

Chapter 2

Plant Water Relations, Plant Stress and Plant Production

Summary Plant water deficit is initiated as the crop demand for water exceeds the supply. The capacity of plants to meet the demand and thus avoid water deficit depends on their “hydraulic machinery.” This machinery involves firstly the reduction of net radiation by canopy albedo, thus reflecting part of the energy load on the plant. Secondly, it determines the ability to transport sufficient amount of water from the soil to the atmosphere via the stomata (which take in CO_2) in order to provide for transpiration, transpirational cooling and carbon assimilation. Water is transported by way the SPAC (soil-plant-atmosphere continuum). SPAC is largely controlled by the resistances in the continuum as determined by root, stem, leaf, stomata and cuticular hydraulic resistances. Resistances are generally a function of the plant basic anatomy, development and metabolism. Some resistance such as those of stomata is also variable depending on plant responses and environment effects.

The primary force driving water against plant resistances is the soil-to leaf gradient of water potential which is expressed in reduced leaf water potential. Reduced leaf water potential may induce osmotic adjustment which helps maintain leaf hydration at low leaf water potential. As plants enter a state of water deficit, hormones, mainly ABA are produced in the root and the shoot, causing an array of responses, most of which cannot be defined as productive in the agronomic sense. Thus, the combination of hydraulic stress and hormonal metabolism carry various impacts on plant adaptation to stress on one hand and reductions in growth and productivity on the other. The most susceptible growth stage to water deficit is flowering and reproduction, which in many crop species cannot be recovered upon rehydration. Some (not all) of the heritable plant traits and adaptive responses to water deficit can be counterproductive in term of allowing high yield potential.

2.1 The Initiation of Plant Water Deficit

Crop evapotranspiration (ET) is affected by both the environment and the crop. Crop factors that affect ET are mainly associated with the dynamics of leaf-area development and senescence and the resistances to water flux developed in the

soil-plant-atmosphere continuum (SPAC). When actual ET is close or equal to maximum ET, the environment exercises most of the control over ET. A reduction in actual ET below maximum ET is associated with the development of a gradient of potentials between the soil and the transpiring organs, leading towards a situation defined as plant water deficit. At the same time, the relative role of the plant in affecting ET becomes greater. Therefore, the role of breeding for water limited environments is anywhere in the domain where $ET_{\text{actual}}/ET_{\text{maximum}} < 1$. It must be made very clear already at this point that breeding programs for water limited environments can be quite different if this ratio is closer to 1 or closer to 0.1, namely if plant water deficit is small or large.

In the dryland agricultural domain where plant production is a major consideration the ultimate purpose is for the plant to deliver water from the soil to the leaves thus allowing sustained leaf gas exchange and the delay of leaf death. The best plant to achieve this purpose is one that is equipped with the appropriate “hydraulic machinery” (Sperry et al. 2002) as well as additional traits to relieve the energy load on the plant as well as manage an effective use of water.

2.2 The Soil-Plant-Atmosphere Continuum (SPAC)

During the day the plant is under heavy energy load (net radiation, R_n) (Sect. 1.3). While a small fraction of this energy is used in photosynthesis, most of it must be dissipated. If this energy is still absorbed by the canopy to its fullest extent then leaves can reach a killing temperature of 40° to 50°C or more. This energy load is dissipated via three physical channels: (1) the “albedo” which is determined by the total reflectivity of the leaf as affected by its optical characters and its architecture; (2) “sensible heat” which is the radiation emitted from the canopy as heat; and (3) the “latent energy” which is dissipated by plant transpiration. In the narrow sense SPAC relates only to water movement through the system (channel 3 above) but it is most relevant towards the subject of this book to discuss all channels of energy dissipation by the plant under this heading.

2.2.1 The Albedo

The Albedo is the ratio of reflected to incident radiation. It is a unit-less measure indicating the diffuse reflectivity of any surface or body. The word is derived from *albus*, a Latin word for “white.” The crop albedo is different from the leaf albedo in that the former is determined by the spectral properties of the exposed soil and the crop leaf canopy. The soil reflective properties are determined largely by its color and wetness, where greater “whiteness” increases the albedo.

The optical characteristics of the single leaf (Fig. 2.1) are determined by leaf pigments, leaf anatomy, leaf age (which is partly expressed in its pigmentation), leaf water status and leaf surface properties. A study of 45 plant species revealed

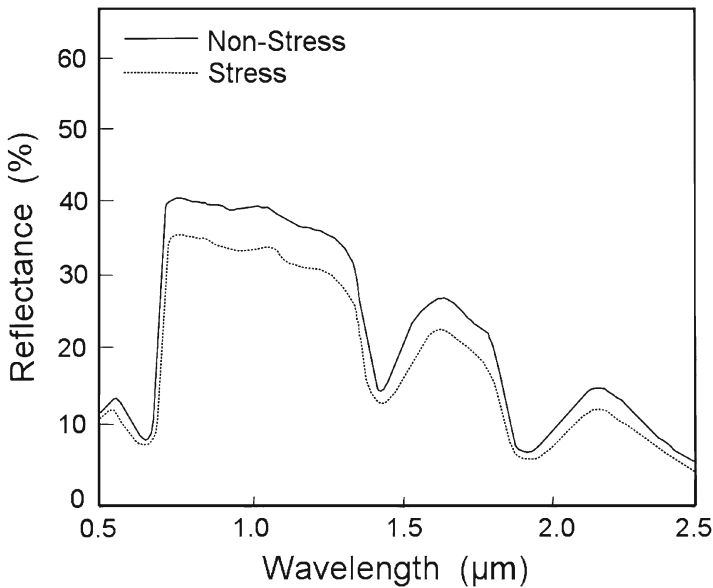


Fig. 2.1 A typical spectral reflectance curve of a typical non-stressed and a drought stressed leaf ranging from short visible to long infrared wavelength drawn as an average according to several sources of data

that both pubescence (presence of hairs) and glaucousness (presence of a thick epicuticular wax) had marked effects on total leaf reflectance (Holmes and Keiller 2002). Pubescent leaves tended to be more effective in reflecting longer wavelengths than the ultraviolet. Surface waxes are very effective reflectors of both UV and longer wavelength radiation. As can be seen in Fig. 2.1, drought stress tends to reduce leaf reflectivity throughout the spectrum.

Research on the spectral properties of leaves was also performed in relations to remote sensing development for vegetation and crops, either from satellite platforms or from the ground. The understanding of the optical properties of leaves and how they change with leaf characteristics and the effect of the environment led to the development of remote sensing techniques which allow to sense plant drought, mineral deficiency and various biotic stresses. Multispectral signatures of crops are now being used to estimate crop growth and even yield, in conjunction with or without crop simulation models. Some of these methods as applied to breeding are discussed in Chap. 4, section “Indirect Methods (Remote Sensing).”

2.2.2 The Water Flux

The hydraulic system within intact plants acts as a true continuum. Water will move from the soil into the plant, through the plant and into the atmosphere in response to a water potential gradient. Water flows along a gradient of decreasing water potential.

Water potential is measured in units of negative pressure such as bars or Mega Pascals (MPa). Free water is defined to have a potential of zero. Water that contains solutes will have a negative potential and it will attract free water across a semi permeable membrane. When water is held by force as the case may be in the pores of soil, the water potential is determined by the force which is required to move this water to a state of free water. This is also the case for water held in the plant.

The physical model of water flux through the SPAC has been developed under the influence of soil physics and with the involvement of soil physicists and crop climatologists. It is still the basis of our understanding of plant water relations. However, as will be seen below there are also “metabolic” or “active” components added to this model more recently.

The movement of water through plants obeys an Ohm’s law analogy, i.e., current equals driving force (the electrical potential gradient) divided by electrical resistance. Thus, water flux is more clearly understood if it is regarded as being driven by a difference in water potential, against a resistance.

Under steady-state conditions, flow through each segment of the SPAC is described as follows:

$$\text{Waterflux} = \frac{\Psi_s - \Psi_r}{r_m} = \frac{\Psi_r - \Psi_l}{r_r + r_x} = \frac{\Psi_l - \Psi_a}{r_s + r_a} \quad (2.1)$$

Where, r_m is the resistance due to the soil matrix, r_r is the root resistance, r_x is the resistance through the xylem in plant stems, r_s is the stomatal resistance, and r_a is the aerial resistance. Ψ_s , Ψ_r , Ψ_l and Ψ_a are the water potential of the soil, root, leaf and air, respectively. Resistances are additive in a series. Figure 2.2 provides a graphical schematic representation of SPAC.

The energy driving water flux through the SPAC is by and large that part of the solar irradiance which is not reflected by the canopy or dissipated as sensible heat. Therefore it must be remembered that water flux through SPAC under the Ohm’s law analogy responds primarily to the seasonal, daily and hourly march of solar radiation and R_n . Other environmental factors are also in effect, such as air humidity (vapor pressure deficit), air temperature and wind. Consequently, plant water status and most prominently leaf water status vary extensively during the day in correspondence to the march of the atmospheric environment. Even passing clouds will affect transpiration on a time scale of few minutes. Normally, leaf water potential will decrease (become more negative) from sunrise towards solar noon with lowest values at or just after solar noon. As the sun begin to set, leaf water potential will increase towards full or almost full recovery at night. It is generally accepted that relatively little transpiration occurs at night but exceptions were noted (Caird et al. 2007). Towards dawn leaf water potential almost completely equates with soil water status, unless the plant is at or close to permanent wilting.

The highly dynamic state of water flux, transpiration and the associated leaf water potentials pose a problem for the comparative measurement of water fluxes or plant water status during the day. There is no problem in hooking up a single plant to various sensors and measuring its daily response from dawn to dusk.

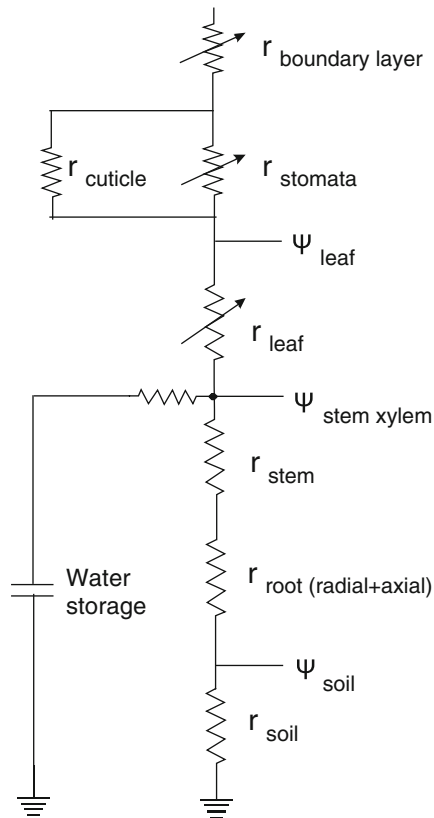


Fig. 2.2 A schematic representation of the soil-plant-atmosphere continuum as an Ohm's law analogy (see text). Arrows on resistance icons represent variable resistances. This is not to say that other resistances are absolutely static under all conditions. (Ψ = water potential; r = hydraulic resistance)

However when different genotypes must be phenotyped and compared for plant water status, it should be done on a reasonable short time span and when the plant is in a relatively stable hydraulic state under a relatively stable environment. Extensive experience shows that plants are relatively stable in terms of water flux and plant water status at dawn and for about 1 to 2 h after solar noon when there is a small plateau in the daily march of transpiration and plant water status. At dawn the plant is under a minimal water deficit while at midday it is at peak stress.

In a well hydrated plant the greatest hydraulic resistance is in the leaf and the smallest resistance is in the stem. These values may vary to some extent in absolute and relative term in different plant species and under different conditions. It is therefore important to understand the dynamics of the various components of plant resistance affecting the SPAC since they are the initial and main controls of plant water status and plant water stress, which we strive to manipulate genetically.

2.2.3 Root Resistance

The root is the most crucial organ for meeting transpirational demand at a reasonable high leaf water status, on the condition that water is available anywhere in the root horizon. Total root conductivity which is the inverse of root resistance ($K_r = 1/R_r$) is positively related to *root length density* in the soil and the *hydraulic conductivity* of the single root axis. High root length density increases the number of contact points between root and soil. This is crucial for water uptake in a drying soil. In order for the root to absorb water, water must be available at the root-to-soil interface. For this situation to occur the root must grow towards water or water must flow towards the root. Water flow in a drying soil towards the root is subjected to very high resistance. High root length density reduces the impact of soil resistance to water flow towards the root. Experience gained with drip irrigation and associated research demonstrated that well watered plants in a reasonably good soil can meet transpirational demand in full even when the root system is small.

The root axis hydraulic resistance is partitioned into radial and axial (longitudinal) resistances. Axial resistance refers mainly to water flow through root xylem vessels. It has been shown that as soon as early metaxylem vessels mature, the axial hydraulic resistance within the xylem is usually not rate-limiting (Steudle and Peterson 1998). However under certain conditions (see below) xylem resistance can increase. Radial resistance is the important component of root resistance, in addition to the root-soil interface resistance.

To pass from the soil solution into root vascular tissues, water must flow radially across a series of concentric cell layers. These layers include the epidermis, the exodermis in roots where it is differentiated, several layers of cortex cells, the endodermis, pericycle, xylem parenchyma cells and finally into the xylem vessel. Three pathways co-exist for radial water transport across living root tissues: through the cell walls (apoplastic path), from cell to cell, along the symplasm through plasmodesmata (symplastic path) or across membranes (trans-cellular path). The cell walls of exo- and endodermal cells possess a particular structure, the Casparian band (or “strip”), which consists of a deposit of suberin and/or lignin. It has been shown that in the exodermis, this structure represents an effective impediment to water flow. It is generally accepted that the Casparian band creates a tight apoplastic barrier to solutes and prevents their backflow from the stele.

It has been argued (Stirzaker and Passioura 1996) that sometimes the sum of the resistances in the plant and the soil was too small to account for the fall in water potential between the leaf and the soil, especially when plants grow in sandy soils, which are prone to dry rapidly. The root-soil interface resistance was suggested to be responsible due possibly to poor root contact with the soil or due to accumulation of solutes at the root interface. It was later shown by White and Kirkegaard (2010) that root contact as driven by extensive root branching and long root hairs is a prime determinant of moisture extraction from dry soil. Accordingly, radial root resistance and root-soil interface resistance (also involving root hairs) in series can be considered as the major resistance of the single root to water uptake.

Whereas radial water flux through the trans-cellular path is important as compared with the apoplastic path, water channels that control water movement through cellular membranes become important controls of radial root resistance. In the presence of heavily suberized roots, the apoplastic component of water flow may be small. Under these conditions, the regulation of radial water flow by water channels becomes dominant. Since water channels are under “metabolic” control, this component represents an “active” element of water transport regulation (Steudle 2000).

Zhu et al. (2010) proposed an interesting hypothesis for enhanced root growth and root-length density. They hypothesized that root cortical aerenchyma (RCA) reduces root respiration in maize by converting living cortical tissue to air volume. This should reduced root metabolic cost and release more energy for root growth. Their data for maize lines of low and high RCA show that high RCA was associated with appreciable increase in root-length density and depth.

Aquaporins are water channel proteins expressed in various membrane compartments of plant cells, including the plasma and vacuolar membranes (Javot and Maurel 2002). While their role in root water uptake and plant water status is well recognized, there are wider implications of aquaporins in plant physiology and plant response to stress (see further below). These membrane proteins belong to the major intrinsic protein (MIP) family, with members found in nearly all living organisms. Plants appear to have a particularly large number of MIP homologues. The complete genome of *Arabidopsis thaliana* has 35 full-length MIP genes. Based on sequence homology, plant MIPs cluster into four subgroups which to some extent reflect different subcellular localizations. Members of the two major subgroups, the plasma membrane intrinsic proteins (PIPs) and the tonoplast intrinsic proteins (TIPs) have been initially localized in the plasma membrane and in the tonoplast, respectively.

Mercury (HgCl_2) acts as an efficient blocker of most aquaporins and has been used to experimentally demonstrate the significant contribution of water channels to overall root water transport. Aquaporin-rich membranes may be needed to facilitate high-rate water flow across the trans-cellular path. Aquaporins are considered to be crucial for radial water transport in roots (Bramley et al. 2007). Roots show a remarkable capacity to alter their water permeability over the short term (i.e., in a few hours to less than 2–3 days) in response to many stimuli, such as day/night cycles or nutrient deficiency. These rapid changes can be mostly accounted for by changes in root cell membrane. The processes that allow perception of environmental changes by root cells and subsequent aquaporin regulation are basically unknown. It seems however that both MIPs and PIPs can be down-regulated or up-regulated by drought stress in *Arabidopsis*, depending also on plant part (Alexandersson et al. 2010). Drought resistance was not promoted by overexpression of PIP1 and PIP2 in *Eucalyptus* (Tsuchihira et al. 2010).

Abscisic acid (ABA) is a well-recognized plant hormone which accumulates in plants under drought and other stresses. It will be extensively discussed further in this and other chapters. ABA mediates many known plant responses to drought stress. It has been shown (Hose et al. 2000; Quintero et al. 1999) that exogenous

ABA enhanced root conductivity. In one detailed study (Hose et al. 2000) ABA applied at concentrations of 100–1,000 nM increased the hydraulic conductivity of excised maize roots both at the organ level (by a factor of 3 to 4) and the root cell level (by a factor of 7 to 27). It was concluded that ABA acts at the plasmalemma, presumably by interacting with aquaporins (Kaldenhoff et al. 2008). Some of the above experiments used exogenous application of ABA. Studies with transgenic plants expressing high endogenous ABA also indicate that ABA promotes hydraulic root conductivity in whole plants, such as the case for tomato (Thompson et al. 2007). ABA therefore facilitates the cell-to-cell radial water flux (Parent et al. 2009) and the uptake of water into the root as soil start drying and transpiration is reduced and when the apoplastic path of water transport is largely excluded.

The involvement of aquaporins and ABA in controlling root conductivity introduce a “metabolic” or an “active” component into the seemingly pure physical model of water flux through the SPAC. It was therefore suggested, for example, that PIP may regulate water transport across roots such that transpirational demand is matched by root water transport capacity (Sade et al. 2009; Vandeleur et al. 2009). As our understanding of aquaporins and their interaction with ABA will develop it might become possible to genetically design root conductivity to improve plant performance under drought stress. There is an apparent need for this option as can be deduced from the example of rice which has an inherently poor root conductivity causing sometimes a plant water deficit even when roots are in water (Miyamoto et al. 2001).

The majority of vascular plants form root associations with fungi to increase their absorption of mineral nutrients. Fungi, which live by absorbing nutrients from their surroundings, are ideal organisms for such associations. There are both *endomycorrhizae* and *ectomycorrhizae* associations. Endomycorrhizae penetrate cells of the root cortex with their hyphae. Mycorrhizae function as sophisticated root hairs; plants that associate with ectomycorrhizae often do not produce root hairs.

It has long been observed that *Arbuscular mycorrhizal* (AM) symbiosis with plant roots enhance plant water status and growth under drought stress as compared with non AM plants (Auge et al. 2001; Davies et al. 2002a; Ortega et al. 2004; Porcel and Ruiz-Lozano 2004; Ruiz-Lozano et al. 2001). The effect of AM in this respect has been traced at least partially to increased root conductivity in drought stressed or non-stressed plants (Aroca et al. 2007). The effect of AM in this respect seems to be genetically independent of the effect of root aquaporins. Studies with lettuce indicated that AM symbiosis enhanced plant tolerance to the depressing effect of exogenous ABA treatment on biomass production (Aroca et al. 2008), again suggesting a positive role of AM on root conductance and its interaction with ABA especially under drought stress. Further discussion of the role of AM symbiosis under drought stress with special reference to maize is available in Boomsma and Vyn (2008). Beyond AM, it is now recognized that various rhizosphere and root inhabiting rhizo-bacteria can impact root and plant hormone signaling pathways by producing ABA, auxins and cytokinins or by mediating plant ethylene levels (Dodd 2009). These can have important but yet unresolved effects on root hydraulic resistance and plant water relations.

Hydraulic lift is the passive movement of water from roots into the dry top soil layer, while other parts of the root system in deeper moist soil layers are absorbing water. Soil water absorbed by deep roots can be released in the upper dry soil profile at night or during periods of low irradiance. Hydraulic lift was first observed in native vegetation and later also in crop plants. In sorghum (Xu and Bland 1993) efflux of water into the dry top soil could first be detected at a dry soil water potential of about 0.55 MPa, Outflow was 5–6% of daily transpiration during periods of highest water use. More water was found to be exuded from roots in the top soil layer in a drought resistant maize hybrid than in a susceptible maize hybrid (Wan et al. 2000). The sizable amount of water from hydraulic lift allowed the resistant hybrid to reach a peak transpiration rate 27–42% higher than the drought-susceptible hybrid on days when the evaporative demand was high. There were two to threefold more primary roots in the deep moist soil in the resistant than the susceptible hybrid. Genetic variation in water transported by hydraulic lift were also found in cotton and ascribed to possible differences in root conductance (McMichael and Lascano 2010).

Large quantities of water, amounting to an appreciable fraction of daily transpiration, can be lifted at night. This temporary partial rehydration of upper soil layers provides a source of water, along with soil moisture deeper in the profile. Nutrients are usually most abundant in the upper soil layers which under dryland conditions become dry. Lifted water may provide moisture to facilitate nutrient availability, microbial processes, and the acquisition of nutrients by topsoil roots. Hydraulic lift was especially noted for P- efficient canola genotypes and it was found to enhance P and K uptake from the top dry soil (Rose et al. 2008). Lifted water into the upper soil zone might also extend root survival in the dry top soil (Bauerle et al. 2008).

2.2.4 Stem Resistance

The classical SPAC model accepts that axial hydraulic resistance of the stem is the smallest relative to that of stomata, leaf and root especially when crop plants and common fruit trees are considered. Understandably an efficient system of conduits must have been developed through evolution to allow plants and trees to meet large transpirational demand of leaf canopies against gravitational force and soil water deficit. The discussion of xylem conductivity is especially unique for the stem with its long conduits. Understandably, this topic has been discussed more extensively for trees than for herbage plants. It is however interesting still to note that improved stem hydraulic conductance was regarded as a reason for the drought resistance of a specific maize hybrid (Li et al. 2009).

The *Cohesion/tension theory* for long distance ascent of water in the xylem (mainly in trees) is based on the fact that water is a polar molecule. When two water molecules approach one other they form a hydrogen bond. The negatively charged oxygen atom of one water molecule forms a hydrogen bond with a positively charged hydrogen atom in another water molecule. This attractive force has several

manifestations. Firstly, it causes water to be liquid at room temperature, while other lightweight molecules would be in a gaseous phase. Secondly, it is (along with other intermolecular forces) one of the principal factors responsible for the occurrence of surface tension in liquid water. This attractive force between molecules allows plants to draw water from the root and then pull it through the xylem (via capillary action) to the leaf.

Recent pressure probe and NMR results often challenge the frequent belief that tension is the only driving force. This seems to be particularly the case for plants faced with problems of height, drought, freezing and salinity as well as with cavitation of the tensile water. Other forces come into operation when exclusively tension fails to lift water against gravity due to environmental conditions. Possible candidates are longitudinal cellular and xylem osmotic pressure gradients, axial potential gradients in the vessels as well as gel- and gas bubble-supported interfacial gradients. Zimmermann et al. (2004) criticized the arguments developed in support of the cohesion/tension theory as an explanation of water ascent in tall trees. This was then followed by a letter of response to the journal signed by no less than 46 scientists, defending the theory against this criticism. Hence, the cohesion/tension theory became a hot issue towards which this review is not making judgement. The controversies were eminent also before the publication of Zimmermann et al. (2004) (e.g., Sperry et al. 2003). An important reason for the controversy is that the xylem is “vulnerable” being sensitive to cavitation and embolism. If air enters the continuous column of water in the xylem, resistance to flow is created.

Rather than embolism being essentially irreversible, it also appears (Sperry et al. 2003) that there is a dynamic balance between embolism formation and repair throughout the day and that daily release of water from the xylem via cavitation may serve to stabilize leaf water balance by minimizing the temporal imbalance between water supply and demand. Sperry et al. (2003) concluded that although the cohesion–tension theory for xylem transport withstood recent challenges, a number of gaps remain in our understanding of xylem hydraulics. These include the extent and mechanism of cavitation reversal and thus hysteresis in the vulnerability curve and the structural basis for differences in air entry pressure (cavitation pressure) for different xylem types.

When various poplar (*Populus* spp.) and willow (*Salix* spp.) clones were tested for cavitation vulnerability (Cochard et al. 2007) it was found that variation in vulnerability to cavitation across clones was poorly correlated with anatomical traits such as vessel diameter, vessel wall strength, wood density and fibre wall thickness; however, a striking negative correlation was established between cavitation resistance and aboveground biomass production, indicating a possible trade-off between xylem safety and growth potential. However, the association between anatomical and structural features of the stem and cavitation vulnerability is apparently still an open issue (Cochard et al. 2009). Further discussion of cavitation vulnerability in relations to drought resistance is presented in Chap. 3, section “Stem Xylem Cavitation.”

Water storage in plants (predominantly in stems) can serve as a buffer against transitional insufficient supply of water from soil. It is more common in cacti and

trees, For example, in tropical forest trees (Stratton et al. 2000) it was found that seasonal and diurnal variation in leaf water potential were associated with differences among species in wood-saturated water content (a measure of water storage in trees). The species with higher wood-saturated water content were more efficient in terms of long-distance water transport, exhibited smaller diurnal variation in leaf water potential and higher maximum photosynthetic rates. The role of water storage in crop plants has not been well investigated and it is assumed to be generally small.

2.2.5 Leaf Resistance (Excluding Stomata and Cuticle)

The partitioning of resistances within the leaf among petiole, major veins, minor veins, and pathways outside the xylem is variable across species. Hydraulic resistances occur both in the leaf xylem as well as in the flow paths across the mesophyll to evaporation sites. Resistance therefore largely depends on the architecture of the specific leaf. Aquaporins may also be involved. A detailed discussion of leaf hydraulics has been published by Brodrib et al. (2010).

The decline in leaf conductivity in response to lower LWP arises from increase in xylem resistance due to cavitation or collapse, and/or from changes in the conductivity of the pathways outside the xylem such as the mesophyll. As leaf conductivity decreases due to dehydration stomata will close when, or before a low LWP becomes damaging. In droughted plants such a mechanism operates in tandem with chemical signals from the roots to close the stomata (discussed below).

Generally, leaf resistance is relatively lowest in crop plants and highest in conifers (Sack and Holbrook 2006).

2.2.6 Stomatal Resistance

Stomata affect leaf resistance by way of stomatal density and stomatal activity. High stomatal density has a role in enhancing leaf conductivity mainly under well watered conditions. As stress develops, stomatal closure becomes the main controls of resistance.

Stomata can be regarded as hydraulically and chemically driven valves in the leaf surface, which open to allow CO₂ uptake and close to prevent excessive loss of water. Movement of these valves is regulated by environmental cues, mainly light, CO₂ and atmospheric humidity. Stomatal response to humidity is of special interest with respect to plant water use in harsh environments (Fletcher et al. 2007). Stomata guard cells can sense environmental signals and they function as motor cells within the stomatal complex. Stomatal movements are controlled by the stomatal guard cells. Turgor changes in the guard cells regulate their movement. Water movement into the guard cell is driven by osmosis. Accumulation of solutes in the guard cell cytoplasm lowers guard cell water potential. Given a high hydraulic conductivity of the plasma

membrane, water will flow into the guard cell and the water potential of the guard cell will equilibrate with that of the apoplast. The inflow of water will cause the turgor pressure to rise and the guard cells to swell. The increase in volume of both guard cells causes opening of the stomatal pore. Stomatal opening depends on the import of K^+ and sometimes also sugar into guard cells. Plasma membrane and vacuolar membrane ion channels and transporter proteins are involved in regulating ion status of guard cells and subsequently the dynamics of their turgor. Ca^{2+} and its interaction with aquaporin are also involved in stomatal regulation (Li et al. 2004).

Stomata open more fully at low CO_2 concentrations. When CO_2 concentration in the sub-stomatal cavity is reduced by mesophyll photosynthesis, stomatal conductivity increases. Thus CO_2 signalling of stomatal activity links the demand for CO_2 to its supply via stomata. However, stomata are similarly sensitive to CO_2 concentration outside the leaf. As a consequence of climate change, more studies are being performed recently on the effect of atmospheric CO_2 concentration on crop plant response. It was found, for example (Wall et al. 2006) that an experimental increase in atmospheric CO_2 improved wheat water status under drought stress due to the increase in daily stomatal resistance.

Light stimulates stomatal opening. Initially it was thought that the effect was transduced via the enhancement of photosynthesis by light. It was later found that the effect was achieved via blue light-specific and photosynthetic-active radiation dependent pathways. This response to blue light has been assigned to the activity of the PHOT1 and PHOT2 blue light receptors located in the plasma membrane. Light sensitivity is high and stomata will respond to shading almost instantaneously. One must remember this when leaning over the plant with a porometer in order to measure stomatal conductance.

Stomata respond to abscisic acid (ABA) by closure. ABA concentration in the leaf tissues increases as the plant sense water deficit. The guard cell receptor for ABA is unknown to the same extent that it is still an enigma for any other plant response to this hormone (e.g., Christmann and Grill 2009). It may involve Ca^{2+} signalling and regulation of plasma-membrane ion transport. Calcium, protein kinases and phosphatases, and membrane trafficking components have been shown to play a role in ABA signalling of guard cell movement, as well as ABA-independent regulation of ion channels by osmotic stress (Luan 2002). Stomata also sense the water status of distant tissues such as roots via the long-distance transport of ABA in the xylem. It is therefore believed now that stomatal activity is regulated by both hydraulic and chemical ABA signals (e.g., Christmann et al. 2007; Schachtman and Goodger 2008).

Aquaporins are also implicated in the control of stomatal conductance not only to water but also to CO_2 (Miyazawa et al. 2008). Deactivation of aquaporins was suggested to be responsible for the significant reduction in the diffusion conductance of CO_2 from the intercellular air space to the chloroplasts (internal conductance) in plants growing under long-term drought.

Stomata are therefore very effective but complex variable resistors in the SPAC which respond to the atmospheric environment on one hand and to plant water status and stress responsive plant chemical signals on the other. The consequences

of stomatal resistance towards photosynthesis and the relationship to water-use and plant productivity are discussed in Chap.3, section “Stomatal Activity and Dehydration Avoidance.”

2.2.7 *Cuticular Resistance*

In parallel to the stomata the cuticle offers a second plant surface hydraulic conductance pathway. Relative to stomata, cuticular resistance is basically non-variable on a short time-scale. When stomata are tightly closed, the cuticle remains the major resistance to transpiration at the leaf surface. If the cuticle is conductive then the effectiveness of the stomata in controlling transpiration is impaired.

The cuticle is a thin (0.1–10 μm thick) continuous membrane consisting of a polymer matrix (cutin), polysaccharides and associated solvent-soluble lipids (cuticular waxes) (Riederer and Schreiber 2001). Cuticular waxes are embedded in the cuticle and are deposited over the cuticle as “epicuticular wax” (EC). Upon the formation of the cuticle and EC, the passage of wax components through the cell wall and cuticle probably occurs via diffusion, possibly in a solvated form enabled by cell wall associated transport proteins. Lipid transfer proteins (LTPs) are thought to be involved in the transfer of lipids through the extracellular matrix. A six-fold increase of free tobacco *LTP* gene transcripts was observed after three drought events (Cameron et al. 2006).

In the following discussions “Cuticular resistance” or “non-stomatal resistance” refer to the resistance of the layer comprising of the epidermis, the cuticle and the EC. EC is a general term for complex mixtures of homologue series of long chain aliphatics like alkanes, alcohols, aldehydes, fatty acids, and esters with the addition of varying proportions of cyclic compounds like pentacyclic triterpenoids and hydroxycinnamic acid derivatives. EC can take various shapes according to plant species and plant organ, ranging from amorphous layer to ribbons, filaments, tubes and plates which can produce impressive photographs by scanning electron microscopy. EC morphology is influenced more by the physicochemical properties of the constituents rather than by the underlying cuticular membrane or the means of delivery to the surface. The shape of the wax deposit can also affect hydraulic resistance. Temperature, light intensity and humidity influence wax morphology via their effect on wax composition and probably the rate of deposition.

The hydraulic resistance of the cuticle varies. Generally it is low in tropical plants and high in xerophytic plants, indicating evolutionary adaptation to water limited conditions. Studies of EC mutants (e.g., Zhang et al. 2005; Burow et al. 2008) and experimental removal of EC by mechanical or chemical means (e.g., Araus et al. 1991) indicate that the presence of EC is very important in increasing cuticular resistance.

Stress affects EC load and cuticular resistance on a time scale of few days (Shepherd and Wynne 2006). High irradiance increase EC load. The response is very likely derived from the role of wax in reflecting excess radiation, including UV. The spectral properties of leaves are affected by EC. This has been well

documented by numerous publications since that of Blum (1975). Low air humidity increases EC load and sometimes it affects the shape of the deposits. It is a well known phenomenon that plants grown from tissue culture at high humidity have little wax and tend to wilt due to excessive cuticular transpiration. Plant water deficit increases EC load (e.g., Cameron et al. 2006; Shepherd and Wynne 2006). Cuticle-associated gene transcripts in leaves were altered in *Arabidopsis* leaves subjected to drought stress and were associated with increased cuticle thickness and abundance of cuticular lipids (Kosma et al. 2009).

It is therefore evident that the full phenotypic expression of EC deposition potential of any given genotype is realized after plants are exposed to an inductive environment, such as drought, low humidity and high irradiance.

ABA promotes EC deposition. ABA treatment of Jojoba shoots resulted in increased EC load on leaves (Mills et al. 2001). CER6 condensing enzyme is involved with epicuticular wax production and it was found that ABA enhanced CER6 transcript accumulation (Hooker et al. 2002).

2.3 Plant Size and the Development of Water Deficit

Besides the factors controlling transpiration at the single leaf level, a most dominant factor in controlling whole plant and crop transpiration is total leaf area. Any amateur gardener knows that a large plant grown in a pot will require irrigation more frequently than a smaller one for the same pot volume. The disregard for the role of plant size in plant water relations has become a prevalent pitfall in pot experiments (Sect. 4.1.5.1). A major avenue by which plant evolution impacted plant adaptation to dry environments was by reduced plant size and growth rate, typical of many xerophytic and native arid land plants. It is also a common observation that when severe water deficit develops lower (older) leaves are desiccated and die first so as to reduce leaf area and plant water use.

At the crop level the demand for water as affected by plant size is controlled by leaf area index (LAI), which is the total area of live leaves per unit ground surface. Crop evapotranspiration (ET) increases with LAI until LAI reaches a maximum threshold beyond which ET does not increase. As the crop matures and leaves senesce, LAI is reduced and so does ET. Plant size and leaf area are important variables in breeding for crop adaptation to water-limited environments (Sect. 3.6).

2.4 Plant Water Status and Plant Stress

Cellular water potential is determined by several components important for cells and their surroundings. These components are derived from the effects of solute, pressure, solids (matrix), and gravity. The effect of gravity is negligible. Accordingly, cell water potential and its components are expressed as follows:

$$\psi_w = \psi_s + \psi_p + \psi_m \quad (2.2)$$

where the subscripts s, p, and m represent the effects of solute, pressure and matrix. Each component is additive algebraically according to whether it increases (positive) or decreases (negative) the ψ_w as compared to the reference potential which is pure, free water. Whereas for free water ψ_w is null, plant cell ψ_w is always negative.

Solute lowers the chemical potential of water by diluting the water and decreasing the number of water molecules able to move compared to the reference, pure water. In the simplest terms, solutes hold the water in the cell against external pull, such as a water potential gradient developed by transpirational demand. In a similar way, wettable matrices have surface attraction that lowers the chemical potential of water. Since solutes and matric force reduce the chemical potential of water below that of free water their sign is negative. The balance in a plant cell is ψ_p (turgor potential or turgor pressure) which is positive as long as all other components allow it. In most whole-plant and crop physiology studies matric potential is neglected and the major dynamics of tissue water status is considered as the interplay and balance between ψ_w , ψ_s and ψ_p . It can be immediately seen that for a given ψ_w if ψ_s will decrease (become more negative) due to solute accumulation, ψ_p (turgor) will increase. Although some experimental results attempted in the past to show that turgor potential can sometimes be negative, this is a very debatable point. It is unresolved if negative turgor is physiologically possible or it is an apparent result of small errors in the measurement of the other components of water status.

Figure 2.3 demonstrates the most crucial facets of these relationships with special reference to the subject of this publication. The reader should concentrate very carefully on this figure and its discussion because here most mistakes are being made (e.g., Blum et al. 1996) in the interpretation of plant water status, turgor and osmotic adjustment.

As soil moisture is being used and water is transpired SWP and LWP (ψ_w) are reduced (becoming more negative). When soil moisture is abundant (high SWP) water will flow through the root and into the leaf with only a small reduction in LWP. When soil becomes drier, its water potential (SWP) is reduced further and LWP must be further reduced in order to create the necessary gradient differential, which would drive (pull) the water up from the drying soil to the leaf through all the soil and plant resistances in between.

The leaf cells contain various organic and inorganic solutes, which determine leaf OP (ψ_s). Therefore OP is lower (more negative) than LWP and the difference between the two is turgor potential (ψ_p). Turgor is lost (null value) when LWP=OP. Two theoretical cultivars are presented in this figure. Both cultivars have the same OP when the leaf is fully hydrated on the day of irrigation. In both cultivars OP is reduced as LWP is reduced. OP reduction is due to the loss of water from the leaf (*concentration effect*) and due to active solute accumulation in cells (*osmotic adjustment*) (OA). For the same LWP OP of cultivar S is reduced less than cultivar R. Therefore in cultivar S turgor is lost (reaching null) at about LWP of -3 MPa 8

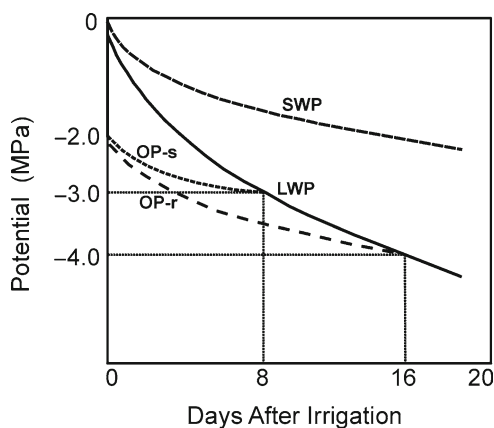


Fig. 2.3 Hypothetical schematic representation of the components of leaf water status during a soil drying cycle. *SWP* – soil water potential; *LWP* – leaf water potential (ψ_w); *OP-s* and *OP-r* represent two different cases of change in osmotic potential (ψ_s) with the reduction in *LWP*. See text

days after irrigation while in cultivar R turgor is lost at -4 MPa at 16 days after irrigation. Cultivar R is able to maintain turgor (and delay its wilting) for a longer period of time due to solute accumulation by OA. It can also be seen that due to its better capacity for OA, cultivar R can continue to draw water from the soil to a lower *SWP*, as compared with cultivar S. Cultivar R can therefore be defined as relatively drought resistant as compared with cultivar S due to a respective difference in OA. A relatively lower *OP* in itself is not an indication of better drought resistance or OA because it can result only from a concentration effect without any net solute accumulation.

One of the very first cellular response to water deficit is *cell wall hardening*, physically expressed in the decreased plastic extensibility and increased elastic modulus of the cell wall. This wall hardening appears to be biochemically related to decreased wall acidification and increased cross linking by phenolic substances such as lignins and diferulate bridges (Fan and Neumann 2004; Fan et al. 2006). Cell wall hardening and tightening around the cytoplasm help maintain turgor as water is lost from cells. However, hardening of the cell wall and its reduced extensibility will diminish and even stop cell growth. There is therefore a certain trade-off between cellular growth and turgor maintenance via cell wall hardening (Neumann 1995). In comparison, osmotic adjustment OA cast little if any direct cost in terms of cellular growth in turn for its effect on turgor maintenance. There is even a notion that plant species which are more capable of maintaining turgor via cell wall hardening tend to lack in OA (Barker et al. 1993).

Cell wall hardening under drought stress is reversible, depending on the rate of cellular dehydration. Chazen and Neumann (1994) claimed that the signal for cell wall hardening under water deficit was totally hydraulic in their study. However, other signals cannot be overruled, such as may be the case for ABA (e.g., Wu et al.

1994). Because of the trade-off between cell wall hardening and cell growth it is not quite clear whether greater cell wall hardening and its greater sensitivity to water deficit and turgor loss would constitute an advantage or a disadvantage in terms of affecting whole plant drought resistance (Marshall and Dumbroff 1999). It seems that crop species might differ in cell wall extensibility response to water deficit (Barker et al. 1993; Lu and Neumann 1998) so that genetic manipulation towards optimized responses under stress is theoretically imaginable. This issue still remains open in terms of application to breeding.

Leaf wilting is a symptom of turgor loss. Hence wilting is an important simple phenotypic expression of a critical stage in plant water status under drought stress and it is used extensively by breeders for phenotyping during selection under drought stress (Sect. 4.2.2.1). Wilting is displayed by various leaf presentations. In the cereals wilting is expressed by leaf rolling (Fig. 2.4). Gradual leaf movement into the rolled configuration is activated by the loss of turgor in special bulliform cells situated between veins along the axis of the leaf. When these cells loose turgor they initiate leaf curvature until tight rolling is reached at zero turgor. Leaf rolling is very sensitive to leaf turgor changes. Plants may present a daily march in leaf rolling according the daily march of plant water status and turgor. Maximum rolling is seen at about or just after solar noon. Cereals leaves roll as a defence mechanism to reduce net radiation load on the leaf. Rolling reduces transpiration and leaf water use and was found to protect PSII functionality from damage (Nar et al. 2009). As such it is an important adaptive trait for a leaf approaching zero turgor, but it is still a symptom of plant stress. When different genotypes are compared on a given day under drought stress, those with advanced leaf rolling are at a relatively lower water status than those that do not express leaf rolling on that day. *Genotypes expressing relatively delayed leaf rolling might have relatively better access to soil water or better osmotic adjustment.* Therefore, in terms of comparative performance under drought stress, delayed leaf rolling is the preferred phenotype.

2.4.1 Osmotic Adjustment (OA)

OA maintains cell water contents by increasing the osmotic force that can be exerted by cells on their surroundings and thus increasing water uptake. For the same leaf water potential, more water is held in leaf cells with greater OA resulting in higher turgor as compared with leaves with less OA (Fig. 2.3).

The adjustment results from compatible organic solutes accumulating in the cytoplasm which decreases the osmotic potential of the cytosol. Typical compatible solutes are sugars, amino acids such as proline or glycinebetaine, sugar alcohols like mannitol, and other low molecular weight metabolites. Inorganic ions may also drive OA as the case is for potassium in wheat (Morgan 1992). When plants are challenged by salinity the cellular accumulation of sodium can also be used for OA, especially if it is balanced by the accumulation of potassium. However there is a critical high sodium concentration that will toxify the cell.



Fig. 2.4 Symptoms of wilting in four plant species. From left to right: tobacco, cotton, rice and sorghum

Small cells require less solute for the same rate of osmotic adjustment (Cutler et al. 1977). The smaller size and smaller leaves typical of xerophytic plants can be partly ascribed to smaller cells and a better capacity for OA.

Some of the solutes used for OA, especially those produced by photosynthesis and used for growth are subjected to a dynamic balance between the demands by the two sinks: growth and OA. Since cell growth (expansion) is reduced by water deficit before photosynthesis (see below), there is an initial availability of carbon for OA when water deficit develops. The increase in OA allows sustaining cellular hydration and thus support continued photosynthesis and growth at slow rate under stress. When solutes used for OA are not those under heavy demand for growth (e.g., potassium, glycinebetaine), OA is relatively non-competitive to growth.

Cellular dehydration is the signal for active solute accumulation and OA generally increases with the reduction in leaf water potential. This is all too often not understood and can cause serious misinterpretation of experimental results concerning OA and drought resistance. This and other issues pertaining to OA and its role in drought resistance are discussed in Chap. 3, section “Osmotic Adjustment.”

2.4.2 *Abscissic Acid (ABA)*

ABA was first discovered as an endogenous compound causing fruit abscission and it was named “Abscisin-ii” (Ohkuma et al. 1963). Later during the 1960s additional research by others found that this endogenous hormone also caused dormancy and was found in large amounts in wilting leaves. Subsequently it was

found that ABA also induced stomatal closure. It was later described as a “stress hormone” because it was produced in plants subjected to various abiotic stresses including salinity, cold and heat all of which can involve cellular dehydration. ABA synthesis and accumulation is highly responsive to tissue water status and it increases with reduction in leaf water potential, turgor or relative water content (RWC). However there is no consensus water status threshold for ABA accumulation in plant tissues.

It is not clear how cellular water deficit induces ABA biosynthesis. The signal may constitute of cellular pressure, membrane modification, solute concentration or cell wall tension. ABA is also produced by roots in response to a drying soil (see below). Plants under drought stress contain significant amounts of ABA in their xylem. Therefore, ABA can potentially reach any plant part which is connected via the xylem. Furthermore, ABA is produced without any stress signaling in certain ripening fruit and developing seed. Detailed analyses of drought affected transcript profiles and comparisons with other studies (Huang et al. 2008) revealed that the ABA-dependent pathways are predominant in the drought stress responses. These comparisons also showed that other plant hormones including jasmonic acid, auxin, cytokinin, ethylene, brassinosteroids, and gibberellins also affected drought-related gene expression, of which the most significant was jasmonic acid. There is also extensive cross-talk between responses to drought and other environmental factors including light and biotic stresses. These analyses suggest that ABA-related stress responses are modulated by various environmental and developmental cues.

The involvement of ABA in stress perception, signaling and gene response has been reviewed and discussed by Zhang et al. (2006), Shinozaki and Yamaguchi-Shinozaki (2007), and Nakashima et al. (2009). The later reviews provide more detail but the general scheme and primary outline remain, as presented in Fig. 2.5.

2.4.2.1 ABA as a Non-Hydraulic Long-Distance Root Signal

ABA is produced in roots when they are exposed to a dry and hard soil. ABA is then found at high concentration in the xylem sap ascending from the root. ABA transported in the xylem signals the various known ABA responses in the shoot (Davies et al. 2005). Xylem sap pH is involved with xylem sap ABA activity where high pH generally enhances ABA effectiveness in the shoot. Soil drying has been shown to increase xylem sap pH. ABA solubility, transport, concentration and activity in different plant organs and cellular compartments are affected by pH. At the same time it was found that xylem sap alkalization under the effect of soil drying is not universal across all species tested (Sharp and Davies 2009). Hence, the role of pH in controlling ABA signaling is not clear and subjected to various theories (e.g., Zhang et al. 2006; Davies et al. 2005; Sharp and Davies 2009).

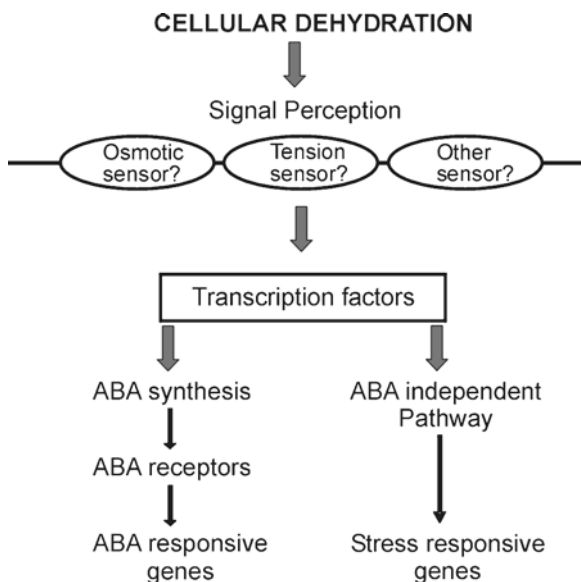


Fig. 2.5 A schematic representation of the molecular basis of drought stress perception and signaling pathways

ABA produced in the root is defined as a “long distance non-hydraulic root signal.” At the very early stages of soil drying when some of the roots are exposed to a drying soil, other (deeper) roots are well supplied with water. Under such conditions the hydraulic status of the shoot is favorable. However, at the same time ABA originating from the drying roots reaches the shoot and cause stomatal closure, arrested growth and other consequences of ABA signaling. This scenario seems to contradict the Ohm’s law analogy of the SPAC in the control of plant water status and its consequences in the plant, as described above. However after some debate in the literature a wide consensus has apparently been reached. The role of the hormonal signal is important at the earlier stages of drought stress while the hydraulic signal comes into full control when stress increases (e.g., Christmann et al. 2007). Galmés et al. (2007) offered an interesting concept where as soil moisture is reduced aquaporins help maintain hydraulic homeostasis while the reduction in soil water status already induces a hormonal signal to close stomata.

This is a very reasonable *modus operandi* for the native plant. The hormonal root signal serves as an “early warning system.” This alarm, coming up from the root via the xylem, causes the most important early effects of ABA in the shoot, namely stomatal closure and retarded leaf growth. Both of these consequences are the effective controls of plant water use. They serve to delay the expected hydraulic signal and the consequent reduction in plant water status and turgor. It should be

pointed out however that a hormonal root signal was not seen in all experiments designed to identify a hormonal root signal impacted by a dry soil (e.g., Christmann et al. 2007; Whalley et al. 2006). It could be possible that this hormonal root signal might have been perturbed by plant domestication and selection in certain cases.

The main question towards application of this knowledge in plant breeding for water-limited conditions is what should be the preferred response model – a sensitive or an insensitive “early warning system?” The “early warning system” is not so fine-tuned towards the control of water deficit response in the plant since other factors besides drought induce ABA production in roots and an increase in its mobility to the shoot, such as certain nutrient relations (Jeschke and Hartung 2000), soil strength salinity (Shaterian et al. 2005) and even certain soil biota (Dodd 2009). Furthermore, other hormones were also found to interact with ABA or with the effect of ABA on the shoot, such as the case for ethylene which can also be produced in the root (Sharp 2002). Beyond and above all these issues it is still not perfectly clear whether ABA in the shoot is a positive or a negative presence when plant production and yield under drought stress is concerned. Thus the role of the hormonal root signal in rainfed dryland crop production is not clear and the prediction of its effect on yield is not forthcoming. Genetic differences for hormonal root signal may exist, such as the case for grapevine (Beis and Patakas 2010). Blum and Sinmena (1995) tried to obtain some answers by isolating ABA insensitive variants of wheat and by studying their function under root signal promoting conditions (through partial root drying). However that study did not produce conclusive results (unpublished). A study with wheat grown in soil in pots (Xiong et al. 2007) concluded that a hormonal root signal produced at high soil moisture content was desirable for drought resistant wheat, thus favoring early stomatal closure at the onset of drought stress. This is in contrast to the current consensus that sustained stomatal conductance and transpiration under stress will support yield (Sect. 3.5.1).

Crop simulation models can be a potentially effective tool to assess if, when and where a hormonal root signal is desirable towards plant production under drought stress. Modeling efforts in this direction were initiated (e.g., Gutschick and Simonneau 2002) but they are still not perfected to the stage where they can be used as a decision support system, especially not with regard to breeding.

It should however be noted that the current emerging consensus among practicing dryland crop plant breeders is that sustained stomatal conductance and transpiration under stress will support yield (Araus et al. 2002; Blum 2009; Munns and Richards 2007). This view is compatible with plants which are less sensitive to ABA in general and to a hormonal root signal specifically.

The only available application of knowledge on hormonal root signal is being made in certain irrigation schemes. Irrigation methods that involve partial root drying (PRD) induce a hormonal signal while the plant remains well hydrated (Davies et al. 2002a, b). Irrigation of part of the roots can be technically achieved in crops normally irrigated by drip or subsurface irrigation. Crops (mainly fruit trees, olives and grapevine) irrigated by PRD show an improvement in irrigation water use efficiency for yield. Yield is often reduced somewhat in comparison with full irrigation

but water use decreases proportionally more. Fruit quality has been found to improve with PRD and this might be a decisive factor in adopting PRD in choice fruit orchards. Still, fruit quality in this context is not a simple characteristic. For example, drought stressed peach produced less but larger fruit. Larger fruit fetches better price but at the same time the fruit was of poor taste (Lopez et al. 2010).

2.4.2.2 ABA Effects in Plants

Several reviews deal with the wide array of effects that ABA causes in plants (Sharp 2002; Wilkinson and Davies 2005; Liu et al. 2005; Zhang et al. 2006). Whereas ABA is often defined as a “stress hormone” which ascribes “drought tolerance” to plants, it is very important to recognize the pros and cons of high ABA concentration in various plant organs. This should allow weighing the different effects and their sum totals under given stress scenarios and given agricultural ecosystem. In view of the huge and growing literature on ABA the reader should be well informed if, where and when ABA is a blessing or nuisance towards plant production in water-limited environments. The fact that ABA is part of the stress response transcription network (Fig. 2.5) does not necessarily imply that it is a positive component of drought resistance in the agronomic perspective.

It has long been established that the most prominent effect of ABA besides stomatal closure is general *shoot growth retardation*. Figure 2.6 is a simple visual representation of the growth inhibition of wheat plants caused by an increasing physiological concentration of ABA in the root medium. Inhibition mainly involved reduced leaf size and tillering, accompanied by some loss of chlorophyll at the higher concentration. When heat stress was applied (right panel) the effect of ABA on growth reduction was amplified. It appears that heat stress and ABA effects were additive. The apparent effect of ABA under heat stress was partly caused by stomatal closure. Plants with closed stomata were less capable of transpirational cooling, causing leaf temperatures to rise to lethal levels at the highest ABA concentration. The highest concentration in itself was not lethal (left panel).

In another experiment (Fig. 2.7) wheat was grown in aerated nutrient solution. PEG was added to impose drought stress. Roots were separated from the nutrient solution by a semi-permeable membrane so as to avoid direct contact of PEG with the root (Sect. 4.2.3.2). ABA reduced growth by about 65% and PEG reduced growth by about 40%, as compared with the control. It can be seen that ABA in the nutrient solution did not provide any protection to wheat growth under drought stress. Rather, it affected growth in an additive fashion to drought stress.

Growth retardation by ABA can be caused by stomatal closure and reduced photosynthesis. In the short term growth retardation by ABA results from the inhibition of both cell expansion and cell division. The retardation of cell division seems to be caused by reduced DNA synthesis through inactivating some DNA-replication origins resulting in a lengthening of the replicon size (Jacqmard et al. 1995). Reduced tillering under the effect of ABA has long been observed in the cereals (e.g., Harrison and Kaufman 1980) and its effect may be assigned to the

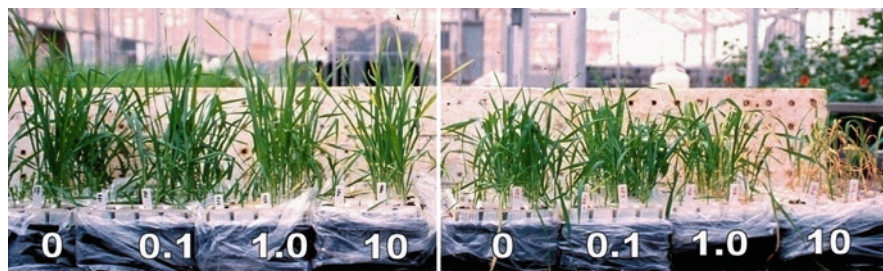


Fig. 2.6 Effect of ABA on wheat growth under two temperature regimes. Plants were grown in the growth chamber in aerated nutrient solution at 15°/25°C (night/day) (control – left panel). Two weeks before this photo was taken the plants in the right panel were transferred to 25°/37°C (chronic heat stress). At the same time ABA was added to the nutrient solution in the different pans, at concentrations of 0–10 μM . Author's unpublished experiment

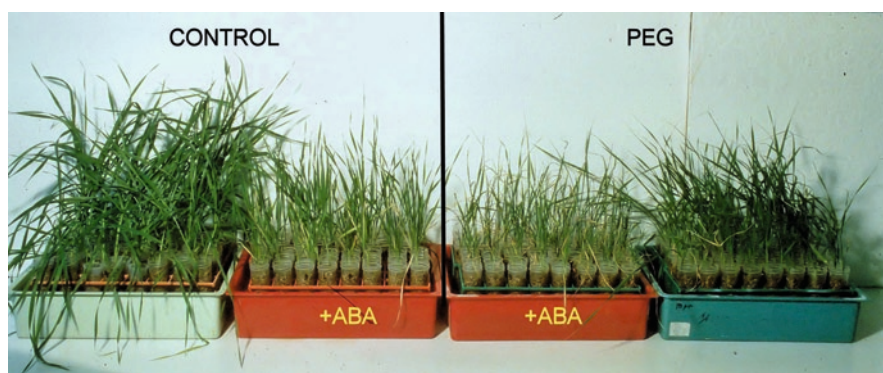


Fig. 2.7 The effect of 50 μM ABA on wheat grown in aerated nutrient solution with or without polyethylene glycol (PEG8000). Wheat was grown in pure nutrient solution until 2 weeks before this photo was taken when PEG was added in three daily increments to reach a final solution water potential of -0.5 MPa so as to impose drought stress. ABA was then added. Wheat was grown in vermiculite in vials where a semi-permeable membrane separates the roots from the nutrient solution (Sect. 4.2.3.2). Author's unpublished experiment

inhibition by ABA of kinetin. There are indications that ABA might enhance growth when endogenous ethylene accumulation is the cause of growth retardation (Sharp and LeNoble 2001). Xylem and apoplastic pH can affect the way in which ABA regulates stomatal activity and leaf growth.

It has long been established that ABA promote *root growth* (e.g., Munns and Sharp 1993). ABA also increase root hydraulic conductivity (see above), presumably by enhancing root aquaporins activity. Since ABA also reduces leaf area, the result is the often observed increase in the root/shoot dry matter ratio under the effect of drought stress. Such higher ratio has a major impact on the crop SPAC and the maintenance crop water status when drought stress develops. Thus, ABA

involvement in root growth and function can enhance plant performance under drought stress in the field. However, this effect should be considered within the complete array of ABA effects on the plant.

ABA cause *flower abscission* (Aneja et al. 2004) in tune with the initial discovery of its effect in plants (Ohkuma et al. 1963). Elevated concentration of ABA in the reproductive structures may inhibit embryonic cell division and subsequently impair *fruit and seed set and development*. In soybean, drought-induced increase in xylem ABA concentration, and not pod water potential, was found to control pod growth (Liu et al. 2003). In wheat, grain set was negatively correlated with the endogenous ABA concentration under drought (Westgate et al. 1996). Application of ABA to wheat leaf sheath of well watered plants inhibits floret development, and decreases the number of fertile florets and grain set (Morgan 1980; Wang et al. 2001). The effect of ABA towards flower sterility is largely mediated by pollen dysfunction (Oliver et al. 2007) following the inhibition of pollen germination and pollen tube growth (Frascaroli and Tuberosa 1993). There is therefore compelling evidence indicating that ABA seriously hampers plant reproduction, which in grain and fruit crops translates into yield reduction.

In the cereals, ABA inhibits *endosperm cell division* on one hand (Mambelli and Setter 1998) and on the other hand it promotes starch accumulation and *grain filling* in wheat and rice (Yang et al. 2004, 2006). This was attributed mainly to the enhanced sink activity by regulation of key enzymes involved in starch synthesis. In contrast to the above results in wheat and rice it has been shown in maize (Cheikh and Jones 1994) that the reduction of grain growth under heat stress involved the inhibiting effect of ABA.

ABA seems to have a role in enhancing *stem reserve mobilization* into the growing grain in rice and wheat (Yang et al. 2001, 2003), which is linked to accelerated leaf senescence. Kinetin delayed senescence and reduced stem reserve mobilization to the grain.

ABA enhances plant *senescence* in contrast to kinetin. This has been seen in the known expressions of senescence such as chlorophyll breakdown (Figs. 2.6 and 2.7) and specific changes in cell ultra structure (e.g., chromatin condensation, thylakoid swelling, plastoglobuli accumulation) and metabolism (e.g., protein degradation, lipid peroxidation) (Munne-Bosch and Alegre 2004). There is therefore compelling evidence that ABA is involved in the breakdown and transport of storage materials from senescing leaves into the developing grain while kinetin acts to conserve leaf viability.

ABA treatment of *Poa bulbosa* L a summer perennial grass geophyte (Ofir and Kigel 1998), resulted in cessation of leaf and tiller production and in the development of typical features of *dormancy*, namely bulbing at the base of the tillers and leaf senescence. Photoperiodic induction and heat stress, both of which are known to induce dormancy in this plant were accompanied by an increase in endogenous ABA concentration at the tiller base. ABA induced grape bud dormancy and the rate of dormancy was proportional to ABA concentration (Or et al. 2000). Dormancy of rose buds cultured in vitro could be broken by fluoridone an inhibitor of ABA synthesis. Dormancy was regained by constant ABA application (Le Bris et al. 1999). High endogenous ABA or high seed embryo sensitivity to ABA

Table 2.1 A summary of ABA effects and consequences in the plant

Trait	Effect
General growth	Decrease
Cell division	Decrease
Cell expansion	Decrease
Germination	Decrease
Tillering	Decrease
Root growth	Increase
Root hydraulic conductance	Increase
Flower abscission	Increase
Pollen viability	Decrease
Seed and fruit set	Decrease
Grain and fruit growth	Decrease
Starch synthesis in cereal grains	Increase
Plant reserve mobilization to the grain	Increase
Leaf senescence	Increase
Dormancy	Increase

retained embryo dormancy in maturing seed of sorghum (Steinbach et al. 1997) and wheat (Rasmussen et al. 1997).

When all of the above results pertaining to the cereal grain are taken together it appears that ABA reduces grain size but enhances stored assimilates transport into the grain and starch synthesis in the grain. If ABA supply to the grain is sustained, it will induce dormancy upon maturation.

Table 2.1 offers a concise summary of the positive and negative consequences of ABA, in terms of the final effect on plant production under drought stress. It helps explain the reduction seen in yield of wheat (Quarrie 1991) and maize (Sanguineti et al. 1996) lines selected for a constitutive capacity for high leaf ABA content. Near isogenic maize lines constitutively producing high or low leaf ABA content were developed by backcrosses. The difference in ABA accumulation was mainly due to one major QTL. The effect of this QTL was evaluated in testcrosses subjected to drought stress and non-stress conditions in the field (Landi et al. 2007). The effect of the high leaf ABA QTL was seen in lower yield under both water regimes indicating a basic negative effect of ABA accumulation on maize yield. Selection for low leaf ABA resulted in higher yielding maize under non-stress and moderate stress conditions (Landi et al. 2001). On the other hand Kholova et al. (2010) found that pearl millet lines resistant to terminal drought stress had constitutively higher leaf ABA content. They argued that water-saving due to apparent moderate water-use under the effect of high ABA was beneficial for sustaining the final stages of growth and grain filling under drought stress. It might be added here also that constitutively high ABA content could perhaps has enhanced stem reserve utilization for grain filling under terminal stress (see above).

It can therefore be speculated very reasonably that ABA evolved as a life conserving mechanism when the plant enters a stress situation. Where drought stress is concerned the first consequences of ABA activity are to reduce water use and

conserve plant hydration via reduced shoot growth, reduced stomatal conductance and promoted root growth and its hydraulic conductance. As stress increases ABA serve to reduce the sink load (see below) on the stressed plants by reducing the number of the developing fruit and/or seed. However, few remaining seed are still retained and filled well. When total plant assimilate production is limited by stress it would be a reasonable strategy to limit the number of sinks in order to produce at least a few viable seeds. Filling of the remaining seed in the cereals is supported by ABA induced stem reserve mobilization. Dormancy is then affected in order to conserve the seed until the next season.

This *survival* strategy is extremely important to the plant in terms of its ontogeny and evolution. However, when this plant is used for the farmer's livelihood, other considerations can be more important and they may not fit the above built-in strategy of ABA regulation (Table 2.1). If we understand this, the way for manipulating ABA signaling towards sustained plant production under drought stress will open. However, one thing must be absolutely clear: ABA cannot be arbitrarily defined (as sometimes seen in the literature) as a "drought resistance hormone." It is a stress hormone.

2.5 Growth and Water Deficit

Cell growth depends on turgor and cell wall extensibility. The relationship is described by the classical Lockhart equation (Lockhart 1965). Expansion rate of a cell equals to $m(P - Y)$, where m is the extensibility of the cell wall, P is the turgor pressure, and Y is a minimum value of P below which the cell will not grow. Passioura and Fry (1992) argued that Y (and sometimes m) may vary in response to changes in P on a time scale of about 10 min. The result is that, apart from the transient responses, cell expansion rate is often maintained at an approximately steady value despite changes in P . This has been later supported by data of others, such as Serpe and Matthews (2000) indicating it to be the case at least for moderate decrease in turgor. Cell wall growth therefore accounts for how m and Y may vary to maintain a constant growth rate despite moderate changes in turgor.

During growth, plant cells secrete proteins called "expansins," which unlock the network of cell wall polysaccharides, permitting turgor-driven cell enlargement. For example, expansins were implicated in the drought responses of maize seedlings, where maintenance of root growth involved increased expansin activity in the growing region (Wu et al. 1996). Drought increases the expression of expansin genes in a spatial and temporal pattern that closely matches the changes in expansin protein activity (Cosgrove 2000).

Inhibition of cell expansion under drought stress involves both the reduction in turgor and the loss of cell wall extensibility. Loss of cell wall extensibility also involves changes in polysaccharide content and structure in the cell wall. In the resurrection plant *Myrothamnus flabellifolius* (Moore et al. 2006) constitutive presence of high concentration of arabinose in cell walls provide the necessary structural

properties to be able to undergo repeated periods of desiccation and rehydration. Genetic engineering of specific cell wall properties was suggested by Cosgrove (2000) as a potential option for drought resistance improvement. However there are vast complexities that still exist in attempting to understand how cells grow especially under environmental cues such as water deficit.

Cell division can occur only after cells reach a certain size. Old views considered that cell growth and enlargement was more sensitive to water deficit than cell division. More recently it has been found for sunflower leaves that cell division and enlargement were similarly affected by water deficit (Granier and Tardieu 1999). In another study by the same group (Tardieu and Granier 2000) it was shown that water deficit reduced the final cell number in leaves by way of increasing cell cycle duration. More studies are required before a universal rule can be established regarding the relative sensitivity to water deficit of cell division and cell enlargement. One must also consider that cell division takes place in certain growth regions of the young leaf while cell enlargement takes place in various parts of young and old leaves. The specific cellular position and environment within the leaf can have a decisive effect on cell sensitivity to measured bulk leaf water deficit.

The integrated and final effect of both cell enlargement and division on leaf growth under stress is the important issue in terms of the whole plant in the field. It has been argued on the basis of experimental work with maize (Reymond et al. 2003) that a single leaf growth under drought stress can be predicted and its genetic background might be resolved. Basic growth process of plant tissues might be under a universal genetic control, whether under non-stress or stress conditions (Welcker et al. 2007). This is certainly an attractive proposition implying that plant growth under drought stress might perhaps be amenable to simple genetic manipulation despite the plant's apparent complexity.

However there are still major plant structural and physiological components to consider where whole plant growth under drought stress is considered. Whole plant structural and morphological features are relatively stable under drought stress as compared with features of dynamic organ expansion. Meristem and organ differentiation seem to be relatively resilient as compared with expansion growth. Any experienced agronomist will confirm that determinate plants subjected to drought stress will nearly always maintain the same number of leaves but leaves become smaller. Hence, differentiation and expansion growth must be treated differently in order to understand and manipulate whole plant response to drought stress.

The leaf canopy constitutes a major control over transpirational demand of the crop as well as the crop light interception. Canopy development and size at any given day in the field is determined by the expansion of all of the growing leaves as well as by leaf number and the senescence of older leaves. Plants subjected to soil moisture deficit develop a gradient of water potential such that leaves at a higher insertion are at lower water potential than leaves at lower insertion – with all the consequences of leaf water potential, turgor and their effect on growth. Leaf expansion is reduced by water deficit before leaf photosynthesis is inhibited. Hence, photosynthate that has been normally used for leaf expansion is now available for either osmotic adjustment or translocation. Light distribution in the canopy

and the extinction coefficient also impose a variable vertical profile of photosynthesis in addition to leaf water potential and leaf age.

Taken together, all this translates into the fact that at any given time each leaf in the canopy is very unique in its own physiology and microenvironment and the response to soil water deficit. If one considers also a flux of ABA (and possibly xylem sap pH) ascending in the xylem along this gradient, then we have a very complex system for simulation. Furthermore, in terms of the purpose of simulation towards plant breeding one has to consider the interpretation of the model. For example, high rate of leaf death under stress will usually be taken as stress inflicted damage to the crop and its productivity. This however is not necessarily always the case as seen in sorghum, a relatively drought resistant plant. When drought stress develops not all green viable leaves respond similarly in stomatal closure. Rather, older leaves senesce and die while upper younger leaves retain full turgidity and open stomata. Thus, whole plant water use is reduced but leaf gas exchange is retained in the most viable and light-exposed part of the canopy (Blum and Arkin 1984). Furthermore, leaf senescence under stress can also be linked to enhanced stem reserves mobilization into the grain as discussed above.

It therefore seems that designing a plant that can sustain growth and productivity when its tissues are dehydrated is not forthcoming. What appears to be the solution at the present state of our knowledge is to design a plant that can avoid dehydration. It also appears that plant reserve mobilization into the growing grain is a powerful resource for enhancing grain yield under stress during grain filling.

2.6 Root Growth Under Drought Stress

When drought stress develops, root-to-shoot ratio increases in terms of final dry matter weight. Total root dry matter very rarely increase in absolute terms under drought as compared with non-stress conditions. However this change in ratio also indicates that root-length density per unit live leaf area generally increases. Root-length density at deep soil may increase relative to root length density at shallow soil.

Four factors are behind the relative (or in rare cases the absolute) increase in root growth under drought stress. These are not totally independent and certain interactions between factors in affecting root growth were noted.

Firstly, Root growth is less sensitive than leaf growth to the same tissue low water potential (Hsiao and Xu 2000). The reason is in the greater osmotic adjustment in the extension region of roots as compared with leaves (Ober and Sharp 2007). In the apical few millimeters of the primary root of maize seedlings, proline concentration increased dramatically under water deficit. It could contribute up to 50% of osmotic adjustment (Sharp et al. 2004). However besides proline certain photosynthetic products also serve as osmoticum in roots. Since leaf expansion is arrested before photosynthesis is affected by shoot water deficit, some of the excess carbohydrates are assumed to be diverted to the root, supporting osmotic adjustment and root growth. Even shoot osmotic adjustment can drive deeper soil moisture extraction (e.g., Chimenti et al. 2006).

Secondly, it has long been established that ABA promotes root growth while it inhibits shoot growth (see above). The role of ABA accumulation in roots in enhancing root growth in a drying soil has been clearly proven by the use of fluroidone (an ABA synthesis inhibitor) and by two ABA knockdown mutants (Sharp et al. 2004; Ober and Sharp 2007). Loss of ABA synthesis capacity hindered root growth only under drought stress. However there were difference in root growth response to drought stress and ABA between the root tip and the immediate growth zone above it, indicating a complex control of ABA function in roots subjected to water deficit. Cytokinins are involved in inhibiting root branching and enhancing primary root growth (Havlová et al. 2008) by preventing the formation of an auxin gradient that is required to pattern lateral root primordia (Laplaze et al. 2008).

Thirdly, cell wall expansion is an important factor in enhancing root growth in a drying soil. The importance of expansin proteins and the expression of expansin genes in this respect have already been discussed above.

Fourthly, plant morphological and developmental interactions can greatly modify root growth in a drying soil and determine root distribution in the soil, especially in the cereals. In sorghum, crown (adventitious) roots are formed in a distinct temporal cycle from buds in the basal stem internodes. When the top soil is wet the initiated crown roots penetrate into the soil, grow and constitute the major part of the root system that occupies the top wet soil (Fig. 2.8). If the

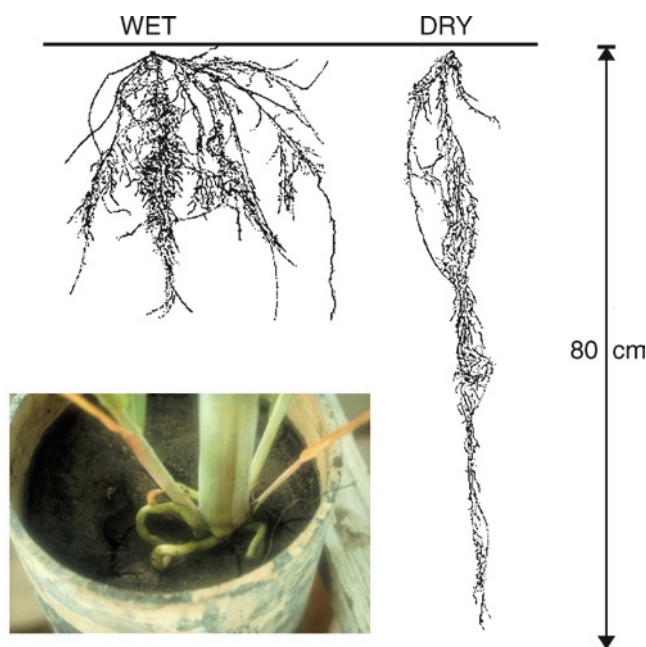


Fig. 2.8 Computer enhanced display of sorghum adventitious (*crown*) roots grown in fully wet soil (*left*) and in soil in which only the top was dry but was wet deeper (*right*) (Blum and Ritchie 1984; with permission). Inset: initiated crown roots that could not penetrate the hard top-soil (see text)

top-soil is dry and hard (while deep soil is still wet), these crown roots do not penetrate the soil (Blum and Ritchie 1984). Photosynthate that would have been used for the growth of these new roots is diverted towards the growth of existing roots, which grow deeper into the soil. Therefore, by limiting crown root number per plant, a dry soil surface causes compensatory growth in existing roots, which subsequently reach deeper soil layers. Different root distribution profile results from the balance between crown root number and crown root growth. Similar results were found by Troughton (1980) in perennial ryegrass where crown roots were associated with tillering. Consequently in a tillering crop plant such as wheat, a drying soil was found to limit root growth at the top 30 cm while promoting root extension and growth into depth (Asseng et al. 1998). Once re-watered, plants reverted to fast root growth at the top soil at the expense of deep soil.

2.7 The Formation of Yield and Drought Stress

Crop biomass production is linearly related to crop transpiration, or water use. The equation first proposed by de Wit (1958) still stands: $B = mT/E_0$, Where B = total crop biomass, m = crop constant, T = crop transpiration and E_0 = free water (potential) evaporation. This equation is the foundation for our understanding that biomass production is linked to transpiration. The primary consideration for enabling total plant production under drought stress is sustained transpiration. All other considerations as much as they may be important are secondary when production is concerned.

The development of a relationship between economic yield (e.g., grain, fruit, fiber, or tuber) and water use is far more complex whereas economic yield is not equated with total biomass. A first approximation is achieved through the introduction of the “harvest index” (HI) to the calculation, where a given crop-specific fraction of the total dry matter is partitioned into economic yield. This approximation is imperfect, as the harvest index changes with the water regime especially when drought stress occurs towards the end of the crop season. As such HI is a complex result and balance of genetic and environmental effects when different genotypes are compared. *HI is not an explanation. It is a result.* HI is useful tool for the analysis of results rather than a tool for obtaining results in breeding. The most well known analysis involving HI is that which is done repeatedly for various crops since the first study in wheat by Austin et al. (1980). They showed that most of the historical genetic progress in grain yield was obtained by a *de facto* increase in HI rather than by an increase in biomass production at a given HI (with few exceptions). However, HI does not help explain the basis of this change in ratio in the course of historical modern plant breeding. The speculation offered here is that selection for yield alone (as done historically) put a selective pressure on morphology and assimilate partitioning process but not on basic plant production (biomass). We have no idea what would have resulted in the historical perspective

if both biomass and yield were persistently selected during the breeding process. Certainly, the occasional voiced or written recommendations to select for HI as a conclusion from the historical analysis in this or other cases is an example of a misguided conclusion based on this ratio. The lesson learned from the historical perspective is that biomass and yield should be selected for while retaining HI.

Most research on yield formation has been done in the cereals. A useful approach to understand yield has already been developed years ago by defining *yield components*. Hence, yield of wheat, barley, sorghum, millet or rice is the multiplication of the number of inflorescences per unit area of land, by the number of grains per inflorescence, by single grain weight. Even the analysis of panicle weight components allowed better understanding of yield formation and heterosis in sorghum (Blum 1970, 1977). The reader can derive the definition of the yield components of maize, sunflower, pulses or cotton etc.

All yield components taken together constitute the “sink” while all assimilate contributing parts of the plant are considered the “source.” Whereas certain yield components can be developmentally interactive, such as grain weight and the number of grains per inflorescence in sorghum, component compensation is an important developmental mechanism for reconstituting yield under or upon recovery from stress - to a limit. For example, if tiller number is reduced by stress, grain mass per inflorescence can increase upon recovery via grain number or grain weight – depending on source activity and sink structure. It is not uncommon to observe an increase in sorghum grain weight under drought stress, due to a decrease in grain number per panicle, or an increase in grain number per panicle in compensation for a decrease in panicle number (Blum 2004).

The plant has a large potential for the creation of yield sinks, beyond what is realized even under a non-stress conditions. Cotton produces more flower buds and wheat produces more tillers or more florets that will ever bear fruit to maturity. Despite constant breeding for a more efficient cereal plant, excessive tillering and the natural degeneration of a proportion of the tillers have been apparently retained in present cultivars. This may have been the result of the selection pressure for stability of yield across different environments. Plants without a capacity for plastic development may lack in adaptation to variable growing condition.

Drought stress can reduce yield by affecting the sink or the source. Source capacity is reduced under drought stress as a result of stress effects on leaf area, gas exchange and carbon storage available for grain filling as well as from an increase in leaf senescence and the increase in rate of certain developmental processes.

The reduction in sink capacity under drought stress is caused by arrested organ differentiation as well as by the dysfunction of the differentiated reproductive organs. Thus, for example, drought stress reduces the number of tillers either by stopping their sequence of differentiation or by death of growing or grown tillers. The number of flowers (or florets) in the inflorescence will be reduced by arrested differentiation or by abortion and degeneration of developed flowers under stress. The reduction in the number of grains developed from a given number of flowers in the inflorescence can be affected by induced sterility of female or male organs as well as by stress induced abortion of embryos.

There is a very large volume of evidence that the most drought stress sensitive plant growth stage is flowering. This can be seen in the classical presentation by O'Toole (1982) with contribution from TC Hsiao (Fig. 2.9) where yield of rice is reduced most when stress occurs during plant reproduction. Peak stress sensitivity is at anthesis and fertilization. This presentation for rice represents well most if not all other cases of grain and fruit bearing crops.

A well demonstrated case for a non-cereal crop has been described for chickpeas where drought stress at the reproductive growth stage caused flower abortion, as well as pistil (or stamen) and pollen failure causing a reduction in total seed number per plant (Fang et al. 2010). The specific sensitivity of reproduction to drought stress is compounded by the fact that plants at flowering are large and pose a heavy demand for water. Reproductive failure is basically irreversible unless non-determinate crop plants are considered. There the failed reproductive organs cannot re-grow but they can be replaced upon recovery by new growth and the differentiation of new reproductive organs. Depending on their inherent drought resistance, non-determinate crop species offer better probability for recovering some yield under later season drought stress.

During its differentiation and early growth the flower or the inflorescence is usually protected by other tissues against excessive water loss, at least in comparison

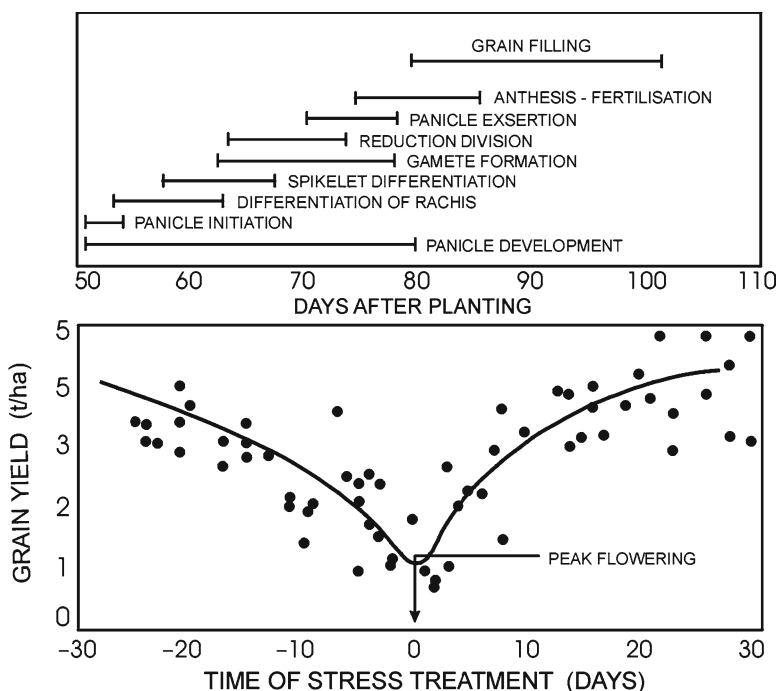


Fig. 2.9 The effect of drought stress applied at different rice growth stages on grain yield (Adapted by O'Toole from personal data by T.C. Hsiao and as presented in O'Toole (1982). With permission) *Bottom panel*: yield when stress occurred at different times during growth. *Top panel*: the respective stages of reproductive development when stress occurred

with exposed leaves. In the cereals and some other crop plant species the inflorescence is relatively protected against evaporation by protective surfaces such as thick cuticle and heavy epicuticular wax load. For these reasons, at least, the water status of the inflorescence may be expected to be better than that of the leaf. Still, a reduction in inflorescence or flower water status under severe stress can occur, thereby causing reproductive failure. However, even in a hydrophyte species such as rice, manipulations to reduce panicle transpiration and improve its water status did not increase its fertility under conditions of soil moisture stress (Garritty et al. 1986). The increase in shoot ABA concentration under drought stress, whether produced in situ or imported from the root (see Sect. 2.4.2.2) is a most likely reason for reproductive failure – irrespective of inflorescence water status.

In Maize, grain water status was reported to be stable under varying conditions (Borras et al. 2003) and ovary turgor under drought stress was the same as under non-stress conditions (Schussler and Westgate 1995). However, in wheat grain filling processes under stress conditions were partly limited by low grain water status as well as by the reduced assimilate supply to the grain (Ahmadi and Baker 2001). It seems that grain water status or sensitivity of grain growth to grain water status is not the only factor controlling grain growth. Each of the above sink-limiting dysfunctions which are caused by drought stress can be mediated by the direct effect of the water deficit of the organ in question, by plant hormones or by reduction in the supply of carbohydrates to the organ. The first two factors were already discussed above. The third one warrants further consideration.

In maize, female florets were more sensitive to reduction in water potential than pollen (Boyer and Westgate 2004). It was further found that invertase activity was inhibited and starch content was diminished in the ovaries. Sucrose infused to the stems of droughted maize rescued many of the ovaries otherwise destined to abort. Sucrose feeding restored some of the ovary starch and invertase activity. These studies indicate that sugar deficiency in maize ovaries was an important cause of abortion under drought stress. Invertase is implicated as a limiting enzyme step for grain yields during drought stress. On the other hand the ovary was more resilient than pollen in drought stressed wheat (Ji et al. 2010) while carbohydrate availability supported anther resilience.

The role of carbohydrate deficiency in pod abortion under drought stress was also evidenced in soybeans (Fulai et al. 2004). Sherson et al. (2003) concluded that the hydrolysis of sucrose by cell-wall invertase and the subsequent import of hexose into target cells appear to be crucial for appropriate metabolism, growth and differentiation in plants.

Sugar concentration in plant tissues constitutes an important signal, and sugar responsive genes have a role in the response of plants to drought stress (Koch 1996; Smeekens 1998). Sugar responsive genes participate in the control of resource distribution among tissues and organs. Carbohydrate depletion up regulates genes for photosynthesis, remobilization, and export, while decreasing mRNAs for storage and utilization. A role for plant hormones (particularly ABA) in sugar-response pathways was found by using various ABA mutants of *Arabidopsis thaliana*. ABA might be important also in regulating tissue response to sugar.

An additional important source for grain filling is carbohydrate reserves stored in the stem in the form of starch or fructan. Whenever the demand by the sink for assimilates grows beyond the supply by the current source, available stem reserves may be used for grain filling. Stem reserves can also be used in tandem with the current assimilate supply by photosynthesis. A large amount of information is available on the importance of stem reserve utilization (SRU) for grain filling especially under drought and heat stress. SRU was found to be important for grain filling in wheat, barley, triticale, rice, maize, sorghum, pearl millet, safflower, sunflower, chickpeas. SRU was ineffective in lupine (Palta et al. 2007). It was concluded that an important physiological component of the increase in wheat yield in the UK from 1972 to 1995 was a larger source for grain filling through increases in stem carbohydrate reserves (Shearman et al. 2005). SRU contribution to grain mass depends on the amount stored and the capacity for remobilization of storage to the grain. Further discussion SRU role in drought resistance is presented in Chap. 3, section “Stem Reserve Utilization for Grain Filling.”

Finally, in the biological sense the sink constitute a load on the source; whereas a large sink dictates a high rate of assimilate demand from the source. Experiments with partially de-grained wheat plants indicated that a large sink signals higher stomatal conductance and gas exchange in the flag leaf (Blum et al. 1988). Under stress conditions this effect brought about a significant reduction in flag leaf water status and a reduction in its capacity for osmotic adjustment. Lower flag leaf stomatal conductance was observed in millet plants after removal of their panicles (Henson and Mahalakshmi 1985). Higher stomatal conductance involved greater transpiration and water-use. This is compatible with the fact that high yielding wheat cultivars (having a large sink) could be identified by their higher rate of transpiration (Reynolds et al. 1994). A large sink load on the source would lead to earlier leaf senescence under stress, as compared with a plant of smaller sink (Khanna-Chopra and Sinha 1988).

Thus, sink load and its effect on plants under stress may be taken as one example of the fact that a high yield potential is basically not compatible with sustainable yield under severe drought stress. Further discussion of this important point with regard to breeding is presented in Sect. 3.3.

The sensitivity of plant reproduction to drought stress must have evolutionary roots. The plant apparently constantly monitors its status with respect to sugar pool and ABA signaling. Besides ABA, other hormonal signals are possibly involved in the monitoring of sink-source relationships. By means which were discussed above the plant under stress can adjust its reproduction in response to water status, hormones and sugars all of which signal the amount of available assimilates (current source). What an agronomist may define as a reproductive failure is in the evolutionary sense a method of survival under drought stress. The reduction in sink size allows the survival of few seeds in tune with the small source. Maintenance of a large sink demand under stress would have resulted in the total failure of reproduction in the face of assimilate shortage.

While this is a most appropriate strategy of survival for natural vegetation, it may not be suitable for crop plants. Agriculture is based on the idea that the farmer

and its supporting research make the decisions on the basis of knowledge and experience pertaining to plants, inputs, soils, water, climate and economics. This is one of the domains where plant genetics should modify and adapt plant responses and signaling systems to the specific agroecosystem in order to economically optimize and stabilize plant production. Philosophically, the farmer is prepared to and capable of taking a greater risk than evolution when it comes to plant reproduction under stress.

References

- Ahmadi A, Baker DA (2001) The effect of water stress on grain filling processes in wheat. *J Agric Sci* 136:257–269
- Alexandersson E, Danielson JÅH, Råde J et al (2010) Transcriptional regulation of aquaporins in accessions of *Arabidopsis* in response to drought stress. *Plant J* 61:650–660
- Aneja M, Gianfagna T, Ng E (2004) The roles of abscisic acid and ethylene in the abscission and senescence of cocoa flowers. *J Plant Growth Regul* 27:149–155
- Araus JL, Febrero A, Vendrell P (1991) Epidermal conductance in different parts of durum wheat grown under Mediterranean conditions – the role of epicuticular waxes and stomata. *Plant Cell Environ* 14:545–558
- Araus JL, Slafer GA, Reynolds MP et al (2002) Plant breeding and drought in C3 cereals: what should we breed for? *Ann Bot* 89:925–940
- Aroca R, Porcel R, Ruiz-Lozano JM (2007) How does arbuscular mycorrhizal symbiosis regulate root hydraulic properties and plasma membrane aquaporins in *Phaseolus vulgaris* under drought, cold or salinity stresses? *New Phytol* 173:808–816
- Aroca R, Vernieri P, Ruiz-Lozano JM (2008) Mycorrhizal and non-mycorrhizal *Lactuca sativa* plants exhibit contrasting responses to exogenous ABA during drought stress and recovery. *J Exp Bot* 59:2029–2041
- Asseng S, Ritchie JT, Smucker AJM et al (1998) Root growth and water uptake during water deficit and recovering in wheat. *Plant Soil* 201:265–273
- Auge RM, Kubikova E, Moore JL (2001) Foliar dehydration tolerance of mycorrhizal cowpea, soybean and bush bean. *New Phytol* 151:535–541
- Austin RB, Bingham J, Blackwell RD et al (1980) Genetic improvement in winter wheat yields since 1900 and associated physiological changes. *J Agric Sci* 94:675–689
- Barker DJ, Sullivan CY, Moser LE (1993) Water deficit effects on osmotic potential, cell wall elasticity, and proline in five forage grasses. *Agron J* 85:270–275
- Bauerle TL, Richards JH, Smart DR et al (2008) Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. *Plant Cell Environ* 31:177–186
- Beis A, Patakas A (2010) Differences in stomatal responses and root to shoot signalling between two grapevine varieties subjected to drought. *Funct Plant Biol* 37:139–146
- Blum A (1970) Nature of heterosis in grain production by the sorghum panicle. *Crop Sci* 10:28–31
- Blum A (1975) Effect of the BM gene on epicuticular wax deposition and the spectral characteristics of sorghum leaves. *SABRAO J* 7:45–52
- Blum A (1977) The basis of heterosis in the differentiating sorghum panicle. *Crop Sci* 17:880–882
- Blum A (2004) Sorghum physiology. In: Nguyen HT, Blum A (eds) *Physiology and biotechnology integration for plant breeding*. CRC Press, Boca Raton
- Blum A (2009) Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Res* 112:119–123

- Blum A, Arkin GF (1984) Sorghum root growth and water-use as affected by water supply and growth duration. *Field Crops Res* 9:131–142
- Blum A, Ritchie JT (1984) Effect of soil surface water content on sorghum root distribution in the soil. *Field Crops Res* 8:169–176
- Blum A, Sinmena B (1995) Isolation and characterization of variant wheat cultivars for ABA sensitivity. *Plant Cell Environ* 18:77–83
- Blum A, Mayer J, Golan G (1988) The effect of grain number (sink size) on source activity and its water-relations in wheat. *J Exp Bot* 39:106–114
- Blum A, Munns R, Passioura JB et al (1996) Genetically engineered plants resistant to soil drying and salt stress: how to interpret osmotic relations? *Plant Physiol* 110:1051
- Boomsma CR, Vyn TJ (2008) Maize drought tolerance: potential improvements through arbuscular mycorrhizal symbiosis? *Field Crops Res* 108:14–31
- Borras L, Westgate M, Otegui ME (2003) Control of grain weight and grain water relations by post-flowering source-sink ratio in maize. *Ann Bot* 91:857–867
- Boyer JS, Westgate ME (2004) Grain yields with limited water. *J Exp Bot* 55:2385–2394
- Bramley H, Turner DW, Tyerman SD et al (2007) Water flow in the roots of crop species: the influence of root structure, aquaporin activity, and waterlogging. *Adv Agron* 96:33–196
- Brodrib TJ, Feild TS, Sack L (2010) Viewing leaf structure and evolution from a hydraulic perspective. *Funct Plant Biol* 37:488–498
- Burow GB, Franks CD, Xin Z (2008) Genetic and physiological analysis of an irradiated bloomless mutant (epicuticular wax mutant) of sorghum. *Crop Sci* 48:41–48
- Caird MA, Richards JH, Hsiao TC (2007) Significant transpirational water loss occurs throughout the night in field-grown tomato. *Funct Plant Biol* 34:172–177
- Cameron KD, Teece MA, Smart LB (2006) Increased accumulation of cuticular wax and expression of lipid transfer protein in response to periodic drying events in leaves of tree tobacco. *Plant Physiol* 140:176–183
- Chazen O, Neumann PM (1994) Hydraulic signals from the roots and rapid cell-wall hardening in growing maize (*Zea mays* L) leaves are primary responses to polyethylene glycol-induced water deficits. *Plant Physiol* 104:1385–1392
- Cheikh N, Jones RJ (1994) Disruption of maize kernel growth and development by heat stress – role of cytokinin abscisic acid balance. *Plant Physiol* 106:45–51
- Chimenti CA, Marcantonio M, Hall AJ (2006) Divergent selection for osmotic adjustment results in improved drought tolerance in maize (*Zea mays* L) in both early growth and flowering phases. *Field Crops Res* 95:305–315
- Christmann A, Grill E (2009) Are GTGs ABA's biggest fans? *Cell* 136:21–23
- Christmann A, Weiler EW, Steudle E et al (2007) A hydraulic signal in root-to-shoot signalling of water shortage. *Plant J* 52:167–174
- Cochard H, Casella E, Mencuccini M (2007) Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. *Tree Physiol* 27:1761–1767
- Cochard H, Holttä T, Herbette S et al (2009) New insights into the mechanisms of water-stress-induced cavitation in conifers. *Plant Physiol* 151:949–954
- Cosgrove DJ (2000) Loosening of plant cell walls by expansions. *Nature* 407:321–326
- Cutler JM, Rains DW, Loomis RS (1977) The importance of cell size in the water relations of plants. *Physiol Plant* 40:255–260
- Davies FT, Olalde-Portugal V, Aguilera-Gomez L et al (2002a) Alleviation of drought stress of Chile ancho pepper (*Capsicum annuum* L cv San Luis) with arbuscular mycorrhiza indigenous to Mexico. *Sci Hort* 92:347–359
- Davies WJ, Wilkinson S, Loveys B (2002b) Stomatal control by chemical signalling and the exploitation of this mechanism to increase water use efficiency in agriculture. *New Phytol* 153:449–460
- Davies WJ, Kudoyarova G, Hartung W (2005) Long-distance ABA signaling and its relation to other signaling pathways in the detection of soil drying and the mediation of the plant's response to drought. *J Plant Growth Regul* 24:285–295
- de Wit CT (1958) Transpiration and crop yields. *Versl Landbouwk Onderz* 64:1–88

- Dodd IC (2009) Rhizosphere manipulations to maximize 'crop per drop' during deficit irrigation. *J Exp Bot* 60:2454–2459
- Fan L, Neumann PM (2004) The spatially variable inhibition by water deficit of maize root growth correlates with altered profiles of proton flux and cell wall pH. *Plant Physiol* 135: 2291–2300
- Fan L, Linker R, Gepstein S et al (2006) Progressive inhibition by water deficit of cell wall extensibility and growth along the elongation zone of maize roots is related to increased lignin metabolism and progressive stelar accumulation of wall phenolics. *Plant Physiol* 140:603–612
- Fang X, Turner NC, Yan G et al (2010) Flower numbers, pod production, pollen viability, and pistil function are reduced and flower and pod abortion increased in chickpea (*Cicer arietinum* L.) under terminal drought. *J Exp Bot* 61:335–345
- Fletcher AL, Sinclair TR, Allen LH Jr (2007) Transpiration responses to vapor pressure deficit in well watered 'slow-wilting' and commercial soybean. *Environ Exp Bot* 61:145–151
- Frascaroli E, Tuberosa R (1993) Effect of abscisic acid on pollen germination and tube growth of maize genotypes. *Plant Breed* 110:250–254
- Fulai L, Christian RJ, Mathias NA (2004) Drought stress effect on carbohydrate concentration in soybean leaves and pods during early reproductive development: its implication in altering pod set. *Field Crops Res* 86:1–13
- Galmés J, Pou A, Alsina MM et al (2007) Aquaporin expression in response to different water stress intensities and recovery in Richter-110 (*Vitis* sp): relationship with ecophysiological status. *Planta* 226:671–681
- Garrity DP, Vidal ET, O'Toole JC (1986) Manipulating panicle transpiration resistance to increase spikelet fertility during flowering stage water stress. *Crop Sci* 26:789–795
- Granier C, Tardieu F (1999) Water deficit and spatial pattern of leaf development Variability in responses can be simulated using a simple model of leaf development. *Plant Physiol* 119:609–620
- Gutschick VP, Simonneau T (2002) Modelling stomatal conductance of field-grown sunflower under varying soil water content and leaf environment: comparison of three models of stomatal response to leaf environment and coupling with an abscisic acid-based model of stomatal response to soil drying. *Plant Cell Environ* 25:1423–1434
- Harrison MA, Kaufman PB (1980) Hormonal regulation of lateral bud (tiller) release in oats (*Avena sativa* L.). *Plant Physiol* 66:1123–1127
- Havlová M, Dobrev PI, Motyka V et al (2008) The role of cytokinins in responses to water deficit in tobacco plants over-expressing trans-zeatin O-glucosyltransferase gene under 35S or SAG12 promoters. *Plant Cell Environ* 31:341–353
- Henson IE, Mahalakshmi V (1985) Evidence for panicle control of stomatal behaviour in water-stressed plants of pearl millet. *Field Crops Res* 11:281–290
- Holmes MG, Keiller DR (2002) Effects of pubescence and waxes on the reflectance of leaves in the ultraviolet and photosynthetic wavebands: a comparison of a range of species. *Plant Cell Environ* 25:85–93
- Hooker TS, Millar AA, Kunst L (2002) Significance of the expression of the CER6 condensing enzyme for cuticular wax production in *Arabidopsis*. *Plant Physiol* 129:1568–1580
- Hose E, Steudle E, Hartung W (2000) Abscisic acid and hydraulic conductivity of maize roots: a study using cell- and root-pressure probes. *Planta* 211:874–882
- Hsiao TC, Xu LK (2000) Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. *J Exp Bot* 51:1595–1616
- Huang D, Wu W, Abrams SR et al (2008) The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. *J Exp Bot* 59:2991–3007
- Jacqumard A, Houssa C, Bernier G (1995) Abscisic acid antagonizes the effect of cytokinin on DNA-replication origins. *J Exp Bot* 46:663–666
- Javot H, Maurel C (2002) The role of aquaporins in root water uptake. *Ann Bot* 90:301–313
- Jeschke WD, Hartung W (2000) Root-shoot interactions in mineral nutrition. *Plant Soil* 226:57–69

- Ji X, Shiran B, Wan J et al (2010) Importance of pre-anthesis anther sink strength for maintenance of grain number during reproductive stage water stress in wheat. *Plant Cell Environ* 33:926–942
- Kaldenhoff R, Ribas-Carbo M, Flexas J et al (2008) Aquaporins and plant water balance. *Plant Cell Environ* 31:658–666
- Khanna-Chopra R, Sinha SK (1988) Enhancement of drought-induced senescence by the reproductive sink in fertile lines of wheat and sorghum. *Ann Bot* 61:649–653
- Kholova J, Hash CT, Lava Kumar P et al (2010) Terminal drought-tolerant pearl millet [*Pennisetum glaucum* (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. *J Exp Bot* 61:1431–1440
- Koch K (1996) Carbohydrate-modulated gene expression in plants. *Annu Rev Plant Physiol Plant Mol Biol* 47:509–540
- Kosma DK, Bourdenx B, Bernard A et al (2009) The impact of water deficiency on leaf cuticle lipids of *Arabidopsis*. *Plant Physiol* 151:1918–1929
- Landi P, Sanguinetti MC, Conti S et al (2001) Direct and correlated responses to divergent selection for leaf abscisic acid concentration in two maize populations. *Crop Sci* 41:335–344
- Landi P, Sanguinetti MC, Liu C et al (2007) Root-ABA1 QTL affects root lodging, grain yield, and other agronomic traits in maize grown under well-watered and water-stressed conditions. *J Exp Bot* 58:319–326
- Laplaze L, Benkova E, Casimiro I et al (2008) Cytokinins act directly on lateral root founder cells to inhibit root initiation. *Plant Cell* 19:3889–3900
- Le Bris M, Michaux-Ferrière N, Jacob Y et al (1999) Regulation of bud dormancy by manipulation of ABA in isolated buds of *Rosa hybrida* cultured in vitro. *Aust J Plant Physiol* 26:273–281
- Li Y, Wang G-X, Xin M et al (2004) The parameters of guard cell calcium oscillation encodes stomatal oscillation and closure in *Vicia faba*. *Plant Sci* 166:415–421
- Li Y, Sperry JS, Shao M (2009) Hydraulic conductance and vulnerability to cavitation in corn (*Zea mays* L.) hybrids of differing drought resistance. *Environ Exp Bot* 66:341–346
- Liu F, Andersen MN, Jensen CR (2003) Loss of pod set caused by drought stress is associated with water status and ABA content of reproductive structures in soybean. *Funct Plant Biol* 30:271–280
- Liu F, Jensen CR, Andersen MN (2005) A review of drought adaptation in crop plants: changes in vegetative and reproductive physiology induced by ABA-based chemical signals. *Aust J Agr Res* 56:1245–1252
- Lockhart JA (1965) An analysis of irreversible plant cell elongation. *J Theor Biol* 8:264–276
- Lopez G, Behboudian MH, Vallverdu X et al (2010) Mitigation of severe water stress by fruit thinning in ‘O’Henry’ peach: implications for fruit quality. *Sci Hort* 125:294–300
- Lu ZJ, Neumann PM (1998) Water-stressed maize, barley and rice seedlings show species diversity in mechanisms of leaf growth inhibition. *J Exp Bot* 49:1945–1952
- Luan S (2002) Signalling drought in guard cells. *Plant Cell Environ* 25:229–237
- Mambelli S, Setter TL (1998) Inhibition of maize endosperm cell division and endoreduplication by exogenously applied abscisic acid. *Physiol Plant* 104:266–272
- Marshall JG, Dumbroff EB (1999) Turgor regulation via cell wall adjustment in white spruce. *Plant Physiol* 119:313–320
- McMichael BL, Lascano RJ (2010) Evaluation of hydraulic lift in cotton (*Gossypium hirsutum* L.) germplasm. *Environ Exp Bot* 68:26–30
- Mills D, Genfa Z, Benzioni A (2001) Effect of different salts and of ABA on growth and mineral uptake in jojoba shoots grown in vitro. *J Plant Physiol* 158:1031–1039
- Miyamoto N, Steudle E, Hirasawa T et al (2001) Hydraulic conductivity of rice roots. *J Exp Bot* 52:1835–1846
- Miyazawa S-I, Yoshimura S, Shinzaki Y et al (2008) Deactivation of aquaporins decreases internal conductance to CO₂ diffusion in tobacco leaves grown under long-term drought. *Funct Plant Biol* 35:553–564
- Moore JP, Nguema-Ona E, Chevalier L et al (2006) Response of the leaf cell wall to desiccation in the resurrection plant *Myrothamnus flabellifolius*. *Plant Physiol* 141:651–662

- Morgan JM (1980) Possible role of abscisic acid in reducing seed set in water-stressed wheat plants. *Nature* 285:655–657
- Morgan JM (1992) Osmotic components and properties associated with genotypic differences in osmoregulation in wheat. *Aust J Plant Physiol* 19:67–76
- Munne-Bosch S, Alegre L (2004) Die and let live: leaf senescence contributes to plant survival under drought stress. *Funct Plant Biol* 31:203–216
- Munns R, Richards RA (2007) Recent advances in breeding wheat for drought and salt stresses. In: Jenks MA, Hasegawa PM, Mohan Jain S (eds) *Advances in molecular breeding toward drought and salt tolerant crops*. Springer, Dordrecht
- Munns R, Sharp RE (1993) Involvement of abscisic acid in controlling plant growth in soils of low water potential. *Aust J Plant Physiol* 20:425–437
- Nakashima K, Ito Y, Yamaguchi-Shinozaki K (2009) Transcriptional regulatory networks in response to abiotic stresses in *Arabidopsis* and grasses. *Plant Physiol* 149:88–95
- Nar H, Saglam A, Terzi R et al (2009) Leaf rolling and photosystem II. Efficiency in *Ctenanthe setosa* exposed to drought stress. *Photosynthetica* 47:429–436
- Neumann PM (1995) The role of cell wall adjustment in plant resistance to water deficits. *Crop Sci* 35:1258–1266
- Ober ES, Sharp RE (2007) Regulation of root growth responses to water deficit. In: Jenks MA, Hasegawa PM, Jain S (eds) *Advances in molecular breeding towards drought and salt tolerant crops*. Springer, Dordrecht
- Ofir M, Kigel J (1998) Absciscic acid involvement in the induction of summer-dormancy in *Poa bulbosa*, a grass geophytes. *Physiol Plant* 102:163–170
- Ohkuma K, Lyon JL, Addicott FT et al (1963) Abscisin II, an abscission-accelerating substance from young cotton fruit. *Science* 142:1592–1593
- Oliver SN, Dennis ES, Dolferus R (2007) ABA regulates apoplastic sugar transport and is a potential signal for cold-induced pollen sterility in rice. *Plant Cell Physiol* 48:1319–1330
- Or E, Belausov E, Popilevsky I et al (2000) Changes in endogenous ABA level in relation to the dormancy cycle in grapevines grown in a hot climate. *J Hort Sci Biotechnol* 75:190–194
- Ortega U, Duñabeitia M, Menendez S et al (2004) Effectiveness of mycorrhizal inoculation in the nursery on growth and water relations of *Pinus radiata* in different water regimes. *Tree Physiol* 24:65–73
- O'Toole JC (1982) Adaptation of rice to drought prone environments. In: *Drought resistance in crops with emphasis on rice*. International Rice Research Institute, Los Banos
- Palta JA, Turner NC, French RJ et al (2007) Physiological responses of lupin genotypes to terminal drought in a Mediterranean-type environment. *Ann Appl Biol* 150:269–279
- Parent B, Hachez C, Redondo et al (2009) Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: a trans-scale approach. *Plant Physiol* 149:2000–2012
- Passioura JB, Fry SC (1992) Turgor and cell expansion: beyond the Lockhart equation. *Aust J Plant Phys* 19:565–576
- Porcel R, Ruiz-Lozano JM (2004) Arbuscular mycorrhizal influence on leaf water potential, solute accumulation, and oxidative stress in soybean plants subjected to drought stress. *J Exp Bot* 55:1743–1750
- Quarrie SA (1991) Implications of genetic differences in ABA accumulation for crop production. In: Davies WJ, Jones HG (eds) *Absciscic acid: physiology and biochemistry*. Bios Scientific Publishers, London
- Quintero JM, Fournier JM, Benlloch M (1999) Water transport in sunflower root systems: effects of ABA, Ca^{2+} status and HgCl_2 . *J Exp Bot* 50:1607–1612
- Rasmussen RD, Hole D, Hess JR et al (1997) Wheat kernel dormancy and plus abscisic acid level following exposure to fluridone. *J Plant Physiol* 150:440–445
- Reymond M, Muller B, Leonardi A et al (2003) Combining quantitative trait loci analysis and an ecophysiological model to analyze the genetic variability of the responses of maize leaf growth to temperature and water deficit. *Plant Physiol* 131:664–675

- Reynolds MP, Balota M, Delgado MIB et al (1994) Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Aust J Plant Physiol* 21:717–730
- Riederer M, Schreiber L (2001) Protecting against water loss: analysis of the barrier properties of plant cuticles. *J Exp Bot* 52:2023–2032
- Rose TJ, Rengel Z, Ma Q et al (2008) Hydraulic lift by canola plants aids P and K uptake from dry topsoil. *Aust J Agric Res* 59:38–45
- Ruiz-Lozano JM, Collados C, Barea JM et al (2001) Arbuscular mycorrhizal symbiosis can alleviate drought-induced nodule senescence in soybean plants. *New Phytol* 151:493–502
- Sack L, Holbrook NM (2006) Leaf hydraulics. *Annu Rev Plant Biol* 57:361–381
- Sade N, Vinocur BJ, Diber A et al (2009) Improving plant stress tolerance and yield production: is the tonoplast aquaporin S1TIP2;2 a key to isohydric to anisohydric conversion? *New Phytol* 181:651–661
- Sanguinetti MC, Conti S, Landi P et al (1996) Abscissic acid concentration in maize leaves – genetic control and response to divergent selection in two populations. *Maydica* 41:193–203
- Schachtman DP, Goodger JQD (2008) Chemical root to shoot signaling under drought. *Trends Plant Sci* 13:281–287
- Schussler JR, Westgate ME (1995) Assimilate flux determines kernel set at low water potential in maize. *Crop Sci* 35:1074–1080
- Serpe MD, Matthews MA (2000) Turgor and cell wall yielding in dicot leaf growth in response to changes in relative humidity. *Aust J Plant Physiol* 27:1131–1140
- Sharp RE (2002) Interaction with ethylene: changing views on the role of abscisic acid in root and shoot growth responses to water stress. *Plant Cell Environ* 25:211–222
- Sharp RG, Davies WJ (2009) Variability among species in the apoplastic pH signalling response to drying soils. *J Exp Bot* 60:4363–4370
- Sharp RE, LeNoble ME (2001) ABA, ethylene and the control of shoot and root growth under water stress. *J Exp Bot* 53:33–37
- Sharp RE, Poroyko V, Hejlek LG et al (2004) Root growth maintenance during water deficits: physiology to functional genomics. *J Exp Bot* 55:2343–2351
- Shaterian J, Georges F, Hussain A et al (2005) Root to shoot communication and abscisic acid in calreticulin (CR) gene expression and salt-stress tolerance in grafted diploid potato clones. *Environ Exp Bot* 53:323–332
- Shearman VJ, Sylvester-Bradley R, Scott RK et al (2005) Physiological processes associated with wheat yield progress in the UK. *Crop Sci* 45:175–185
- Shepherd T, Wynne GD (2006) The effects of stress on plant cuticular waxes. *New Phytol* 171:469–499
- Sherson SM, Alford HL, Forbes SM et al (2003) Roles of cell-wall invertases and monosaccharide transporters in the growth and development of *Arabidopsis*. *J Exp Bot* 54:525–531
- Shinozaki K, Yamaguchi-Shinozaki K (2007) Gene networks involved in drought stress response and tolerance. *J Exp Bot* 58:221–227
- Smeekens S (1998) Sugar regulation of gene expression in plants. *Curr Opin Plant Biol* 1:230–234
- Sperry JS, Hacke UG, Oren R et al (2002) Water deficits and hydraulic limits to leaf water supply. *Plant Cell Environ* 25:251–263
- Sperry JS, Stiller V, Hacke UG (2003) Xylem hydraulics and the soil plant-atmosphere continuum: opportunities and unresolved issues. *Agron J* 95:1362–1370
- Steinbach HS, Benech-Arnold RL, Sanchez RA (1997) Hormonal regulation of dormancy in developing sorghum seeds. *Plant Physiol* 113:149–154
- Steudle E (2000) Water uptake by plant roots: an integration of views. *Plant Soil* 226:45–56
- Steudle E, Peterson CA (1998) How does water get through roots? *J Exp Bot* 49:775–788
- Stirzaker RJ, Passioura JB (1996) The water relations of the root-soil interface. *Plant Cell Environ* 19:201–208
- Stratton L, Goldstein G, Meinzer FC (2000) Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant Cell Environ* 23:99–106

- Tardieu F, Granier C (2000) Quantitative analysis of cell division in leaves: methods, developmental patterns and effects of environmental conditions. *Plant Mol Biol* 43:555–567
- Thompson AJ, Andrews J, Mulholland BJ et al (2007) Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. *Plant Physiol* 143:1905–1917
- Troughton A (1980) Production of root axes and leaf elongation in perennial ryegrass in relation to dryness of the upper soil layer. *J Agric Sci Camb* 95:533–538
- Tsuchihira A, Hanba YT, Kato N (2010) Effect of overexpression of radish plasma membrane aquaporins on water-use efficiency, photosynthesis and growth of Eucalyptus trees. *Tree Physiol* 30:417–430
- Vandeleur RK, Mayo G, Shelden MC et al (2009) The role of plasma membrane intrinsic protein aquaporins in water transport through roots: diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. *Plant Physiol* 149:445–460
- Wall GW, Garcia RL, Kimball BA et al (2006) interactive effects of elevated carbon dioxide and drought on wheat. *Agron J* 98:354–381
- Wan CG, Xu WW, Sosebee RE et al (2000) Hydraulic lift in drought-tolerant and -susceptible maize hybrids. *Plant Soil* 219:117–126
- Wang Z, Cao W, Dai T et al (2001) Effects of exogenous hormones on floret development and grain set in wheat. *Plant Growth Regul* 35:225–231
- Welcker C, Boussuge B, Bencivenni C et al (2007) Are source and sink strengths genetically linked in maize plants subjected to water deficit? A QTL study of the responses of leaf growth and of anthesis-silking interval to water deficit. *J Exp Bot* 58:339–349
- Westgate ME, Passioura JB, Munns R (1996) Water status and aba content of floral organs in drought-stressed wheat. *Aust J Plant Physiol* 23:763–772
- Whalley WR, Clark LJ, Gowing DJG et al (2006) Does soil strength play a role in wheat yield losses caused by soil drying? *Plant Soil* 280:279–290
- White RG, Kirkegaard JA (2010) The distribution and abundance of wheat roots in a dense, structured subsoil – implications for water uptake. *Plant Cell Environ* 33:133–148
- Wilkinson S, Davies WJ (2002) ABA-based chemical signalling: the co-ordination of responses to stress in plants. *Plant Cell Environ* 25:195–210
- Wu YJ, Spollen WG, Sharp RE et al (1994) Root growth maintenance at low water potentials – increased activity of xyloglucan endotransglycosylase and its possible regulation by abscisic acid. *Plant Physiol* 106:607–615
- Wu YJ, Sharp RE, Durachko DM et al (1996) Growth maintenance of the maize primary root at low water potentials involves increases in cell-wall extension properties, expansin activity, and wall susceptibility to expansins. *Plant Physiol* 111, 765–772
- Xiong Y-C, Li F-M, Zhang T et al (2007) Evolution mechanism of non-hydraulic root-to-shoot signal during the anti-drought genetic breeding of spring wheat. *Environ Exp Bot* 59:193–205
- Xu XD, Bland WL (1993) Reverse water flow in sorghum roots. *Agron J* 85:384–388
- Yang JC, Zhang JH, Wang ZQ et al (2001) Activities of starch hydrolytic enzymes and sucrose-phosphate synthase in the stems of rice subjected to water stress during grain filling. *J Exp Bot* 52:2169–2179
- Yang JC, Zhang JH, Wang ZQ et al (2003) Involvement of abscisic acid and cytokinins in the senescence and remobilization of carbon reserves in wheat subjected to water stress during grain filling. *Plant Cell Environ* 26:1621–1631
- Yang JC, Zhang JH, Ye YX et al (2004) Involvement of abscisic acid and ethylene in the responses of rice grains to water stress during filling. *Plant Cell Environ* 27:1055–1064
- Yang JC, Zhang J, Liu K et al (2006) Abscisic acid and ethylene interact in wheat grains in response to soil drying during grain filling. *New Phytol* 171:293–303
- Zhang J-Y, Broeckling CD, Blancaflor EB et al (2005) Overexpression of WXP1, a putative *Medicago truncatula* AP2 domain-containing transcription factor gene, increases cuticular wax accumulation and enhances drought tolerance in transgenic alfalfa (*Medicago sativa*). *Plant J* 42:689–707

- Zhang J, Jia W, Yang J et al (2006) Role of ABA in integrating plant responses to drought and salt stresses. *Field Crops Res* 96:111–119
- Zhu J, Brownjonathan KM, Lynch P (2010) Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). *Plant Cell Environ* 33:740–749
- Zimmermann U, Schneider H, Wegner LH et al (2004) Water ascent in tall trees: does evolution of land plants rely on a highly metastable state? *New Phytol* 162:575–615



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