Over millions of years, plants have evolved a sophisticated network of K⁺ transport systems. This Botanical Brieﬁng provides an overview of K⁺ transporters in various leaf tissues (epidermis, mesophyll, guard cells and vascular system) at both the cellular and organelle levels. Despite the tremendous progress in our knowledge of genes encoding K⁺ transport systems in plants, understanding has not developed of coordinated functioning and operation of these genes or proteins in the context of whole plant physiology and plant±environment interaction. This Botanical Brieﬁng is aimed at ﬁlling that gap by analysing electrophysiological and molecular evidence for mechanisms coordinating K⁺ transport between various leaf cells and tissues in changing environments.

INTRODUCTION

Potassium is the most abundant inorganic cation in non-halophytes, contributing up to 6 % of plant dry weight. As a major inorganic osmolyte, K⁺ is crucial for cell osmo-regulation and turgor maintenance and, hence, for cell expansion, stomatal function, tropisms and leaf movement. Being an activator of a large number of enzymes, K⁺ plays a key role in photosynthesis, protein synthesis, and oxidative metabolism. It also affects phloem transport and provides charge balance during vectorial ion transfer across cellular membranes (Marschner, 1995).

Being complex and heterogeneous structures, plants have evolved a sophisticated and highly specialized K⁺ transport system to meet the different requirements for K⁺ in various cells and tissues and many reviews addressing various molecular and electrophysiological aspects of K⁺ transport in plants have been published recently (Maathuis and Amtmann, 1999; Schachtman, 2000; Mäser et al., 2001, 2002; Very and Sentenac, 2002; Pilot et al., 2003). Most of these deal with regulation of K⁺ uptake and transport in roots. As almost all K⁺ found in plant tissues is taken up by roots, it is not surprising that K⁺ transport systems in roots are the most studied, although the majority of K⁺ in a plant is found in the stems and leaves. In contrast to root cells, our knowledge of the properties and regulation of membrane K⁺ transport in leaves is much more limited (Piñeros and Kochian, 2003).

Recent advances in molecular biology have allowed tremendous progress in our knowledge of genes encoding K⁺ transport systems in plants (Mäser et al., 2001). However, with a possible exception of guard cells (Assmann and Shimazaki, 1999; Blatt, 2000; Schroeder et al., 2001), understanding of the coordinated functions and operation of these genes/proteins in the context of whole plant physiology and plant–environment interaction has not developed at the same rate. In this Brieﬁng, an attempt is made to ﬁll this gap and address electrophysiological and molecular aspects of coordination of K⁺ transport between various leaf cells and tissues under natural conditions.

HETEROGENEITY OF LEAVES

The heterogeneous nature of leaves is obvious: there are striking differences between leaves in venation, stomatal alignment and stomatal density. It is not surprising, therefore, to ﬁnd that the nutritional demands and, consequently, regulation of ionic uptake are remarkably different in various cells, even of one leaf.

Heterogeneity of leaf ionic environment

The cells of the mesophyll and of the epidermis are very different anatomically, with their vacuoles occupying around 61–75 % and up to 99 % of the cell volume, respectively (Karley et al., 2000a). In addition, epidermal cells are virtually unable to produce organic solutes and rely heavily on inorganic ions (mainly K⁺) for osmotic adjustment (Fricke et al., 1994). In mesophyll cells, the total contribution of organic osmolytes is much higher (20–30 %; Gonzales et al., 2002) than in epidermal cells, although K⁺ remains the dominant osmoticum (Shabala et al., 2000; Gonzales et al., 2002). A difference in K⁺ composition between epidermal and mesophyll cells is an obvious consequence of their different solute compositions (Leigh, 2001). Cytosolic K⁺ homeostasis is a characteristic feature of mesophyll cells and is maintained at the expense of the supply to the epidermis, where cytosolic K⁺ may decline to very low levels (Cuin et al., 2003). This homeostasis enables protection and maintenance of optimal photosynthetic activity of the mesophyll cells. The process underlying differential accumulation of ions by leaf cells can include both the regulation of supply of certain ions and the capacity for ion uptake (Karley et al., 2000b).

Apoplastic free K⁺ concentrations are usually much lower than symplastic and have been reported between 2 and
These values may change dramatically as a result of altered light (Roelfsema and Hedrich, 2002) or salinity (Leigh, 2001).

**Heterogeneity of leaf physiological responses**

The heterogeneity of leaf physiology is illustrated by two examples: leaf extension growth and stomatal ‘patchiness’. There are striking differences between growth patterns of different regions of the leaf lamina and yet expansion of various leaf tissues is highly coordinated. It is believed that the epidermis normally restricts leaf expansion (Van Volkenburgh, 1999), presumably due to the fact that epidermal cells usually have lower turgor than mesophyll cells. Even within the epidermis, a significant difference was measured between K⁺ uptake at the growing (leaf base) and at the fully extended (leaf tip) regions of corn leaves (S. Shabala and B. Zivanovic, unpub. res.). Although the molecular and ionic mechanisms underlying these differences are yet to be studied, it is reasonable to suggest that either K⁺ concentration in the apoplast or functional expression of K⁺ transporters will vary significantly between the apical and basal regions of the leaf, depending on growth patterns. It is also possible that post-transcriptional modulation of transport activity may determine these differences.

On a smaller scale, stomatal ‘patchiness’ is another example of heterogeneity of leaf physiological characteristics. It has been demonstrated that in many species and under various experimental conditions, stomatal conductance and behaviour differ between regions of the leaf, forming patches up to several millimetres across (Mott and Buckley, 1998). Based on membrane potential measure-
ments, Roelfsema et al. (2001) showed that, in planta, stomatal guard cells exhibit at least three different physiological states under apparently identical environmental conditions. It was speculated that local production and distribution of chemical ‘signals’ facilitates these differences (Mott and Buckley, 1998). Keeping in mind the apoplastic coupling between epidermal and guard cells and the fact that leaf apoplastic K+ concentration is strongly correlated with the leaf venation (Shabala et al., 2002), it is possible to suggest that K+ distribution in the leaf apoplast is one of the factors determining stomatal ‘patchiness’ and heterogeneity in leaf photosynthesis.

FUNCTIONAL EXPRESSION OF PLASMA MEMBRANE POTASSIUM TRANSPORTERS IN LEAF TISSUES

General features of K+ transporters in plants

A large number of genes encode proteins involved in K+ transport in plants. In arabidopsis, these transport mechanisms fall into several distinct categories (Mäser et al., 2001, 2002; Very and Sentenac, 2002): (a) two families of K+ channels (Shaker-type and KCO channels; 15 genes in total); (b) Trk/HKT transporters [Na+/K+ symporter (Schachtman, 2000); one gene]; (c) KUP/HAK/KT transporters [H+/K+ symporter (Kim et al., 1998); 13 genes]; (d) K+/H+ antiporter homologs (six genes); (e) cyclic-nucleotide-gated channels (CNGC; 20 genes in arabidopsis; Very and Sentenac, 2002); and (e) glutamate receptors (GLRs; 20 genes; Very and Sentenac, 2002). The Shaker-type channels are further subdivided into SKOR and GORK channels (both depolarization-activated), KAT channels and AKT channels. AKT channels contain an ankyrin-binding motif, which is lacking in KAT type channels (Mäser et al., 2001). An important feature of plant Shaker-like K+ channels is that they can form heterotetrameric structures (Pilot et al., 2003), allowing plants to tune the K+ transport activity in various cells, independently in each organ/tissue, in relation to environmental conditions. A brief summary of the functional expression of plasma membrane K+ channels in various leaf tissues in Arabidopsis thaliana is given in Table 1, and some details of the functions and intracellular location of K+ transporters in leaves of various plant species are shown in Table 2. The diversity of K+ transport mechanisms at the plasma membrane of a ‘generalized’ leaf cell is summarized in Fig. 1.

Stomatal guard cells

Two major types of K+ channels are present at the plasma membrane of guard cells; voltage-dependent K+-selective inward (KIR) and outward (KOR) rectifying channels (Pilot et al., 2001; Schroeder et al., 2001; Szyroki et al., 2001; Zimmermann et al., 2001). KIR channels are activated by membrane hyperpolarization and mediate stomatal opening, whereas KOR channels are opened by voltages more positive than EK and mediate stomatal closure.

Recent transcription–PCR experiments with isolated guard cell protoplasts showed that in addition to KAT1, the K+ channels AKT1, AKT2/3, AtKCl1 and KAT2 (all KIRs) were expressed (Szyroki et al., 2001), suggesting that KAT1 inward-rectifying K+ channels may not play as dominant a role in K+ uptake in guard cells as previously believed (Assmann and Wang, 2001). It was also shown that KAT1 and KAT2 can form heteromultimeric channels (Pilot et al., 2001; Zimmermann et al., 2001), leading to more flexibility when adapting to altered developmental and/or environmental conditions. Several other channels of unknown voltage-dependence (AtKCl1, AKT5 and AKT6) were also shown to co-localize in arabidopsis guard cells (Dietrich et al., 2001). It is thought that such a multiple ensemble of K+ channels provides greater versatility and much more efficient regulation of K+ homeostasis in guard cells compared with only one type of KIR channel. The only certain candidate in the arabidopsis genome to mediate stomatal closure is GORK, a voltage-gated outwardly rectifying K+ channel of the guard cell membrane (Hosy et al., 2003).
In addition to specific K⁺-selective channels, guard cells also possess a wide range of non-selective cation channels (NSCC), either depolarization- or hyperpolarization-activated (Demidchik et al., 2002). These channels are likely to be involved in release of solutes during turgor adjustment and, to some extent, functionally complement GORK channels. Finally, there is strong evidence that guard cells possess mechanosensitive (or stretch-activated, SAS) channels at the plasma membrane (Cosgrove and Hedrich, 1991). These channels are K⁺ permeable and change their open probabilities as a result of volume or turgor changes.

As well as their voltage-dependence, K⁺ channels in guard cells are regulated by several other factors, the most obvious of which is pH. Both apoplastic (Pilot et al., 2001; Roelfsema and Hedrich, 2002) and cytosolic (Dietrich et al., 2001) acidification lead to the activation of inward K⁺ currents in guard cells. The effect is voltage-dependent (Roelfsema and Hedrich, 2002). Most other second messengers such as cytosolic Ca²⁺, IP₃, GTP, G-proteins, polyamines, reactive oxygen species (ROS) and phosphorylation events also exert direct control over K⁺ channel activity (Assmann and Shimazaki, 1999; Blatt, 2000; Schroeder et al., 2001; Kohler et al., 2003). It has also been shown that guard cells may utilize voltage-dependent K⁺ channels as targets of the osmosensing pathway by regulating channel opening probability by the osmogradient across the plasma membrane of guard cells (Liu and Luan, 1998).

Mesophyll

Molecular studies suggested that both AKT1 and AKT2/3 genes are expressed in arabidopsis leaf mesophyll (Dennison et al., 2001; Cherel et al., 2002). A specific feature of AKT2/3 channels is their weak dependence on the membrane potential, sensitivity to ATP and an inverted pH regulation (Marten et al., 1999). Being only weakly controlled by the membrane potential, AKT2/3 channels are able to conduct both inward and outward currents.

Electrophysiologically, K⁺-permeable channels at the plasma membrane of mesophyll cells were characterized as KIRs (Kourie and Goldsmith, 1992; Karley et al., 2000a), and KORs (Spalding et al., 1992; Blom-Zandstra et al., 1997; Pineros and Kochian, 2003). These KOR channels are regulated by Ca²⁺ and G-proteins (Krol and Trebacz, 2000) and may play a role in stabilizing cell membrane potential (Pineros and Kochian, 2003). Also, Ca²⁺-sensitive, depolarization-activated NSCCs were found at the plasma membrane in arabidopsis mesophyll cells (Spalding et al., 1992).

In addition to KIR channels there is a need for active K⁺ transporters in mesophyll cells, since environmental fluctuations, such as light/dark transitions, may leave Eₘ positive to Eₚ (Shabala and Newman, 1999), making the function of KIR channels impossible. Both HAK/KT/KUP and HKT type transporters are present at the plasma membrane of leaf mesophyll cells (Table 2; Leigh, 2001; Golldack et al., 2002; Su et al., 2002).

Epidermis

Only a few electrophysiological studies have specifically targeted K⁺ transporters from epidermal cells other than stomata. Two time-dependent Ca²⁺-regulated K⁺-selective channels (resembling guard cell KIR and KOR, respectively) were found in subsidiary cells of maize (Majore et al., 2002). Time-dependent inward K⁺ currents were also reported for barley epidermis (Karley et al., 2000a) and there is evidence that NSCCs may also be present in leaf epidermal cells (Elzenga and Van Volkenburgh, 1994; Majore et al., 2002). At the molecular level, expression of AKT2 genes (Cherel et al., 2002) and the HAK/KT/KUP K⁺ transporters (Su et al., 2002) have been attributed to epidermal cells.

Vascular tissues

Phloem loading with assimilates is accompanied by a significant increase in symplastic K⁺ concentration, required to maintain electrical neutrality during vectorial H⁺ transfer. The most abundant K⁺ channels in the phloem tissue are AKT3 (Marten et al., 1999; Cherel et al., 2002) and their homologues (Golldack et al., 2003). The unique characteristics of this channel (its weak voltage dependence, inhibition by physiological concentrations of external Ca²⁺ and by extracellular acidification, and the ability to be open in the entire physiological voltage range; Marten et al., 1999), allow AKT3 to mediate both K⁺ influx and efflux, determining the diverse roles of AKT3 in the phloem. Another major type of K⁺ channel detected in minor veins is KAT2 (Pilot et al., 2001), involved in K⁺ loading into the phloem sap.

There is both electrophysiological and molecular evidence for the presence of high affinity K⁺ transporters, in addition to channels, in the leaf vascular system. McHAKs transcripts showed signals in the leaf vascular bundles (Su et al., 2002) and the HKT1 transporter was localized in cell layers bordering the vascular tissue in leaves (Schachtman, 2000).

POTASSIUM TRANSPORT WITHIN LEAF CELLS

Vacuole

Several types of K⁺ permeable channels are known to be present in the tonoplast (Fig. 2). The most abundant are slow-activating (SV) and fast-activating (FV) vacuolar channels. The SV channel is permeable to both mono- and divalent cations and is activated by cytosolic Ca²⁺ and positive vacuolar voltage. The FV channel is selective for monovalent cations only, activated by positive voltages, and may be blocked by divalent cations (for a review, see Allen and Sanders, 1997). Both SV and FV channels are ubiquitous in plant tissues, including mesophyll and guard cell vacuoles (Allen and Sanders, 1997; Pottosin et al., 1997; Tikhonova et al., 1997). In addition, guard cells possess another channel specifically selective for K⁺ (Allen and Sanders, 1997). This so-called VK channel is voltage-independent and activated by Ca²⁺ (Schönknecht et al., 2002) as well as by cytosolic alkalization (Allen and Sanders, 1997). Recently, a two-pore A. thaliana KOR channel, named AtKCO1, was cloned and localized to the
tonoplast of both mesophyll cells and guard cells (Czempinski et al., 2002; Schönknecht et al., 2002). Finally, there is evidence for mechanosensory SAS channels to be present at the tonoplast (Alexandre and Lassalles, 1991).

At least two other types of transporters may also contribute to K⁺ transport across the tonoplast. Firstly, Banuelos et al. (2002) targeted the rice OsHAK10 (a member of KUP/HAK/KT family) gene to the tonoplast and suggested that such a transporter may be needed to release K⁺ from the vacuole to the cytoplasm when the vacuolar concentration is low. Secondly, there is evidence that NHX1 (a vacuolar Na⁺/H⁺ exchanger) has some affinity for K⁺ and may operate in K⁺ transport during low Na⁺ conditions (Pottosin and Schönknecht, 1996). Several of these channels show bimodal gating (Pottosin and Schönknecht, 1996). However, some channels showed only moderate voltage dependence (Pottosin and Schönknecht, 1996), suggesting that additional mechanisms to regulate the thylakoid cation channel activity might be involved.

Chloroplast

The transport barrier in the chloroplast is the inner membrane, which contains transporters for a selected numbers of low molecular weight substrates. The outer membrane contains specific pore-forming proteins and is permeable to substances with molecular weight of several kDa (Pottosin, 1992). Most of these 'pores' are also able to conduct ions (for a review, see Neuhaus and Wagner, 2000).

Massive light-driven transport of H⁺ into the thylakoid lumen is electrically balanced by the counter flow of other ions (Hinnah and Wagner, 1998). This process is mediated by weakly voltage-dependent cation-selective channels, equally permeable to K⁺ and Mg²⁺ (Pottosin and Schönknecht, 1996). Several types of cation-permeable channels have been found at thylakoid membranes of different species (Pottosin, 1992; Pottosin and Schönknecht, 1996; Hinnah and Wagner, 1998). All of them belong to the NSCC class. Channel conductance varied greatly from 60 pS (Pottosin and Schönknecht 1996) to very high values (non-selective porin-like maxi channel with 1016 pS conductance; Pottosin, 1992). Most of these channels show bimodal gating (Pottosin, 1992). However, some channels showed only moderate voltage dependence (Pottosin and Schönknecht, 1996), suggesting that additional mechanisms to regulate the thylakoid cation channel activity might be involved.

Mitochondria

ATP-sensitive K⁺ channels (mitoKATP) have been reported for various animal tissues (Ferranti et al., 2003). For plant mitochondria, studies on K⁺ transporters are still at an early stage. It appears that the only reported evidence comes from Petrussa et al. (2001), who provided evidence that plant mitochondria possess a K⁺ selective, voltage-dependent channel, which is opened by cyclosporin, regulated by the redox state and inhibited by nucleotides. The hypothetical role of this new ATP-sensitive K⁺ channel was attributed to mitochondrial volume regulation, thermogenesis, apoptosis and/or prevention of ROS formation in plants. As studies on ROS have recently received a great deal of attention from plant scientists (Demidchik et al., 2003; Kohler et al., 2003), there is obviously a strong need for more studies on the role and mechanisms of K⁺ transport across the mitochondrial membranes.

REGULATION OF K⁺ TRANSPORTER ACTIVITY BY ENVIRONMENTAL STIMULI

Light

Light stimulates expansion growth of leaves via cell wall acidification and increased cell turgor, both resulting from light activation of H⁺-ATPase (Van Volkenburgh, 1999). The most rapid response of growing cells to light is electrical depolarization (Elzenga et al., 1995; Van Volkenburgh, 1999) caused by an influx of Ca²⁺ (Shabala and Newman, 1999). This response could be either a part of a signal transduction pathway leading to growth regulation or, more likely, reflect a part of the growth mechanism itself.

Guard cells. There are both red light (RL) and blue light (BL) components within the action spectrum of stomatal opening. RL stimulates photosynthetic activity within the chloroplast, thereby providing an energy source for H⁺ extrusion (Dietrich et al., 2001). This process is mediated by chlorophyll located in guard cell protoplasts. BL also drives guard cell photosynthesis acting via a cryptochrome or zeaxanthin (Assmann and Wang, 2001; Dietrich et al., 2001; Zeiger et al., 2002) receptor.
Several mechanisms mediate RL and BL control over activity of K+ transporters in guard cells. First, most guard cell K+ channels are voltage-dependent (see above) and thus are coupled with light-induced stimulation of the H+-ATPase (Dietrich et al., 2001). Secondly, light-induced apoplastic acidification provides an additional mechanism for K+ gating (Blatt, 2000). Finally, many guard cell K+ channels are Ca2+ sensitive (Blatt, 2000; Dietrich et al., 2001), and light-induced elevation in cytosolic free Ca2+ is a widely reported phenomenon (Schroeder et al., 2001). In addition to chlorophyll-mediated light signalling in guard cells, there is growing evidence that phytochrome is another photoreceptor involved in control of stomatal aperture (Zeiger et al., 2002).

Epidermis. Both BL and RL cause significant changes in net K+ flux across the plasma membrane of epidermal cells (S. Shabala and B. Zivanovic, unpub. res.). It has been proposed that BL stimulates the H+ pump by direct interaction between the BL photoreceptor and the pump, while RL may influence pump activity indirectly by modulating passive ion conductances of Ca2+ and K+ channels [Van Volkenburgh (1999) and references within]. Phytochrome is also likely to be involved as shown in experiments with pcd2 phytochrome-deficient pea mutants (Elzenga et al., 2000).

The precise roles of light-stimulated ion fluxes in leaf epidermis, apart from H+ efflux, are obscure. As membranes cannot stretch, it was suggested that phytochrome-mediated Ca2+ influx across the plasma membrane enhances vesicle fusion, wall synthesis and growth in leaf cells (Van Volkenburgh, 1999). The role of phytochrome-mediated K+ fluxes from epidermal cells remains unresolved.

Mesophyll. Transient increase in K+ uptake across the plasma membrane of leaf mesophyll cells has been reported (Spalding et al., 1992; Blom-Zandstra et al., 1997; Shabala and Newman, 1999), most likely due to an increase in the open probability of KIR channels (Spalding et al., 1992). As light-induced up-regulation of K+ channel activity was not observed in chlorophyll deficient cells, it was concluded that this process is mediated by photosynthesis (Blom-Zandstra et al., 1997). This view is further supported by the presence of a significant lag period (tens of seconds; Spalding et al., 1992; Shabala and Newman, 1999) between the onset of illumination and K+ flux changes (presumably due to diffusion of the unknown activator produced by illuminated chloroplasts). The physiological role of light-induced K+ influx in leaf mesophyll remains obscure. The transient character of this process (Shabala and Newman, 1999) suggests that K+ influx is involved in the charge balance, rather than directly contributing to an increase in cell turgor.

Temperature

Information about direct effects of temperature on activity of ion channels (and, specifically, K+ channels) remains rudimentary. Ilan et al. (1995) reported that inward- and outward-rectifying channels in Vicia guard cell protoplasts had different temperature-dependent activation kinetics. Temperature effects on the voltage-dependence of the open probability of KIR channels were explained by temperature-induced shifts in the electric field in the vicinity of the channel, whereas the bell-shaped response in the number of active KOR channels was explained by temperature effects on membrane fluidity and, thus, on the activity of the channels. Indeed, critical temperature of recovery of K+ transporters in corn epidermal cells showed strong correlation with the phase transition of membrane lipids (Shabala and Shabala, 2002). Therefore, decreased availability of KOR channels was interpreted as a reflection of immobilization (‘locking’) of the channel gates at some ‘superclosed’ conformation (Ilan et al., 1995). This issue remains highly speculative and requires further investigation.

Salinity

Plant adaptation to salt stress involves significant ‘reprogramming’ of K+-channel gene expression, especially in leaves (Goldack et al., 2003; Pilot et al., 2003) and includes strong and progressive increase in the level of AtKCl transcript and a decrease in AKT2 mRNA accumulation. This effect is especially pronounced in the leaf epidermis (Dennison et al., 2001) and was specific to Na+ toxicity, but not to changes in osmotic potential. Expression of McHAK2 and McHAK3 was stimulated in leaves of the ice plant in response to high salinity (Su et al., 2002). The most exceptional stimulation was in phloem cells, while expression of HKT1 homologues in rice and barley were both strongly inhibited by salinity (Su et al., 2002). At the intracellular level, salinity blocks a substantial portion of FV channels, presumably by increasing the level of endogenous polyanamines in the cell cytosol (Brüggemann et al., 1998).

Drought

K+ channel activity in guard cells is known to be regulated by ABA (Assmann and Shimazaki, 2001; Luan, 2002). Biosynthesis of ABA in both root and shoot tissues is significantly enhanced by soil drying and/or salinity (reviewed in Wilkinson and Davies, 2002). Soil drying also increases the pH of the xylem stream, reducing the ability of the leaf symplastic compartments to sequester ABA, thus amplifying the ABA effects. In addition, in dry soil, there is a significant reduction in xylem sap K+, reducing K+ availability as a guard cell osmoticum (Wilkinson and Davies, 2002). Taken together, these factors are believed to be responsible for stomatal closure under drought conditions (Luan, 2002; Wilkinson and Davies, 2002).

Regulation of K+ channels may be mediated by either ABA-induced increase in cytosolic free Ca2+, which activates KIR (Assmann and Wang, 2001; Schroeder et al., 2001; Kohler et al., 2003), or via an ABA-induced Ca2+- independent pathway (Blatt, 2000). The latter is probably mediated by the pH effect on activity of FV and SV vacuolar channels (Assmann and Wang, 2001); not
involvement of ROS is also possible (Kohler et al., 2003). Also, not only gating properties and/or open probability of K⁺ channels, but their expression per se might be affected by ABA (Pilot et al., 2003). Finally, mechanosensory (SAS) channel involvement cannot be ruled out (Cosgrove and Hedrich, 1991).

CONCLUSIONS

As stated by Assmann and Wang (2001), the ‘emergent collective behaviour’ of stomata adds one more layer of complexity to stomatal function under real-world conditions. In the case of regulation of K⁺ transport in plant leaves, there is obviously more than one such layer of complexity. Precise intracellular and tissue locations of leaves, there is obviously more than one such layer of research. Power of the tools of molecular biology with an under

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ing. There is a strong need for in planta functional studies of specific mutants to quantify the relative contributions of particular members of a gene family to plant adaptive responses to the environment. An amalgamation of the power of the tools of molecular biology with an understanding of the plant’s functioning as an ‘entity’ has always been and remains the highest priority for future research.

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LITERATURE CITED


