenase (LOX) products, also called oxylipins, the majority of which are oxygenated C6 compounds that are derived from the peroxidation of unsaturated fatty acids; and volatiles product from the shikimate pathway (phenylpropanoids, e.g. methyl salicylate). Low-molecular-weight VOCs, such as ethylene, methanol, ethanol, formaldehyde, acetaldehyde and acetone, are formed via other biosynthetic routes.

The number of known volatiles has increased steadily in recent decades, not least owing to the emergence of breakthrough technologies and improvements to already existing analytical techniques used for VOC measurement. For example, the design of portable gas chromatographs and electronic noses enables the *in situ* monitoring of VOCs released by organisms (Kunert *et al.*, 2002; Laothawornkitkul *et al.*, 2008), and the development of proton-transfer mass-spectrometry enables real-time measurements of various classes of trace gases at the sub-ppb level (Harren and Cristescu, 2013). Plant release of VOCs can be measured non-destructively when using appropriate enclosure techniques

(Niinemets *et al.*, 2011), under close-to natural conditions or in fully controlled environments. This fact has prompted great interest in using VOC measurements for the *in vivo* monitoring of metabolic processes and the determination of the developmental, phenological, and health status of plants or plant organs. For example, methanol emissions are associated with cell growth, probably owing to the methanol produced by the demethylation of pectin during cell-wall formation (e.g. Oikawa *et al.* (2011) and references therein). Thus far, the majority of efforts have been towards the use of VOC signatures as indicators of stress responses in plants and, more particularly, of responses to biotic stress. A large number of plant VOCs are produced specifically in response to biotic stresses, most notably the LOX volatiles, methyl-salicylate, monoterpenes such as  $\beta$ -ocimene and linalool, various sesquiterpenes, and the two homoterpenes DMNT ((E)-4,8-dimethyl-1,3,7-nonatriene) and TMTT ((E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene) that originate from the sesquiterpene (E)-nerolidol and the diterpene (E,E)-geranyl-linalool, respectively (McCormick *et al.*, 2012). For example, in tomato plants, increased emissions of methyl-salicylate (among other VOCs) was associated with caterpillar (Vercammen *et al.*, 2001) and spider-mite parasitism (Dicke *et al.*, 1998; Kant *et al.*, 2004), and infestations with tobacco mosaic virus (Deng *et al.*, 2004) and *Botrytis cinerea* (Jansen *et al.*, 2010). Although certain VOCs are typical in many stress responses, numerous studies have shown that the quantity and composition of VOCs released differs with the type and intensity of stress (McCormick *et al.*, 2012; Niinemets *et al.*, 2013). For example, using an electronic nose, Laothawornkitkul *et al.* (2008) discriminated VOC bouquets among cucumber, pepper and tomato leaves subjected to mechanical damage and diverse pests and diseases.

Changes in VOC signatures may also indicate abiotic stress. Above all, wounding and mechanical stress can produce large amounts of volatile LOX products that could even be detected under field or greenhouse conditions without using plant enclosure systems (Jansen *et al.*, 2010; Ruuskanen *et al.*, 2011). In addition to LOX products, aromatic crop plants, such as tomatoes, release bursts of terpenes from their trichomes upon mechanical damage. Emissions of LOX volatiles and terpenes were also found to increase after exposure to ozone (Penuelas *et al.*, 1999) and to cold and heat treatments (Copolovici *et al.*, 2012). In the latter study, the emissions increased gradually with the severity of stress. Water logging, i.e. an excess of water, and the resulting hypoxia in the root zone were shown to trigger foliar ethanol and acetaldehyde emissions that originated from fermentation in the root cells (e.g. Copolovici and Niinemets, 2010). Regarding water shortage, numerous studies have described the effects of drought on constitutive VOC emissions ranging from decreased emissions to no effect or increased emissions (for an overview, see Penuelas and Staudt, 2010). However, apart from ethylene (Shakeel *et al.*, 2013), emissions of specific VOCs induced by WD have rarely been reported. Ebel *et al.* (1995) reported increased LOX emissions from apple trees during severe drought. Nevertheless, several independent studies have reported that WD stimulated biotic

stress-induced VOC emissions (Gouinguene and Turlings, 2002; Niinemets *et al.*, 2013; Takabayashi *et al.*, 1994), perhaps by accentuating ROS formation and the associated stress signalling (see above).

The VOCs produced by the plant in response to biotic stress are not only symptoms but may form part of the defence reaction to cope with the aggressor. Stress-elicited VOCs may directly deter the attacker or act as olfactory cues to orientate predators and parasitoids of the pest to the plant under attack (McCormick *et al.*, 2012 and references therein). Genetic manipulation of these defensive traits in plants may serve as a form of pest control in agriculture. For example, the introduction of a sesquiterpene biosynthetic pathway into cultivated tomatoes resulted in improved herbivore resistance (Bleeker *et al.*, 2012). In addition to their potential role as defence compounds to deter pests, stress-induced VOCs may be involved in within-plant and between-plant signalling, thereby regulating the protective responses of plants against both biotic and abiotic stresses. As discussed above, several well-known phytohormones (or their derivatives) implemented in stress responses and priming are volatiles, including ethylene, NO, methyl-salicylate and methyl-jasmonate. Other VOCs with strong potential to act in the plant stress signalling network are volatiles containing  $\alpha,\beta$ -unsaturated carbonyl groups (molecules collectively referred to as reactive electrophile species), such as the LOX volatile (E)-2-hexenal (Frag and Pare, 2002) and  $\beta$ -cyclocitral, a terpenoid formed from the non-enzymatic breakdown of  $\beta$ -carotene by singlet oxygen (Ramel *et al.*, 2012).

Thus, there is increasing evidence that the quality and quantity of VOCs released by plants indicate not only the presence of stress but also its intensity and the plants' capacity to cope with stress. Therefore, *in vivo* monitoring of VOC signatures from plants offers a novel avenue for the control of abiotic and biotic stresses in crop management and in phenotyping platforms for breeding or engineering stress-resistant genotypes. The potential use of stress volatiles as defence elicitors and as olfactory cues for recruiting natural enemies in agroecosystems has been tested (Holopainen *et al.*, 2009; James, 2005) and shown to be promising.

#### *Alternative non-destructive methods to determine fruit quality and plant health status*

There are several non-destructive methods available to determine fruit quality and plant physiological status. Here, we describe briefly nuclear magnetic resonance (NMR), near-infrared spectroscopy (NIRS), parameters based on measurements of UV/visible wavelengths such as the photochemical reflectance index (PRI) or Dualex/Multiplex (Force A, ©), and analysis of fluorescence transient of chlorophyll *a*, which are often used for monitoring plant physiological status but rarely fruit quality. These methods are based on the measurement of physical properties that correlate with the physiological status of plants but also with quality criteria, such as electromagnetic (or optical) properties that could relate to fruit appearance, mechanical properties to texture, and chemical properties to flavour (Abbott, 1999).

NMR has primarily been used to study plant anatomy, changes in water content and transport in stems or in root systems and has rarely been used to assess internal fruit quality. The quantification of extracts of fruit offers the possibility of quantitative measurements of each compound contributing to fruit quality but requires extraction of the compounds (Deborde *et al.*, 2009). However, even without extraction, NMR permits an evaluation of maturity, worm damage, or bruises (Chen *et al.*, 1989).

Visible/near-infrared spectroscopy has been recently preferred over infrared thermography for the screening of genotypes in controlled environments by measuring different plant traits, such as leaf water content (Zhang *et al.*, 2012), leaf nitrogen content (Ulissi *et al.*, 2011), seed viability (Kranter *et al.*, 2010), and metabolic content in fruits (Clement *et al.*, 2008). NIRS measurements correlate with sensory analyses of apple (Mehinagic *et al.*, 2003) and mandarin (*Citrus reticulata* B.; Gomez *et al.*, 2006) and have been applied to measure colour, total soluble solids, and vitamin C in orange (Magwaza *et al.*, 2013). NIRS spectra reflect the unique chemical fingerprint of organic material and thus are potentially important for non-destructive assessments of fruit quality.

Spectral analysis in the UV/visible wavelength range has been used to characterize other factors involved in fruit quality or leaf chlorophyll content. For example, this method was used in grape to detect anthocyanins, which absorb in the visible light, and flavonoids, which absorb in light in the UV range (Rustioni *et al.*, 2013; Tuccio *et al.*, 2011).

The PRI has been also used to evaluate the epoxidation state of xanthophylls and the light use efficiency of photosynthesis. These spectral analyses use visible wavelengths (from 531–570 nm) and have enabled the detection of short-term stress responses to nitrogen stress and WD and evaluations of specific carotenoid content in fruits (Araus and Cairns, 2014; Murshed *et al.*, 2013; Suarez *et al.*, 2012).

However, all of these spectral analyses are based on calibrations using predictive statistical models, which depend on extensive databases. Moreover, these techniques may not be appropriate for fruit species with heterogeneous internal structure, such as the tomato (de Oliveira *et al.*, 2014; Jouquet *et al.*, 2014). Other instruments based on optical properties like Dualex or Multiplex permits to assess the phenolic content in grape berries (Cerovic *et al.*, 2008) and to evaluate its change in relation to WD and fruit maturity (Esteban *et al.*, 2001).

Parameters of chlorophyll fluorescence derived from measurements performed using a pulse amplitude-modulated fluorimeter have been used to follow the maturation of mangoes fruits (Lechaudel *et al.*, 2010). Chlorophyll fluorescence measurements could also be used for post-harvest detection of damaged or infested fruits containing chlorophyll in peel like lemon (Nedbal *et al.*, 2000). Besides minimal fluorescence, maximal fluorescence and variable fluorescence, innovative parameters such as the performance index of Strasser (Strasser *et al.*, 2004) could be used in the future on fruits to assess their physiological status in response to WD.

Thus, fruit quality traits, including colour, soluble sugar, and organic acid contents or nutritional value, can be

quantified using these different methods. All of these methods can be used *in situ* with the exception of NMR.

### *Process-based models: promising tools for the analysis and prediction of fruit quality during water deficit*

Because the variations in fruit quality under WD involve many mechanisms and feedback loops at the plant and fruit levels, a modelling approach may help define relevant strategies for irrigation and designing ideotypes of plants adapted to drought, i.e. genotypes capable of maintaining yield and producing high-quality fruits. Indeed, process-based models are appropriate tools for integrating knowledge from the gene to the fruit (Struik *et al.*, 2005), predicting the behaviour of complex systems such as fruits in fluctuating environments (Génard *et al.*, 2007) and analysing gene–environment interactions (Bertin *et al.*, 2010). Thus, the virtual fruit model (Génard *et al.*, 2007) may be a basis for understanding fruit quality in response to environmental fluctuations and analysing interactions between WD and other environmental or genetic factors or cultural practices. This model describes water and carbohydrate transport combined with stimulations of cell-wall extension driven by the influx of water and turgor pressure. The original virtual fruit model was developed based on the peach; however, the model has proven to be quite generic and has been adapted for different species, including tomato (Liu *et al.*, 2007), mango (Lechaudel *et al.*, 2005) and grape (Dai *et al.*, 2009). Interestingly, the virtual tomato model has been recently combined with a plant model that describes water and carbon fluxes within the plant architecture and the induced gradients of water potential and phloem sap concentration in carbon within the plant (Baldazzi *et al.*, 2013). This integrated model would be a powerful tool for understanding the complex interactions between water and carbon balance in response to WD at the plant and fruit levels. This model focuses on fruit fresh and dry mass and soluble compound content but it could be improved in the future for the prediction of other quality traits, including the accumulation of healthy compounds such as vitamins and carotenoids. Future developments of this model could encompass genetic factors (Bertin *et al.*, 2010), which would make it suited not only for generating novel ideas for future research, but also as a tool for breeding programs.

## Conclusions

Global climate change entails many threats and challenges for the majority of crops. Above all, a reduction in yield is expected in many parts of the world, and drought is generally believed to represent one of the most important negative results of climate change. Fruit crops will certainly also suffer from the increased extension of drought conditions; however, yield is arguably not as important for fruit as for grain crops or oil crops. Yield does matter for fruit crops, but quality criteria are as important if not more important. Fruits are expected to supply health benefits and to bring hedonistic pleasures

associated with specific aromatic compounds. We may thus distance ourselves from the dominant deleterious effect of drought on crop performance and consider the potential benefits. In this review, we discussed fundamental and agronomic research and demonstrated that fruits from drought-stressed plants may be superior, in particular with respect to the content of health-promoting phytochemicals. The stimulation of secondary metabolism may also be beneficial to plant natural defences. A reduction in pesticide use may represent an additional benefit for consumers and, thus, the fruit industry. However, existing data also strongly suggest that taking advantage of stress will require a better understanding of the underlying mechanisms of drought adaptation, and much work remains along these lines. Laboratory studies of the effect of a single severe stress applied during a very short period of time should be de-emphasized in the future. Instead, as shown in this review, we must increase our understanding of the effects of variable and repeated periods of drought applied at different periods of the crop cycle, possibly combined with other forms of stress, because these conditions more accurately reflect actual crop conditions. Integrated models must be developed to address the complexity involved and to generate novel research ideas and avenues for plant physiologists. We also require novel monitoring tools that are based on innovative ideas, such as VOC signatures and parameters derived from measurements of chlorophyll fluorescence. Fortunately, the information analysed as part of this review is sufficiently mature and promising to encourage researchers who are considering a shift in their approach to drought research.

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