Stomatal Responses to Drought Stress and Air Humidity

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1. Introduction

Water is one of the most important substances for both plant and animal survival. Plants require water for photosynthesis, nutrient uptake and transportation as well as cooling (Farooq et al., 2009). Plants are sessile organisms and in contrast to most animals they are unable to move when the environment becomes unfavorable. Accordingly, plants have to be able to respond and adapt to the local environmental changes. Since water is essential for plant survival, the ability to tolerate water stress is crucial.

To be able to grow plants need to take up water from the soil and CO_2 from the atmosphere and use it in photosynthesis. This is done by CO_2 uptake through the stomatal pore, where water is simultaneously transpired. Water transpiration drives the water uptake by the roots and transport through the xylem. When the stomata are open CO_2 is taken up while water is transpired. When the stomata are closed little CO_2 is taken up and the transpiration is lowered. By opening and closing the stomata plants can regulate the amount of water lost, by sacrificing CO_2 uptake, when the environmental conditions are unfavorable.

Water stress can be defined as reduced water availability; either by water scarcity (drought) or osmotic stress (high salt concentrations) or water logging; too much water. Water stress may reduce photosynthesis, respiration and ion uptake, change the metabolic and growth patterns in the plant and in severe cases result in plant death (Jaleel et al., 2009a). In nature water stress is common either for long or short periods of time, depending on the local climate. Most plants therefore have some adaptation or response to enhance the growth and survival rate during water stress and subsequent recovery.

In agriculture and horticulture drought stress is one of the major problems, causing major crop losses every year as well as loss of aesthetic value in ornamentals. In agriculture crop loss is due to reduced numbers of tillers, spikes and grains per plant and reduced grain weight (Farooq et al., 2009). With the global human population rapidly increasing, simultaneously as water scarcity increases, the loss of crop will be even more serious than before. The discovery and development of stress tolerant crops to avoid yield loss during water stress is therefore very important. In the greenhouse industry, energy saving for economic profit is important to be able, but it also affects the plants. To reduce the amount of energy needed for CO_2 and heating in the greenhouses, energy-efficient semi-closed

greenhouses can be used. In these greenhouses the ventilation is reduced to a minimum, which consequently results in increased relative air humidity inside. This increase in air humidity affects the plants in different ways and might result in plants that are less tolerant to water stress (Torre and Fjeld, 2001).

In this review different plant responses to water stress will be discussed, with most attention to drought and the role for abscisic acid (ABA) as a plant stress hormone. In addition, consequences of plant development under high relative air humidity, which reduces the plants ability to respond to water stress, will be discussed.

2. Plant responses to water stress

Plants growing in deserts or high salinity habitats are all exposed to more or less constant water stress. To survive such conditions plants have developed growth strategies such as increased water use efficiency with C_4- or CAM metabolism (Keeley and Rundel, 2003), succulent growth and extensive root systems (Henry et al., 2011). These strategies are good in a dry environment, but in more "favourable" conditions at least some of these plants may, due to lower growth rates, more easily be outcompeted by other less drought tolerant plants. Other adaptations to plant life in dry environments are thick cuticula and wax layers, depressed stomata and high density of trichomes. Thick cuticula and wax layers reduce extra-stomatal transpiration, and depressed stomata and trichomes create a thicker boundary layer outside the stomata, where the humidity gradient is more gradual, thereby reducing the stomatal transpiration.

Plants living in saline environments (e.g. beaches, salt marshes) commonly keep a low osmotic potential in their cells, which facilitates water uptake. They usually also have the ability to exclude or excrete salt from their cells to avoid to too high salt concentrations. A variety of perennials commonly avoid water stress during the winter by entering dormancy and often shedding leaves (deciduous woody species) before the onset of the harsh conditions when water is unavailable due to frost. However, plants keeping the leaves on through the winter commonly face water stress in the spring when air temperatures are high while the soil is still frozen.

Even if they do not live in particularly dry places, most plants will occasionally encounter water stress for shorter or longer periods of time. Most of these plants do not have many of the adaptations of desert plants and must respond to the water stress in other ways. When these plants are exposed to water stress, such as drought or saline conditions, to survive they must be able to retain as much water as possible. If the plants are not able to cope with the water stress, they will not be able to survive. The sensitivity and response time to drought differs between different species and slow growing species have been found to be more sensitive (Aasamaa and Sober, 2011). Repeated drought encounters increases the sensitivity to environmental changes that induce stomatal closure, while the sensitivity to changes that induce stomatal opening is decreased (Aasamaa and Sober, 2011). In response to water stress plants have developed several different mechanisms that increase the desiccation tolerance and water retention. These responses can be divided into short term and long term responses (Figure 1).

2.1 Long term responses

During prolonged water stress plants must be able to survive with low water content and maintain a minimum amount of water, through water uptake and retention. To cope with

prolonged drought stress plants respond with energy demanding processes that alter the growth pattern, chemical content of the plants and the up or down regulation of genes.

2.1.1 Biochemical changes

When the water availability is reduced, plants change the biochemistry to be able to retain as much water as possible and take up whatever water they can. During water stress plants produce and accumulate compatible solutes such as sugars, polyols and amino acid to lower the osmotic potential in the cells to facilitate water absorption and retention (Xiong and Zhu, 2002). Some of the compatible solutes also contribute to maintaining the conformation of macromolecules by preventing misfolding or denaturation (Xiong and Zhu, 2002). Plants also produce higher levels of the plant stress hormone ABA during water stress and this affects their growth pattern and stress tolerance (details under growth changes and stomatal functioning).
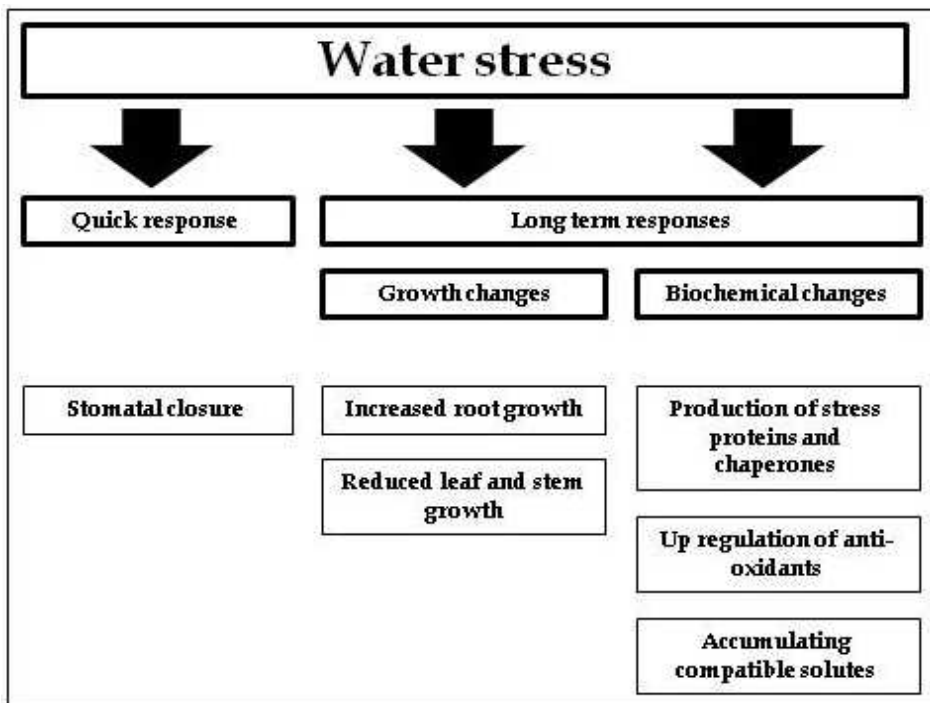

Fig. 1. Plant responses to water stress.

A group of proteins called late embryogenesis abundant like (LEA) proteins are also produced during water stress. These LEA-like proteins are highly hydrophilic, glycine-rich and highly soluble and have been found to be regulated by ABA (Xiong and Zhu, 2002). The LEA-like proteins are thought to act as chaperones, protecting enzymatic activities (Reyes et al., 2005) and preventing misfolding and denaturation of important proteins (Xiong and Zhu, 2002). Some of the LEA-like proteins have similar features as ribosomal proteins and are thought to interact with RNA (Garay-Arroyo et al., 2000).

Decreased transpiration and decreased CO_2 and nutrient uptake during water stress result in changes in metabolic pathways such as photosynthesis and respiration, as well as changes in ion uptake, transport and extrusion (Xiong and Zhu, 2002). Some of these changes can lead to oxidative damage. Reactive oxygen species, such as H_2O_2, O_2^-, OH and OH_2, are by-products in electron transport chains and have unpaired electrons that can attract electrons from other components. Reactive oxygen species can therefore cause damage to a variety of compounds such as DNA, RNA, proteins, lipids and chlorophyll and thus damage membranes and change cell metabolism and eventually lead to senescence. Many antioxidant systems, both enzymatic and non-enzymatic, are up-regulated in response to the increased reactive oxygen species levels during water stress. These antioxidants scavenge the reactive oxygen species and reduce the oxidative damage. The enzymatic antioxidants, such as superoxide dismutase, peroxidase, ascorbate peroxidase, catalase, polyphenol oxidase and gluthathione reductase can detoxify reactive oxygen species (Prochazkova et al., 2001; Jaleel et al., 2009b). The non-enzymatic anti oxidants, including vitamins (A, C and E), glutathione, carotenoids and phenolic compounds, can scavenge reactive oxygen species by donating an electron or a hydrogen atom (Prochazkova et al., 2001; Jaleel et al., 2009b).

2.1.2 Growth changes

During water stress the water content of the plant decreases, which causes the cells to lose turgor pressure and shrink. The loss of turgor pressure in the cells inhibits turgor dependent activities such as cell expansion, which affects the growth of the whole plant. Some studies show that ABA can function as a signal to reduce leaf growth rate, both when ABA is applied exogenously or generated by water stress (Wilkinson and Davies, 2010). Reduced cell growth during water stress has e.g. been found to decrease the stem length in *Arabidopsis thaliana* soybean (*Glycine max*), potato (*Solanum tuberosum*), ocra (*Abelmoschus esculentus)* and parsley (*Petroselinum crispum*) (Heuer and Nadler, 1995; Specht et al., 2001; Park et al., 2007; Petropoulos et al., 2008; Sankar et al., 2008). Similarly reduced cell enlargement reduces the leaf expansion in *Populus* (Ren et al., 2007). By reducing the leaf expansion the leaves become smaller and therefore transpire less. In some cases water stress can even lead to leaf abscission. This has e.g. been seen in *Populus* and paper birch (*Betula papyrifera)* (Giovannelli et al., 2007; Gu et al., 2007). The reduction of cell volume also concentrates the solutes in the cells and compresses the plasma membranes causing them to increases in thickness.

To increase water uptake and maintain a minimum osmotic pressure during drought many plants increase their root growth, either deeper or laterally. By increasing the root growth the area for water uptake becomes larger and water further away and deeper in the soil may be reached. This growth response has been found in e.g. maize, madagaskar periwinkle (*Catharanthus roseus)* and date palm (*Phoenix dactylifera*) (Djibril et al., 2005; Jaleel et al., 2008; Trachsel et al., 2010).

2.2 Short term response

When plants suddenly encounter drought it is important to respond as quickly as possible. A faster drought response means that less water is lost and the survival rate of the plants is increased. The most important quick response is stomatal closure. Stomata consist of two guard cells surrounding the stomatal pore. When the stomata are open water is transpired and CO_2 enter the leaf through the stomatal pore. During water stress the stomatal pore can be closed to reduce water loss. By closing the stomatal pore the

water use efficiency is increased (Farooq et al., 2009), reducing the amount of water lost per CO_2 molecule assimilated. Several mechanisms work together to close the stomata, such as hydro passive closure and chemical signals from the plant stress hormone ABA. Increased levels of ABA also causes increased hydraulic conductivity in the roots and xylem, enabling the plants to transport more water and thereby recover more rapidly after water stress (Kudoyarova et al., 2011).

3. Stomatal functioning

Development of stomata if often considered one of the most important developments in plant evolution (Brodribb and McAdam, 2011). By being environmentally controlled gateways into the plants controlling CO_2 uptake and transpiration they are central determinants of photosynthesis, cooling and nutrient uptake (Farooq et al., 2009). To be able to balance CO_2 uptake and water transpiration through stomatal movement is therefore an important response to changes in the environmental conditions. Low transpiration due to stomata closure means less cooling of the leaves and less uptake and transportation of nutrients.

3.1 Stomatal signaling and movement

Stomatal closure occur when the two guard cells surrounding the stomatal opening lose turgor pressure and close the opening (Outlaw, 2003). There are many signals that induce stomatal closure, among these the best known signal is probably ABA. In the signaling pathway towards stomatal closure there are several secondary messengers, such as Ca^{2+}, H_2O_2 and NO (Atkinson et al., 1990; Zhang et al., 2001; Neill et al., 2002; Garcia-Mata and Lamattina, 2009) that contribute to the stomatal closure. Passive loss of turgor pressure also results in stomatal closure.

Since stomatal closure has negative effects on CO_2 uptake, photosynthesis, transpirational cooling as well as water and nutrient uptake it is important to close the stomata only when the benefit of water retention outweighs the negative effects. To be able to close the stomata during unfavourable conditions there are several mechanisms and signalling pathways leading to stomatal closure. These pathways can be divided into hydro passive and active stomatal closure (Figure 2).

3.1.1 Hydro passive stomatal closure

Hydro passive stomatal closure occurs when the water evaporation from the guard cells is too low to be balanced by water movement into these cells. The water content in the cells is then rapidly reduced to the extent where the osmotic pressure is reduced and the cells lose turgor pressure and shrink (Luan, 2002). When this happens the guard cells are unable to maintain the shape and the stomatal pore is covered.

Some studies have shown that passive stomatal closure is important in ferns and Lycopods, but not in Angiosperms and Gymnosperms (Franks and Farquhar, 2007; Brodribb and McAdam, 2011). This is because in Angiosperms and Gymnosperms the guard cells closely interact with their subsidiary cells. When the guard cells lose turgor pressure the subsidiary cells also lose turgor pressure and the force from the subsidiary cells pulls the guard cells apart, opening the stomata. This hydro passive opening is called the "wrong-way" response (Franks and Farquhar, 2007). In contrast the guard cells of ferns and Lycopods do not interact closely with their subsidiary cells.

The loss of turgor pressure in the subsidiary cells in these plants does therefore not result in the guard cells being pulled apart. The simultaneous loss of turgor in the guard cells will in these plants be enough to close the stomata.
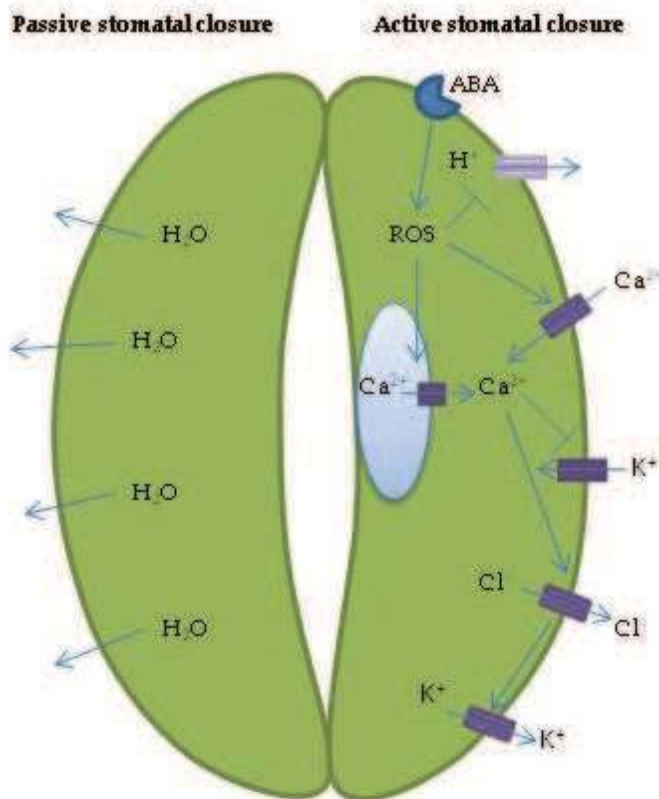

Fig. 2. Hydro passive and active stomatal closure pathways.

3.1.2 Active stomatal closure

ABA as well as elevated levels of CO_2 activates signalling pathways leading to stomatal closure (Kim et al., 2010). ABA is produced in the roots and leaves during water stress and is transported to the guard cells. ABA is transported into the guard cells by ATP-binding cassette (ABC) transporters that are located in the plasma membrane (Kang et al., 2010). When the ABC transporters are knocked out the ABA uptake is lower, stomata remain more open during drought and the stress tolerance is decreased (Kang et al., 2010). The ABA signals are first recognised by several receptors. PYR/PYL/RCAR (PYRABACTIN RESISTANCE/ PYRABACTIN RESISTANCE –LIKE/REGULATORY COMPONENT OF ABA RESPONCE) proteins have been shown to function as ABA receptors (Klingler et al., 2010). Another protein GCR2 (G protein coupled receptor) has also been shown to be a ABA receptor (Liu et al., 2007).

The size of the stomatal opening is regulated by the turgor pressure and cell volume of the guard cells (Schroeder et al., 2001; Kim et al., 2010). Regulation of stomatal opening is linked

to transport of ions and water through channel proteins across the plasma and vacuole membrane (Kim et al., 2010). ABA induces the production of reactive oxygen species (e.g. H_2O_2), which in turn acts as a trigger for NO production, inhibition of membrane proton pumps and Ca^{2+} influx across both the plasma and vacuole membranes. H^+-ATPases that are hyperpolarizing the plasma membranes must be inhibited to induce ABA mediated stomatal closure (Merlot et al., 2007). The increased Ca^{2+} levels activate slow and rapid type anion channels, generating an anion efflux from the cells. The anion efflux depolarizes the membrane, which in turn causes K^+ efflux through K^+_{out} channels across both the vacuole and the plasma membrane. Simultaneously Ca^{2+} also inhibits K^+_{in} channels (Wasilewska et al., 2008). Malate is also converted to starch reducing the osmotic potential and turgor pressure further (Kim et al., 2010). The plasma membrane is thus depolarised, the turgor pressure and cell volume reduced and the stomata close (Kim et al., 2010).

4. ABA biosynthesis and metabolism

Increased content of ABA during water stress has been found in all photosynthetic organisms. The biosynthesis of ABA have previously been thought to occur only in the roots, but more recent studies show that ABA is also synthesized in mesophyll cells, vascular tissue and stomata. As stated above increased levels of ABA in leaves induces and regulates stomatal closure, while the increased levels of ABA in roots increase the hydraulic conductivity increasing the water uptake and transportation (Parent et al., 2009). The amount of ABA in the tissue is regulated in several metabolic steps, both in the biosynthesis and inactivation steps.

ABA is synthesized from phytoene (Figure 3), a carotenoid produced from pyruvate and glyceraldehydes-3-phosphate (Cutler and Krochko, 1999; Liotenberg et al., 1999). In the plastids phytoene is converted to ζ-carotene by phytoene desaturase and then to β-carotene, lycopene and zeaxanthin. Zeaxanthin is converted first to antheraxinthin and then to violaxanthin by zeaxanthin epoxidase (ZEP). Violaxanthin is then converted to xanthoxin by 9-cis-epoxycarotenoid dioxygenase (NCED). Xanthoxin is then converted further in the cytosol. The main pathway from xanthoxin to ABA is through abscisic aldehyde. Xanthoxin is then converted to abscisic aldehyde by an enzyme related to a short-chain dehydrogenase/reductase SDR). Abscisic aldehyde is further oxidized to ABA by abscisic aldehyde oxidase (AAO) (Seo and Koshiba, 2002). It has been found that genes regulating at least the last steps in the ABA biosynthesis (NCED and AAO) are the most important and are strongly up regulated during water stress, showing the important role of ABA as a rapid stress response (Qin and Zeevaart, 1999; Seo et al., 2000).

ABA is further regulated by several inactivation pathways (figure 3) (Cutler and Krochko, 1999). There are two main such pathways. The first is inactivation by oxidation. ABA is then oxidized to 8'-hydroxy ABA and subsequently to phaseic acid (PA) and 4'dihydrophaseic acid (DPA). The conversion of ABA to 8'-hydroxy ABA is catalysed by the enzyme (+)-ABA 8'-hydroxylase (Kushiro et al., 2004) and the enzyme phaseic reductase catalyzes the conversion of PA to DPA (Cutler and Krochko, 1999). (+)-ABA 8'-hydroxylase is highly regulated by environmental factors, such as air humidity (Okamoto et al., 2009). The other inactivation pathway is by conjugation to ABA glucose ester, which is hypothesised to be a storage form of ABA (Cutler and Krochko, 1999). This conjugation is catalyzed by ABA glucosyltransferase (Lee et al., 2006). Several experiments provide evidence that ABA

glucose ester can be cleaved enzymatically by β-D-glucosidase (Dietz et al., 2000; Lee et al., 2006). The liberated ABA can then induce metabolic and changes and stomatal closure.
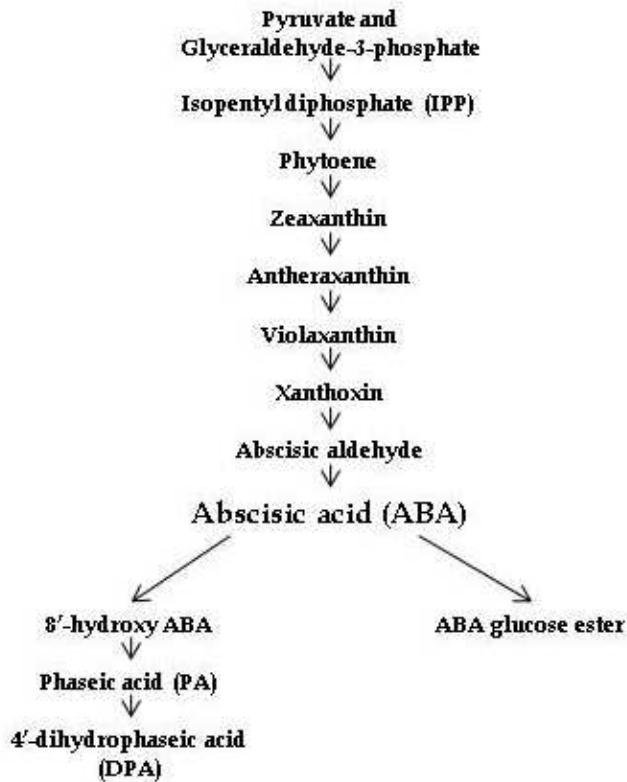
Pyruvate and
Glyceraldehyde-3-phosphate
↓
Isopentyl diphosphate (IPP)
↓
Phytoene
↓
Zeaxanthin
↓
Antheraxanthin
↓
Violaxanthin
↓
Xanthoxin
↓
Abscisic aldehyde
↓
Abscisic acid (ABA)

8'-hydroxy ABA   ABA glucose ester
↓
Phaseic acid (PA)
↓
4'-dihydrophaseic acid
(DPA)

Fig. 3. Biosyntehesis of ABA from pyruvate and glyceraldehydes-3-phosphate and ABA metabolism by oxidation to PA and DPA and conjugation to ABA glucose ester.

5. Stomatal development under high relative air humidity

Plants grown under high relative air humidity have malfunctioning stomata that are unable to close in response to darkness, ABA and desiccation (Fordham et al., 2001). This results in high stomatal conductance and frequent leaf drying. Also, plants grown *in vitro* under high relative air humidity have low ABA levels, but when moved to an *ex vitro* environment with lower relative air humidity the ABA levels increase (Hronkova et al., 2003). Furthermore, *Wrightia tomentosa* plants grown under high relative air humidity *in vitro*, had 29.4 % malformed stomata (Joshi et al., 2006). These stomata were described as large, spherical and wide open, lacking the ability to close. In comparison stomata of *in vivo* developed plants were smaller, elliptical and depressed. Other studies have shown similar results, where *in vitro* propagation has resulted in stomata that are unable to close in response to environmental and biochemical stimuli (Brainerd and Fuchigami, 1982; Santamaria et al., 1993; Sciutti and Morini, 1995).

The efficiency of stomatal openings for CO_2 uptake and water transpiration is not only determined by the size of the opening, but also by the number of stomata (Metwally et al., 1971). More stomata can take up more CO_2 and transpire more. In research done in different humidities it has also been found that the number of stomata per leaf increased with development in higher soil humidities, but when calculated as number of stomata per area the number decreased in higher humidities (Metwally et al., 1970; Metwally et al., 1971). The stomatal index, the number of stomata relative to the number of epidermal cells, was also found to increase with soil moisture (Schürmann, 1959). Similar experiments have been preformed with air humidity, increased air humidity results in increased stomatal density (Sciutti and Morini, 1995). The stomatal density has been found to increase in plants with decreased ABA concentrations, which also have increased transpiration (Lake and Woodward, 2008). In *Vicia* faba drought and salinity stress has been found to increase the stomatal density and stomatal index, facilitating water uptake under water stressed conditions (Gan et al., 2010).

In the greenhouse industry the stomatal functioning and transpiration influences the post harvest quality of the plants. The value of ornamental plants is dependent on the aesthetic condition. Loss of aesthetic value can be due to water stress, where high transpiration rates shorten the shelf life. When ornamental plants are grown in large scale industries it is important to produce stress tolerant plants that have long shelf lives. In greenhouses there is an artificial environment, where the day length, temperature, relative air humidity (RH) and watering regimes are controlled to be able to produce as many plants as possible with as little cost as possible, without reducing the quality of the plants. This has resulted in energy-efficient greenhouses, which conserve energy (CO_2 and temperature) by rarely opening the ventilation. This consequently increases the relative humidity inside the greenhouses. Furthermore, much of the plant breeding is done in greenhouses, particularly when it comes to ornamentals.

Roses developed under high relative humidity (>85%) have 6-8 days shorter shelf life and greater water loss than plants grown under lower humidities (Mortensen and Fjeld, 1998; Torre and Fjeld, 2001). When roses are cultivated in high relative humidity environments in greenhouses they develop large, malfunctioning stomata, similar as the malfunctioning stomata produced under *in vitro* conditions (Torre and Fjeld, 2001; Torre et al., 2003). When these plants are moved to a dryer environment the stomata are unable to close, which results in high water loss and less stress tolerant plants that quickly lose their ornamental value (Torre and Fjeld, 2001).

The shorter shelf life of plants developed under high humidity is a major problem in the greenhouse industry. One of the important challenges is therefore to find new environmental regimes that save energy, but still produce high quality and stress tolerant plants. When plants grown in high relative humidity are treated with a 6 hour low humidity period in the middle of every day, the stomata remain functional (Mortensen et al., 2007; Pettersen et al., 2007). Similarly using 18 hour light period instead of 24 hours also result in more water retention and longer shelf life in roses (Mortensen et al., 2007).

Plants grown under constant high relative humidity contain less ABA than plants grown under lower relative humidities and some of the stomata of these plants are larger and malfunctioning (Nejad and van Meeteren, 2005, 2007). One of the main hypotheses explaining the malfunctioning stomata in high humidity is development with low ABA concentrations (Nejad and van Meeteren, 2007; Okamoto et al., 2009). If the plants developed under high relative humidities are treated with ABA during development, the

stomata respond as if they were developed under lower relative humidities (Nejad and van Meeteren, 2007). In plants moved from high humidity to lower humidities regained stomatal functioning in leaves that were still actively expanding, but not in fully developed leaves (Nejad and van Meeteren, 2008). Similarly if leaves developed under high relative humidity were given ABA application, the stomatal functioning was restored in young expanding leaves, but not in fully developed leaves (Nejad and van Meeteren, 2008).These experiments implicate that ABA is involved in the development of functioning and malfunctioning stomata, although there is also contradicting results. In *Arabidopsis thaliana* it has been shown that ABA-deficient and ABA-insensitive mutants responded similarly as wild type plants to changes in humidity (Assmann et al., 2000). Plants developed under low ABA conditions also have higher stomatal density (Lake and Woodward, 2008), indicating that ABA is important in both the development of stomata size and density.

ABA application in lower concentrations, applied to plants can reduce transpiration rate and increase the shelf life of *Salvia splendens* and a number of other ornamentals, by inducing stomatal closure (Pompodakis et al., 2004; Waterland et al., 2010a; Waterland et al., 2010b; Kim and van Iersel, 2011). On the other hand, application of high ABA concentration caused early leaf abscission in *Salvia* (Kim and van Iersel, 2011). Also, ABA application decreased the shelf life of miniature potted roses (Muller et al., 1999), possibly due to high concentrations.

6. Conclusion

The ability of plants to be able to regulate the size of the stomatal opening is a very important mechanism to control water loss and survive. This ability is especially important during water stress, when loss of water can have serious consequences for the plants. Water stress can cause reduced growth and in severe cases plant death. To minimize the negative effects of water stress the plants respond by changing their growth pattern, producing stress proteins and chaperones, up-regulation of anti-oxidants, accumulation of compatible solutes, increasing the amount of transporters involved in water and ion uptake and transport and by closing the stomata. If the plants are unable to quickly respond to water stress, by closing the stomata and thereby conserve as much water as possible, the consequences are more severe and plants wilt and die more quickly. This is a major problem in plant propagation of ornamentals. Plants developed under high relative air humidity develop malfunctioning stomata, which are unable to close in response to water stress. When these plants are later placed in dryer conditions they quickly lose their ornamental value and wilt. Treatments with ABA or periods of high temperature or low relative air humidity during development can offset this malfunctioning and produce functioning stomata, even in high humidity.

7. References

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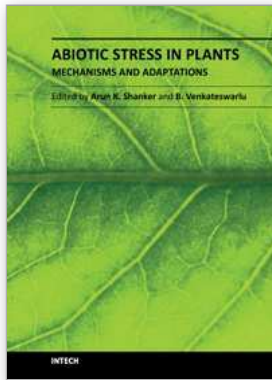
Abiotic Stress in Plants - Mechanisms and Adaptations

Edited by Prof. Arun Shanker

World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly dived into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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