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Drought Stress

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8.1 Introduction

Drought is considered the most limiting factor to crop production worldwide (Boyer 1985; Costa et al. 2007). Water is an increasingly scarce resource in many important regions for vegetable production, for example, in California, USA; in the Guanzhong Plain, China; or in the south of Spain (Cabello et al. 2009; Tang et al. 2013; Olen et al. 2016; Coyago-Cruz et al. 2017). Drought stress events are anticipated to increase in the light of the changing climate. Competition for water will also increase as the world population is growing. Therefore, the more efficient use of water for irrigation is an important target in agriculture (Somerville and Briscoe 2001).

Notably, a mild and short water deficit can improve the quality of some crops. Under controlled conditions, a precisely regulated, crop-adapted water supply can result in a considerable rise of valuable components such as antioxidants, enzymes, sugars, acids and minerals (Sanders and Arndt 2012; Acevedo et al. 2013; Albert et al. 2016; Bogale et al. 2016; Coyago-Cruz et al. 2017; Hazrati et al. 2017). This implies a great potential to improve both the efficiency of water use and the quality of our horticultural plant products (Costa et al. 2007). This chapter aims to explain physiological adaptation strategies of plants to drought and to present methods for the successful application of this knowledge to produce vegetables and medicinal plants that are enriched in the desired metabolites.

8.2 Function of Water in Plants

Water is the most important substance in plants: the water content of nonwoody plant tissue is about 70–95%, and all physiological processes are dependent on the presence of water (Lambers et al. 2008). Water is the transporting medium for nutrients and metabolites, allowing transport between the various plant organs and the cells. In other words, water is the solvent that enables cellular organization and homeostasis. It is taken up from the soil by the roots and transported to the above-ground parts of the plant through the xylem. The smallest and mostly insignificant amounts of water can also enter the plant through (1) opened stomata or (2) epidermal water exchange. The absorbed water is not pure but contains many dissolved nutrient ions and some small organic substances that are required in various metabolic processes inside cells. Last but not least, water cools cells under heat stress (Farooq et al. 2012).

Cellular membranes are semipermeable, which means that ions, large charged metabolites and other compounds cannot disperse freely. For this reason, specialized proteins inside cell membranes, the so-called transporter proteins, actively regulate the influx and efflux of ions and metabolites across the membranes. Water, however, can cross cell membranes with much less restriction, partly flowing directly through the membranes and partly through aquaporins. The aquaporins are specialized channels (proteins inside the cell membranes) that allow the rapid exchange of water in plant cells. In an isothermal system (i.e. when the temperature on both sides of the membrane is equal), water diffuses through a semipermeable membrane from a region with the smaller solute (e.g. ion or metabolite) concentration to a region with the higher solute concentration, aiming to balance the solute concentration per volumetric unit of water across the membrane, even though this target can rarely ever be achieved in practice because of the dynamics of metabolism. The more solutes dissolved in the water, the stronger is its chemical potential. This is called the osmotic potential (Ψ_π). It is measured by the pressure unit called the megapascal (MPa), which describes the pressure that is needed to press the water out (Nabors 2004). The osmotic potential always has negative values.

To make water diffuse from the xylem into the cell, the solute (e.g. ion) concentration inside the cell must be higher than the solute concentration in the xylem. In other words, the osmotic potential inside the cell must be lower (more negative) than that outside, viz. in the xylem, so that the water is 'attracted' and flows from the xylem into the cell.

Because of the lower osmotic potential, the pressure exerted by the water inside the cell is higher than that outside, pressing the outer cell membrane (the plasma membrane) against the cell wall. As a result, the cell is kept in shape. This force is called the turgor pressure. Typical turgor pressures in plants range between 1.0 and 5.0 MPa (Lambers et al. 2008). An appropriate turgor pressure is essential for regular cell functions, metabolism and growth, as it ensures the connectivity between adjacent cells and thus the stream of the cytosol (the aqueous phase between the plasma membrane and the cellular compartment) through the plasmodesmata (channels connecting cells) and thus enables transport. A loss of turgor will result in the loss of cell stability, a visible effect that we call wilt.

Only 1–5% of the water taken up by the roots is finally kept by plants, as the rest is lost via transpiration through the stomata (Kramer and Boyer 1995; Lambers et al. 2008). This may seem inefficient. However, transpiration is the main driving force for the water stream into/through the plants, enabling nutrient uptake and distribution, and serves as a temperature regulator inside the plant (Kögler and Söffker 2017). Without transpiration, the leaf temperature can rapidly rise to lethal values.

Clearly, in the case of a lessening water supply, the plant has to react rapidly because almost all physiological processes are affected under drought (Kögler and Söffker 2017). By 'react', we mean that the plant has to induce mechanisms that help it (1) to take up water via its roots and (2) to maintain cell turgor (i.e. avoid the loss of water).

8.3 What Happens in Plants During Drought Stress?

In general, drought stress is an imbalance between the water supply and the plant's water demand (Tardieu 1996). It occurs when the water demand of the plant cannot be fulfilled, i.e. when too little water is available or less water is taken up than is needed for optimal growth and development (Brouwer et al. 1989). This can be the case when the transpiration rate from the leaves surpasses the water uptake by the roots, e.g. because of (1) insufficient precipitation, (2) too little soil water content or (3) the retention of water held in small pores at large suction tensions (Salehi-Lisar and Bakhshayeshan-Agdam 2016; Lambers et al. 2008).

As a reaction to a drying soil, the roots produce the phytohormone abscisic acid (ABA) (Avolio et al. 2018). ABA is transported through the xylem up to the leaves, where it accumulates as drought continues. High concentrations of ABA lead to a loss of water in the guard cells, so that the stomata close (Nabors 2004; McAdam et al. 2010). Taking only some seconds to some minutes, the closing of the stomata is a fast reaction of plants to reduced water availability (Kuromori et al. 2018). In some instances, stomata close even before any change occurs in the plant's water status (Karuppanapandian et al. 2017). Thus, fast mechanisms must be present that sense and perceive changes in soil water content.

However, the stomata are not only the exit for transpiring water but also the entry for CO_2, the basic material for carboxylation after the light reaction (see ▶ Chap. 14). This is the reason that the closure of the stomata results in markedly lower carbon assimilation (Flexas et al. 2004). What happens to photosynthesis if there is not enough CO_2, as may occur under drought conditions when the guard cells close the stomata? Photosynthesis comprises two main reactions: the light reaction and the dark reaction (Calvin cycle). During the light reaction, chloroplastidial chlorophyll pigments absorb energy from the sunlight. This energy is used to split water, a process that releases a free electron. The electron is passed through redox proteins (the electron transport chain), finally providing the energy for the enzymatic reduction of $NADP^+$ to $NADPH+H^+$. $NADPH+H^+$ is a strong reductant, viz. a storage for electrons, which are needed to energize a myriad of anabolic reactions. The photosynthetic transfer of electrons also energizes the phosphorylation of ADP to ATP. ATP acts a long-term storage for energy. $NADPH+H^+$ and ATP are used in the dark reaction, the Calvin cycle, by providing the energy for the incorporation of inorganic carbon (CO_2) into organic C-skeletons (e.g. triose phosphates). In C_3 plants, triose phosphate is the first stable carbohydrate, being the precursor for the synthesis of all other metabolites in the plant. Hence, a water deficit can reduce CO_2 concentrations in the photosynthetic plant cells because of stomatal closure. By this means, a water deficit can result in stunted growth as less carbon is assimilated.

8.4 Plant Reactions to Drought Stress

8.4.1 Adjusting the Osmotic Potential (Ψ_Π)

Some species are able to maintain photosynthetic activity and plant growth under a reduced water supply. This is because they manage to maintain their cellular turgor (Avolio et al. 2018). How do they do this? These plants can make a so-called osmotic adjustment: this means that under drought stress, they actively accumulate certain osmotically active substances in their cells to lower the osmotic potential (i.e. to make it more negative) (see also ▶ Chap. 7). The accumulation of such highly soluble and almost electrically neutral compounds (called osmolytes or osmoprotectants) happens mainly in the chloroplasts and in the cytosol (Zivcak et al. 2016). This leads to water being attracted from the surroundings, e.g. the vasculature or the apoplast, ultimately driving uptake from the soil solution (Kramer and Boyer 1995; Sanders and Arndt 2012). As a result, turgor pressure is maintained, allowing normal cellular homeostasis. The stomata can remain opened, enabling the uptake of a sufficient amount of CO_2 so that photosynthesis and the Calvin cycle can run normally and growth is not reduced (Zivcak et al. 2016). Simultaneously, an upregulation of genes occurs that encode enzymes for the synthesis of aquaporins, leading to a higher number of aquaporins in the cell membranes so that the water uptake of plant cells is facilitated (Avolio et al. 2018).

By implementing a short and well-controlled water shortage, the horticulturist can induce this process of osmotic adjustment with the aim of changing the sugar to acid ratio in a plant. This is because many of the osmotically active compounds (osmolytes) that accumulate during osmotic adjustment are soluble sugars (sucrose, hexose, trehalose) (Sanders and Arndt 2012). The sugar content in an aqueous solution can be measured with a refractometer and is expressed in degrees Brix (°Brix; see ► Chap. 19) (Kuscu et al. 2014). Thus, the accumulation of sugars during the process of osmotic adjustment normally results in a sweeter taste, e.g. in tomato fruits (see ► Chap. 19).

In addition to sugars, some other substances contribute to the osmotic adjustment. Among them are organic acids, amino acids or K^+, Na^+ and Cl^- (Lemoine et al. 2013; Zivcak et al. 2016). Valine, leucine, isoleucine, glutamic acid, aspartic acid, threonine and, importantly, proline (Pro) belong to the amino acids that are produced under conditions of drought. Pro is one of the most relevant osmotically active compounds (Girousse et al. 1996). The Pro concentration typically increases when drought stress becomes more severe (Hazzoumi et al. 2015; Khan et al. 2015; Slama et al. 2011). Pro exerts a protective effect on cell structures and has been shown to be an effective scavenger of reactive oxygenic species. As its concentration rises during numerous stress situations, it can be used as an indicator for the extent of stress in plants (Avolio et al. 2018; Kanayama and Kochetov 2015). Since Pro confers an acid taste (Yahia et al. 2011), the content of Pro and other drought-inducible acids is relevant for the modulation of the taste, viz. the sugar to acid ratio in plant-based food.

However, the composition and the quantity of osmotically active compounds vary widely not only between different species but also between cultivars. The ability to actively adjust the osmotic potential as a reaction to drought stress seems to be genetically determined (Acevedo et al. 2013; Albert et al. 2016). The reader should also note that the adjustment of the osmotic potential is limited to some extent. If the drought stress becomes too severe, turgor loss and wilting cannot be avoided. However, mild drought stress conditions can have a positive effect on product quality as described above.

8.4.2 Rise of Antioxidants in Drought-Stressed Plants

Furthermore, drought stress induces an increase of the oxidative capacity, which is of potential interest for the horticulturist if they intend to improve the quality of vegetables and medicinal plants.

Stomata close when the plant suffers a water deficit. This closure results in a limited CO_2 supply entering the plant and thus in a reduced photosynthesis rate. Apart from the reduced biomass accumulation, a disturbance of the photosynthetic reactions has another important consequence (◘ Fig. 8.1).

Because of the lower availability of CO_2, the activity of the Calvin cycle is reduced, and less $NADPH+H^+$ is oxidized to $NADP^+$. However, electrons are continuously delivered via the photosynthetic electron transport chain to reduce $NADP^+$ to $NADPH+H^+$. As a smaller number of them can be bound to $NADP^+$, more free

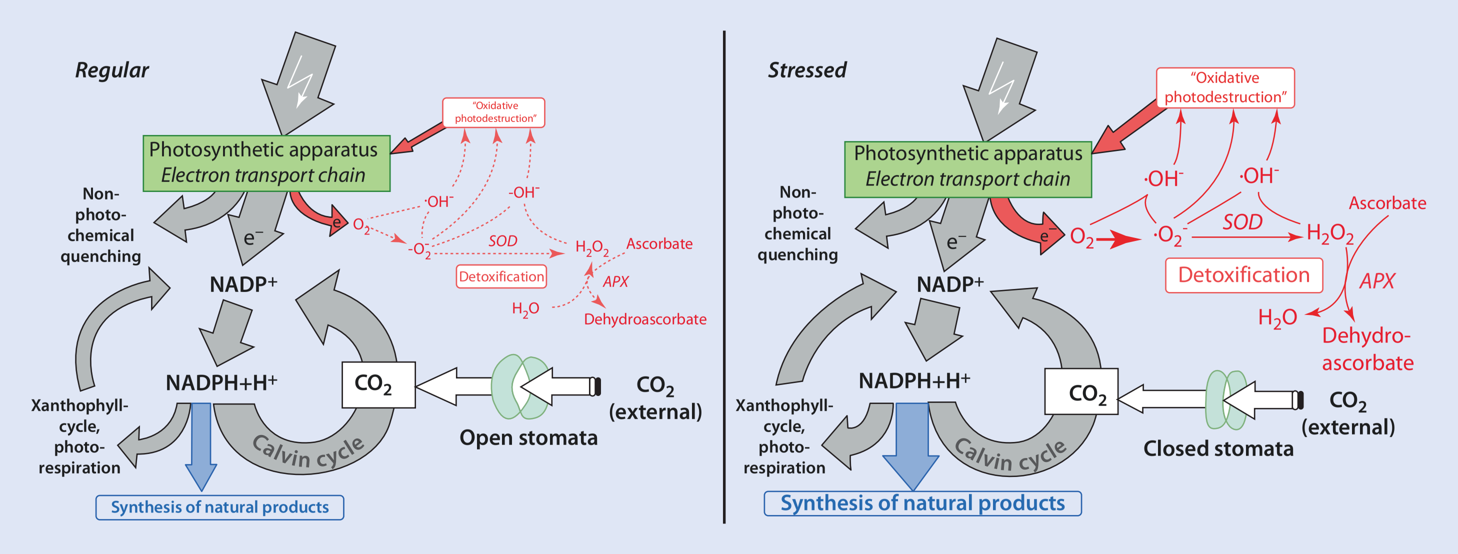

Fig. 8.1 Energy dissipation in plants under regular and stressful conditions. Closed stomata result in a lower CO_2 supply and, hence, in reduced Calvin cycle activity. The surplus of energy is used to enhance the activity of the xanthophyll cycle and for the synthesis of secondary plant compounds. On the other hand, a rise of reactive oxygenic species (ROS) occurs, which is followed by a higher synthesis of antioxidants. (Diagram taken from Selmar and Kleinwächter (2013a), with permission from Elsevier, license number 4417080028213, issued August 27, 2018)

electrons spontaneously reduce molecular oxygen and form oxygen radicals that give rise to the formation of excessive reactive oxygenic species (ROS) (see also ▶ Chap. 7) (Selmar and Kleinwächter 2013a; Saed-Moucheshi et al. 2014). The main ROS are singlet oxygen ($^1O_2$), the superoxide anion ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2) and the hydroxyl radical ($HO^{\bullet}$). When photosynthesis is blocked, these substances are mainly produced in the chloroplasts. ROS such as H_2O_2 can cross biological membranes and function as signalling molecules in plants (Mittler 2017). However, when their level exceeds a certain threshold, ROS cause damage. Especially the hydroxyl radical ($HO^{\bullet}$), which is the highest reactive oxygenic radical, can have very destructive effects on cellular components, damaging not only proteins and lipids but even RNA and DNA (Mittler 2017; Saed-Moucheshi et al. 2014). As a reaction to this undesirable process, the plant synthesizes antioxidants to scavenge the ROS and to avoid damage (see ▣ Fig. 8.1). The main function of these antioxidative agents is to provide an electron that is transferred to the radical. By this means, the radical is detoxified and cannot randomly oxidize other cellular structures.

The ROS-scavenging antioxidants can be enzymatic and non-enzymatic (Grant 2012). Among the enzymatic antioxidants, the enzyme group of the superoxide dismutases (SODs) can transform the superoxide anion ($O_2^{\bullet-}$) to O_2 and H_2O_2, the latter of which is then detoxified by other enzymes (catalases, ascorbate peroxidise (APX), guaiacol-type peroxidases and enzymes of the ascorbate-glutathione cycle) (Mittler 2002; Saed-Moucheshi et al. 2014). Among the non-enzymatic antioxidants, ascorbic acid (vitamin C) is particularly important because of its capacity to quench not only $O_2^{\bullet-}$ and $^1O_2$ but also even hydroxyl radicals ($HO^{\bullet}$). Furthermore, carotenoids, flavonoids, anthocyanins and tocopherols play a role in ROS scavenging (Saed-Moucheshi et al. 2014).

In addition to their importance in intrinsic defence mechanisms, antioxidants are known for their positive effect on human health (e.g. as anticancerogens, antiproliferatives) and are highly desired substances in food (Foyer and Fletcher 2001; Kunwar and Priyadarsini 2011). Therefore, the accumulation of antioxidants in food crops implies an improvement of food quality.

The reduced carbon assimilation under drought stress also results in the accumulation of human health-promoting carotenoids. This is because a reduced activity of the Calvin cycle results in a surplus of photosynthetic energy that is stored either in fully reduced reduction equivalents ($NADPH+H^+$) or in ATP. The energy is channelled to the xanthophyll cycle, which synthesizes, among other compounds, carotenoids (▣ Fig. 8.1). Carotenoids are accessory pigments that are able to dissipate the surplus in light energy and thus to protect leaves from photobleaching (Gruszecki and Strzałka 2005). The plant has another advantage when energy is consumed by those processes: $NADPH+H^+$ is oxidized into $NADP^+$, which can again accept electrons from the photosynthetic electron chain. This helps to avoid the formation of ROS as electrons do not react with molecular oxygen since they are transferred to $NADP^+$. Additionally, the enhancement of the reductive power (electron surplus) caused by drought stress gives rise to the synthesis of highly reduced secondary plant metabolites such as isoprenoids, phenols or alkaloids (see ▶ Chap. 3). Especially in medicinal plants such as sage (*Salvia officinalis*), these secondary metabolites confer beneficial attributes to the plant (Selmar and Kleinwächter 2013a, b). However, if the horticulturist is aiming to enrich these compounds by the induction of drought stress, care must be taken, because if the drought stress becomes too severe, any excessive production of ROS cannot be sufficiently buffered by the production of the antagonistic antioxidants. In consequence, the ROS will damage the membranes resulting in destroyed chloroplasts and accelerated leaf senescence.

The reader should further note that the described energy dissipation processes also take place under regular circumstances (i.e. when stomata are opened), but to a minor degree (◘ Fig. 8.1), because plants usually gain much more energy from light than is needed for CO_2 fixation (Wilhelm and Selmar 2011).

8.5 Additional Effects of a Deficient Water Supply

Of course, a water deficiency-induced lack of CO_2 will lead to decreased plant growth, as it directly affects the amount of assimilated triose phosphate, which is the precursor for all metabolites. However, for fruit crops, this is not necessarily a disadvantage. The whole vegetative part of the plant might however be smaller, as the plant aims to maintain the development of the generative parts, viz. the fruit production. For instance, drought-stressed tomato plants are known to allocate a higher share of photoassimilates to their fruits (Lemoine et al. 2013; Albert et al. 2016). Albert et al. (2016) observed that, in general, plant vigour (measured in stem and leaf size) and yield were both reduced under drought but that yield was less reduced than plant vigour. This suggests that tomato plants limit their vegetative growth more severely than their fruit production (generative growth) under water scarcity. Additionally, Nitsch et al. (2012) assumed that ABA stimulates cell enlargement in tomato fruits. As ABA is accumulated in the shoot during drought stress, this might also be a reason for the maintenance of fruit size, despite the stressful conditions.

Furthermore, although plants under drought stress may reduce their above-ground biomass accumulation, their root growth is less reduced and, in some cases, is even increased because, under drought stress, certain plants 'invest' in root growth to acquire new water pools. As a consequence, they show higher root-to-shoot ratios under drought, e.g. tomato (*Lycopersicon esculentum*), melon (*Cucumis melo*) or alfalfa (*Medicago sativa*) (Khan et al. 2015; Lemoine et al. 2013; Sharma et al. 2014; Slama et al. 2011). A larger root system, however, implies a greater potential for not only water uptake but also nutrient uptake and can thus contribute to a higher nutrient concentration inside the plant (Nangare et al. 2016).

Moreover, a lack of cellular water is associated with a so-called concentration effect of bioactive and flavouring compounds in plants. Fruits or leaves might be smaller according to the lower water content, but the taste is much more intense as the concentrations of the flavour-active components are higher. Apart from the active accumulation of osmolytes, the metabolites concentrate passively because of the reduced fruit enlargement and the continuous water consumption as, for example, in tomato (Kanayama and Kochetov 2015). The horticulturist should keep this in mind when facing consumer demands, since the nutrient content itself and the taste are important quality parameters of plant-based foods.

In addition to the improving of the quality of plants and their products, a deficit in irrigation is associated with the potential to save a considerable amount of water. The water-use efficiency of plants is generally higher under a deficient water supply (Nangare et al. 2016). Zwart and Bastiaanssen (2004) state that 20–40% of irrigation water can be saved if deficit irrigation is applied properly. For tomato plants, Linker et al. (2016) have calculated a saving potential of 30% [60%] of irrigation water when accepting a 5% [10%] decline in maximal yield. Cabello et al. (2009) have shown that melon (*Cucumis melo* cv. Sancho) can be grown under moderate deficient irrigation (90% ETc) without losses in yield and quality. Lobos et al. (2016) have reported that the postharvest quality (firmness, titratable acidity, soluble solids, antioxidant activity) of highbush blueberries (*Vaccinium x corymbosum* cv. Brigitta) is not affected by a mild water deficit treatment (replacing 75% of actual evapotranspiration) that is started during flowering, i.e. 1–2 weeks before the full bloom stage, and ended after harvest is complete.

8.6 Methods of Creating a Controlled Water Deficit for Plants

Drought stress can be induced either by regulated deficit irrigation (RDI) or by partial rootzone drying (PRD). In the RDI treatment, the complete rootzone is exposed to a water deficit during certain noncritical phenological periods (for a further explanation, see below). In consequence, vigour is lower so that plants consume less water (Galindo et al. 2018). The plant water status must be kept within narrow limits (Jones 2004), which is hard to achieve in the open field but is possible in Controlled Environment Horticulture (CEH). In general, RDI should be applied when fruit growth is minimal, i.e. during the stage between the fruit cell division and the fruit enlargement stage when vegetative parts are growing rapidly (Goodwin and Boland 2002; see also below).

On the contrary, during PRD, only a part of the root system is exposed to drought, while the rest is fully irrigated. In certain intervals (e.g. 3–5 days for tomato) depending on a critical soil water content, the irrigation treatment is exchanged between the root zones, so that each part is alternatively exposed to drought and re-watering (Bogale et al. 2016; Galindo et al. 2018). By applying this method, the drying root part induces ABA production, sending a systemic drought stress signal to the shoot, an event that is followed by osmotic adjustment (Xu et al. 2011). At the same time, the fully irrigated root part ensures a favourable plant water status, thus reducing the risk of a severe (harmful) water deficit (Galindo et al. 2018). With PRD, a minimization of excessive vegetative growth is possible, which is essential, especially in modern high-density plantations, whereas yield can be maintained and even be of higher quality at a relatively low risk to damage (Goodwin and Boland 2002). Furthermore, root growth is increased as soon as the dried root parts are rewetted. Mingo et al. (2004) have observed a 55% larger root biomass of tomato plants after PRD treatment (compared with RDI). The resulting mild drought stress induces an accumulation of osmotically active compounds and/or antioxidants, synthesized by the mechanisms explained above. The same is true under RDI.

The effect of the irrigation treatments also depends on species and cultivar. Therefore, species-specific knowledge is essential before RDI or PRD can be applied. First, the producer has to be aware of the specific water demand of the crop. For many species, values for crop evapotranspiration (ETc) are available according to the various developmental stages (e.g. FAO 2018). However, specific circumstances (growth conditions) can cause a divergence from these values. The measurement of relevant parameters in situ is more exact, for example, the measurement of the soil moisture or soil water potential, the real evapotranspiration, the plant tissue water status (e.g. the relative water content (RWC) of the leaves), the stomatal conductance (using porometer) or the water content (thermal sensing, balance of pots or sap-flow sensors). Examples of the imposition of a controlled drought stress are given in ▣ Tables 8.1, 8.2, 8.3, 8.4 and 8.5.

▣ **Table 8.1** Leaf water potentials under control and drought stress conditions for tomato and mung bean

Species	Well-watered	Mild drought stress	Severe drought stress	Values obtained in	Reference
Tomato (*Solanum lycopersicum* L.)	−0.2 to −0.7 MPa	−1.0 to −1.2 MPa	–	Greenhouse	Coyago-Cruz et al. (2017)
Mung bean (*Vigna radiata* (L.) Wilczek var. B1)	–	−0.5 MPa	−1.0 to −1.5 MPa	Petri dishes, plastic boxes	Das and Kar (2013, 2017)

▣ **Table 8.2** Crop evapotranspiration (ETc) under well-watered and dry conditions

Species	Well-watered	Mild drought stress	Severe drought stress	Values obtained in	Reference
Tomato (*Solanum lycopersicum* L. cv. 'Matina', 'Cochoro'), genetic overall variability	100%	50–40%	–	Greenhouse	Ripoll et al. (2016), Albert et al. (2016), Bogale et al. (2016)
Tomato (*Solanum lycopersicum* L. cv. Ryna®)	100%	80%	60%	Field, India	Nangare et al. (2016)
Melon (*Cucumis melo* L. cv. Sancho)	100%	90%	60%	Field, Spain	Cabello et al. (2009)
Pear-jujube trees (*Ziziphus jujube* Mill.)	100%	50%	–	Solar greenhouse	Feng et al. (2017)
Peach trees (*Prunus persica* cv. Golden Queen)	100%	40%	–	Field, Australia	Goodwin and Boland (2002)

Table 8.3 Soil water potential under well-watered and dry conditions for *Ilex paraguariensis*

Species	Well-watered	Mild drought stress	Severe drought stress	Values obtained in	Reference
Ilex paraguariensis (cv. San Isidro 49)	−0.04 MPa	−1.0 MPa	−2.0 to −3.0 MPa	Controlled environmental conditions	Acevedo et al. (2013)

Table 8.4 Relative soil humidity under well-watered and dry conditions for tomato

Species	Well-watered	Mild drought stress	Severe drought stress	Values obtained in	Reference
Tomato (*Solanum lycopersicum* L.)	65%	30–25%	–	Greenhouse	Albert et al. (2016)

Table 8.5 Percentage field capacity (FC) indicating various degrees of drought stress in various species

Species	Well-watered	Mild drought stress	Severe drought stress	Values obtained in	Reference
Alfalfa (*Medicago sativa*)	100%	33%	–	Greenhouse	Slama et al. (2011)
Aloe vera (*Aloe vera*)	100%	60%	–	Greenhouse	Hazrati et al. (2017)
Cassia (*Cassia obtusifolia* L.)	100%	70%	40%	Pot/field	Xue et al. (2018)
Hot pepper (*Capsicum annuum* L.)	100%	70% throughout the season, 90% during late fruit bearing	–	Greenhouse	Yang et al. (2017)
Parsley (*Petroselinum crispum* L.)	100%	50%	30–10%	Pot	Najla et al. (2012)

Knowledge about the developmental stages of the crop is of utmost importance when the aim is to adjust metabolism by the induction of drought stress because, in certain stages, water deficiency can lead to severe yield losses and a reduction of fruit quality. Moreover, this stage-dependent sensitivity is not the same among the species. Fruity crops can be extremely sensitive to drought stress during certain developmental phases, especially during flowering.

This is the reason that, for example, with regard to tomato plants, the right time to begin with RDI is the developmental stage after flowering (Albert et al. 2016; Coyago-Cruz et al. 2017). When drought-stressed during flowering, tomato plants react with flower abortion, resulting in high yield losses (Zegbe-Dominguez et al. 2003). Moreover, the fruit setting stage in tomato plants is also sensitive to drought stress (Harmanto et al. 2005; Nangare et al. 2016).

Hot pepper (*Capsicum annuum* L.) has been demonstrated to have improved fruit quality (increased content of total soluble solids and vitamin C and better fruit firmness) and only a slight yield reduction when the soil moisture is kept at 70% of field capacity (FC) during the growth season and at 90% during late fruit bearing and the harvesting stage (Yang et al. 2017). For citrus species, a slight water deficit during the ripening phase (summer and autumn) results in an increase of total soluble solids and acidity (Pérez-Pérez et al. 2008; Okuda et al. 2008).

In contrast, for *Aloe vera*, a medicinal plant whose leaves are the plant organ that is harvested, deficient irrigation can be adopted from the moment when plants have grown to a certain size threshold (>20 cm) until harvest, resulting in higher concentrations of anthocyanins (Hazrati et al. 2017). The leafy culinary herb parsley (*Petroselinum crispum*) has also been shown to react to deficit irrigation with an increased production of chlorophyll, β-carotenes, vitamins and anthocyanins when submitted to water stress treatment (50% FC) beginning 2 months after sowing until harvest (Najla et al. 2012). Rowland et al. (2018) assume that, for numerous other herb crops (basil, coriander, parsley, mint, thyme, lemongrass), a controlled mild water stress can contribute to improved quality (in terms of, for example, essential oils and antioxidant capacity).

In a study with potato plants, tuber yield was increased when plants were submitted to a PRD treatment during the early season, although yield was reduced when PRD was applied throughout the season, because of the reduced leaf size (source for carbohydrates accumulating in the tubers) (Xu et al. 2011).

The choice of the cultivar is another critical factor. With regard to tomato, the pattern of accumulated bioactive compounds can vary considerably among cultivars (Bogale et al. 2016; Albert et al. 2016; Coyago-Cruz et al. 2017). For example, whereas the content of total carotenoids increased in certain cultivars ('Summerbrix' and 'Lazarino', both cherry varieties), a decrease was observed in others (Coyago-Cruz et al. 2017). The vitamin C and lycopene content increased in the cultivar 'Matina' and decreased in the cultivar 'Cochoro' under RDI and PRD treatments (Bogale et al. 2016). Albert et al. (2016) reported that the variable reaction of the diverse tomato cultivars to drought is mainly caused by the genotype. Among the 141 accessions tested, 50 showed improved fruit quality while maintaining yield. Overall, drought-induced fruit size reduction was concluded to be more pronounced for common tomato cultivars than for cherry tomato cultivars (Albert et al. 2016).

A cultivar-specific response to drought has also been described for melon (*Cucumis melo* L.) (Sharma et al. 2014), alfalfa (*Medicago sativa*) (Slama et al. 2011) and parsley (*Petroselinum crispum* L.) (Najla et al. 2012).

Apart from drought stress, a lower water availability is often associated with salt and heat stress for plants, so that the impact of drought on plants cannot always be distinguished from other abiotic stress factors (Vicente-Serrano et al. 2012; Selmar and Kleinwächter 2013a; for further information, see ▶ Chap. 7 for salt stress and ▶ Chap. 9 for heat stress).

Finally, the economic impact of drought-induced yield reductions should be calculated, as the improvement of the quality must at least counterbalance the eventual losses in yield quantity (Santos Pereira et al. 2002; Zegbe et al. 2006). For example, in *Aloe vera*, the highest aloin and anthocyanin contents are produced under the most severe drought stress; however, the leaf yield and plant growth are negatively affected by drought, so that the best overall results are obtained when the drought treatment is kept at a moderate level (60% of FC) (Hazrati et al. 2016, 2017; see ◘ Table 8.5). Nangare et al. (2016) have observed that a mild water deficit (80% of crop evapotranspiration (ETc), viz. the daily water requirement) does not decrease the marketable fruit yield of tomato, whereas a stronger water deficit (60% of ETc) results in a yield loss of about 25%.

Although, to date, deficit irrigation is still sparsely applied, it is likely to gain more importance in the near future, as it provides a useful option both for coping with the anticipated water scarcity attributable to climate change and for improving the quality of several horticultural products.

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