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Controlled water deficit as abiotic stress factor for enhancing the phytochemical content and adding-value of crops

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A B S T R A C T

In the recent years, there has been a great necessity to increase crop productivity of staple crops in order to provide the food that is needed by a growing world population. Nowadays, not only crop yield is important, but also the ability to keep and, if possible, increase their bioactive compounds, the content of which is beneficial effects on human health, which have been widely reported. Nevertheless, various abiotic stresses affect crop productivity. Especially if the stress is prolonged, plant growth and productivity are severely diminished. In this sense, water scarcity constitutes a crucial constraint for agricultural productivity. Drought is one of the most serious abiotic stresses that restricts plant growth, development and productivity, and affects their physiological and biochemical mechanisms. However, there is evidence that a controlled water deficit (WD) may improve fruit quality through higher concentration of flavor compounds and phytochemicals. This review presents information about how a controlled WD may be used as an abiotic stress factor of crop phytochemicals, thereby improving health benefits for all consumers.

1. Introduction

Drought is considered one of the most common and devastating environmental stress, which affects plant growth, biomass accumulation, cell division, stem elongation, root proliferation, disturbed stomatal oscillations and diminish crop productivity. These plants responses vary depending on the severity of stress and the crop growth stage. Under this type of stress, the response of plants to cope with all these affectations varies from morphological to molecular, including physiological and biochemical. In this review, we describe some biochemical mechanisms used by plants to acclimate to drought conditions, mainly focused on the synthesis of secondary metabolites since, although drought stress reduces the growth of plants, it also increases the content of secondary metabolites.

The effect of water stress on increasing the production of secondary metabolites is very important for crops, so that, in addition to protective role for plants, there is an increase in the concentration of compounds involved in the quality of the crop on the taste and its nutraceutical capacity. The problem is how to manage crops effectively under limited water supply conditions. Growers must not only consider the impact of drought on productivity, but also on how plants control their primary and secondary metabolism. This question is complex because the trade-offs between productivity, defense and quality depend on the intensity, duration, and repetition of WD events. They also depend on the stage of development of the plant during the stress period and the effects of other stressors.

Here we provide an updated review of current knowledge of the effects of drought on crop quality in relation to the production of beneficial compounds for human health. We focus on horticultural and fruit crops because of the importance of secondary metabolism in their quality and the importance of vegetables and fruits in the human diet.

2. Importance of water and impact of water stress on plants

Water in plants accounts for approximately 80–95% of growing tissues. Its importance ranges from allowing the movement of molecules within and between cells, to their influence on the structure and stability of molecules such as proteins, polysaccharides and others (Kirkham, 2004). In addition, processes such as growth and proliferation, exocytosis, endocytosis, changes in cell form, hormone signaling, metabolism, excitability, cell migration, nutrient collection, waste filtration, necrosis and apoptosis are regulated by cellular volume and the hydrodynamics of water (Wehner et al., 2003; Zonia and Munnik, 2007). Taking into account the great importance of water in plants, a limited or excessive amount of water for plants is a factor that induces adverse or stressful situations.

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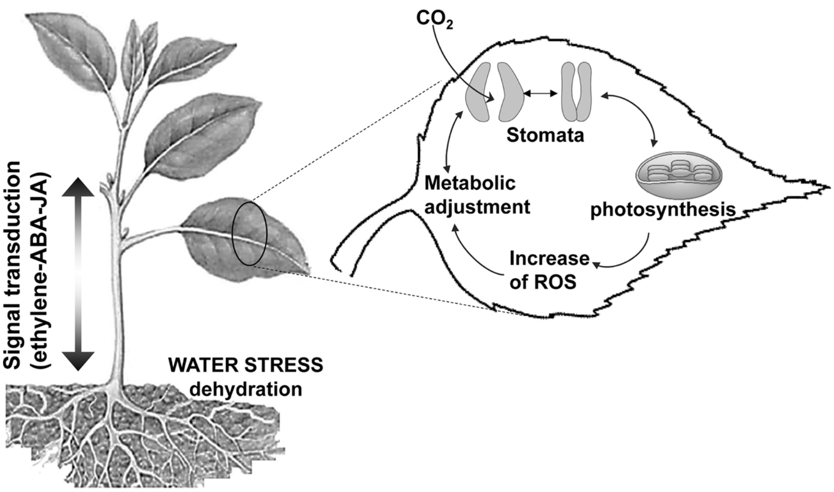

Fig. 1. Illustration of plants response to WD. When plants are subjected to water stress, endogenous abscisic acid (ABA) is rapidly produced, triggering a cascade of physiological responses, including stomatal closure, which is regulated by a signal transduction in the cell. Water stress induce the accumulation of reactive oxygen species (ROS), resulting in oxidative stress in the plant. All these responses lead to an adjustment in the growth rate of plants as an adaptive response for survival. Adapted from: (Osakabe et al., 2014).

One of the main responses to water stress is the modification of gene expression, related to the production of key enzymes in the osmolyte synthesis pathway, proteins with protective function, antioxidant enzymes, transcription factors, and other proteins involved in the responses to water stress (Xiong et al., 2002). Among the proteins most important for their potential protective effect are LEA (Late Embryogenesis Abundant Proteins) (Cushman, 2001) and those that function as antioxidants that are overexpressed during water stress (Laloi et al., 2004). Together with non-protein compounds, these detoxify plants from free radicals. These radicals, such as superoxide and hydrogen peroxide, are generated due to an increase in the rate of O_2 photoreduction in chloroplasts (Fig. 1) (Robinson and Bunce, 2000). Among the main enzymes are superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxidase (POD), glutathione reductase (GR) and monodehydroascorbate reductase (MDAR) (Apel and Hirt, 2004). Among the non-enzymatic antioxidants (phytochemicals) used by a wide range of plant species to neutralize stress-induced reactive oxidative species (ROS) (Sofo et al., 2005) are phytochemicals such as α-tocopherol, β-carotene, and flavonoids – all of which have been found in various plant species (Tattini et al., 2004; Zobayed et al., 2007).

3. Phytochemicals: plants secondary metabolites, and their implications on human health

In recent years, natural products such as fruits and vegetables have attracted the attention of consumers as a source of so-called phytochemicals. Phytochemical substances are organic constituents of plant origin. In general, they are not nutrients and provide the plant with physiological properties such as protective effects against pests and diseases (Howes and Simmonds, 2014). Phytochemicals also appear to be responsible, at least in part, for the health-promoting role in humans associated with the consumption of fruits and vegetables and food derived from them. Specifically, phytochemicals – secondary metabolites of plants- are low molecular-weight bioactive compounds. According to their structures and functional characteristics, phytochemicals can be mainly classified into broad categories such as polyphenols, terpenes, nitrogen-containing compounds, and organosulfur compounds (Lu and Zhao, 2017).

Phenolic compounds have various roles as defending plants, determining certain distinguishing features of different woods and barks, and establishing flower color and flavors. They are derived from shikimic acid and malonic acid pathways (Fig. 2). They are subdivided into groups characterized by the number of phenolic rings and by the structural elements that link these rings: (1) phenolic acids with the subclasses derived from hydroxybenzoic acids, such as gallic acid, and from hydroxycinnamic acid, containing caffeic, ferulic, and coumaric acid; (2) the large flavonoid subclass, which includes flavonols, flavones, isoflavones, flavanones, anthocyanidins, and flavanols; (3) stilbenes; and (4) lignans and polymeric lignins (Tsao, 2010). This family of compounds is being widely investigated for its potential benefits against cancer, as well as in cardioprotection, neuroprotection, urinary tract health, and antiaging effects (Nandamuri et al., 2017).

Terpenes or terpenoids are perhaps the largest group of secondary metabolites. They are constituents of many types of plant essential oils. Terpenoids are derived by repetitive fusion of branched five-carbon units based on isopentane skeleton. These monomers generally are referred to as isoprene units and for this reason are often called isoprenoids. Terpenes are synthesized by the mevolonic acid pathway (Fig. 2) and classified by the number of units of isoprene they contain (Pichersky and Raguso, 2016). Terpenes of two isoprene units (10 carbons (C110)) are called monoterpene; those of three (C15) sesquiterpenes, those of four (C20) diterpenes, triterpenes having 30 carbons and tetraterpenes 40 (Singh and Sharma, 2015). This group of compounds includes hormones (gibberellins and abscisic acid), carotenoid pigments (carotenoids and xanthophylls), sterols (ergosterol, sitosterol, cholesterol), derived from sterols, latex and essential oils. Some of them are interesting for their use as aromas and fragrances in food and cosmetics; others are important because of their anticarcinogenic properties, antiulcerous, antimicrobial and others (Singh and Sharma, 2015).

Alkaloids were originally defined as pharmacologically active, nitrogen-containing basic compounds of plant origin. Since ancient times, they have been widely used for their medicinal properties. These compounds are classified according to the nitrogen-containing ring system (pyrrolidine, piperidine) and their biosynthetic origin, amino acids, amines, alcamides, cyanogenic glycosides and glucosinolates (Khadem and Marles, 2011). They play an important defense role against herbivores and microorganisms because most of them are very toxic (Jimenez-Garcia et al., 2013).

In the last decades, these phytochemicals have been extensively investigated for their bioactive properties. Recognition of the biological properties of those compounds has fueled the current focus of this field. Among the biological properties of phytochemicals are their antioxidant- and free radical-scavenging capacity and anti-inflammatory action, which are also the bases of other bioactivities and health benefits, such as anticancer, anti-aging, and protective action for cardiovascular diseases, diabetes mellitus, obesity and neurodegenerative disorders (Cilla et al., 2017).

The major role of phytochemicals has been mainly associated with their antioxidant activity since overproduction of reactive oxygen species and reactive nitrogen species in the human body is involved in the pathogenesis of many chronic diseases due to the oxidant effects of those radicals. The highly oxidative environment, and many processes involved in metabolism may result in the production of more oxidant (Liu, 2003).