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REVIEW

Participation of phytohormones in the stomatal regulation of gas exchange during water stress

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Abstract

Almost all processes in the life of a plant are directly or indirectly affected by both stresses and phytohormones. Nevertheless, apart from abscisic acid, the role of phytohormones in plant response to water stress is far from being fully elucidated. This review tries to answer the question whether interactions between abscisic acid and some other phytohormones might be important in the regulation of stomatal opening during water stress and subsequent rehydration. Firstly, it describes the changes in the contents of individual endogenous phytohormones during water stress. Then, it deals with the effects of applied phytohormones on stomatal opening, and on transpiration and photosynthetic rates in different plants species. Finally, it focuses on the alleviation or stimulation of absicic acid-induced stomatal closure by application of other phytohormones.

Additional key words: abscisic acid, auxins, brassinosteroids, chlorophyll, cytokinins, ethylene, gibberellins, jasmonates, leaf water potential, net photosynthetic rate, stomatal conductance, transpiration rate.

Introduction

Stomata occupy a central position in the pathway for the transport of water vapour, CO_2, and O_2. The regulation of stomatal conductance (g_s) is the main mechanism by which plants control gas exchange and leaf temperature (*e.g.* Jones 1998, Salleo *et al.* 2000). Many stimuli regulate the aperture of stomata and they achieve this by controlling the pressure potential of the two guard cells that surround the stomatal pore. The changes in pressure potential are a consequence of the uptake or loss of water, driven by changes in the concentrations of cations, particularly K^+, and anions. These are mostly transported through the ion channels located in the plasmalemma and tonoplast of the guard cells.

During water stress, stomata respond to hydraulic as well as chemical signals. Their relative importance is likely to depend on plant size and growth conditions (*e.g.* Blackman and Davies 1985, Tardieu and Davies 1993, Whitehead 1998, Thomas and Eamus 1999). The hydraulic signals involve changes in pressure potential in the xylem as well as changes in water content in the guard cells and other epidermal cells. Guard cells can be both the sensors and transducers of air humidity signals (Assmann *et al.* 2000).

Available evidence suggests that abscisic acid (ABA) synthesised in the roots under water stress and transported to the leaves may act as a root-to-shoot chemical signal of

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Abbreviations: ABA - abscisic acid; BA - N^6-benzyladenine; CK - cytokinin; E - transpiration rate; GA_3 - gibberellic acid; g_s - stomatal conductance; IAA - indole-3-acetic acid; IBA - indole-3-butyric acid; iP - isopentenyladenin; iPA - isopentenyladenosine; JA - jasmonic acid; Kin - kinetin; MeJA - jasmonic acid methyl ester; NAA - α-naphthaleneacetic acid; NCED - 9-*cis*-epoxycarotenoid diogenase; PAA - phenoxyacetic acid; P_N - net photosynthetic rate; RWC - relative water content; Z - zeatin; ZR - zeatin riboside.

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water stress conditions and, together with ABA synthesised in the leaves themselves, induce stomatal closure (for review see, *e.g.*, Davies and Jeffcoat 1990, Mansfield and Atkinson 1990, Liang *et al.* 1996, 1997a,b). ABA has been implicated as a key component in water deficit-induced responses, including those triggered by drought, salinity, and low temperature. ABA not only alters stomatal opening but also increases the root hydraulic conductivity (*e.g.* Zhang *et al.* 1995, Hose *et al.* 2000, 2002). In addition to its role in protecting plants against potentially lethal stresses, ABA helps to maintain near-homeostasis of leaf water status when plants are subjected to mild water deficits or to changes in evaporative demand (Borel *et al.* 2001).

However, other compounds might play a role in the chemical signalling of stress conditions. In the light of the important regulatory role played by cytokinins and auxins in modulating plant growth and development, it seems feasible also to anticipate their involvement in response of plants to adverse environmental conditions (Hare *et al.* 1997, Brault and Maldiney 1999, Itai 1999). However, the role of these and other phytohormones is not yet clear.

Many excellent reviews have been written concerning changes in ABA content and compartmentation during water stress, as well as the response of stomata to ABA signalling (for recent reviews, see *e.g.*, Assmann and Armstrong 1999, Blatt 2000, Rock 2000, Ng *et al.* 2001, Schroeder *et al.* 2001, Wilkinson and Davies 2002). Therefore, this review only briefly mentions the most important recent findings about ABA and is focused on fragmentary knowledge of the stress induced changes in contents of other phytohormones and their possible direct effects on stomata and interactions with ABA.

ABA synthesis, degradation and accumulation during water stress

ABA is found in all photosynthetic organisms and its amount is determined by the dynamic balance between biosynthesis and degradation. The most probable route of ABA biosynthesis starts from the carotenoids 9′-*cis*-violaxanthin or 9′-*cis*-neoxanthin, from which xanthoxin is formed by plastid enzyme 9-*cis*-epoxycarotenoid diogenase (NCED). Subsequently, xanthoxin is converted by xanthoxin oxidase to abscisic aldehyde, and this one by abscisic aldehyde oxidase to ABA (for recent review see Cutler and Krochko 1999, Zeevaart 1999, Hose *et al.* 2002). During water stress, NCED gene (*AtNCED3*) expression, and activity of aldehyde oxidase increase in both leaves and roots (Thompson *et al.* 2000, Iuchi *et al.* 2001, Zdunek and Lips 2001). There is still little information available about the mechanism of the signalling pathway from water stress perception to activation of genes encoding key enzymes of ABA biosynthesis, but interaction between plasmalemma and cell wall seems to be essential to triggering of the water stress-induced ABA accumulation (Zeevaart 1999, Zhang *et al.* 2001a). According to Jia *et al.* (2001) the changes in cellular volume, rather than the water relations parameters, initiate ABA accumulation. Protein phosphorylation might be involved in the signalling of water stress-induced ABA accumulation (Zhang *et al.* 2001b).

ABA is synthesized in leaves and roots of the plant, and also by soil microorganisms, and may move freely from plant to soil and *vice versa*. It can also move rapidly through the plant in both the xylem and the phloem (Jeschke *et al.* 1997). In roots and leaves ABA can be transported in apoplast or symplast. ABA is transported in the active free form or as inactive conjugated forms (predominantly abscisic acid glucose ester, Sauter and Hartung 2000, Sauter *et al.* 2002). Diffusion is the dominant transport mechanism for ABA within cells and the tonoplast permeability is usually lower than that of plasmalemma (Hose *et al.* 2002). Since both ABA and water flow are similarly retarded due to the presence of Casparian bands in root endodermis, ABA concentration remains unaffected (Freundl *et al.* 2000). ABA compartmentation in different tissues is largely caused by changes in pH (*e.g.* Sauter *et al.* 2001). Therefore, one way by which drought could modify the concentration of ABA in apoplast would be to change pH (Thompson *et al.* 1997, Wilkinson and Davies 1997).

The main catabolic pathway leads to phaseic acid and dihydrophaseic acid formation. ABA degradation probably occurs in the cytoplasm because phaseic acid forming enzymes are located in the endoplasmic reticulum (Daeter and Hartung 1995). Even if a higher rate of ABA metabolism was found in epidermal than mesophyll cells (Daeter and Hartung 1995), more ABA was metabolized in the leaf mesophyll due to its much higher volume. The capacity of leaves to metabolize xylem-delivered ABA has been found to be high (Jia *et al.* 1996, Zhang *et al.* 1997a). This fact might prevent stomatal closure by ABA under well-watered conditions (Thompson *et al.* 1997) or might be important for reopening of stomata after rehydration. The rate of catabolism of xylem-delivered ABA is usually faster than the rate of re-export (Zhang *et al.* 1997b). Significantly reduced ABA degradation was found in maize under water stress and with pH increase (Jia and Zhang 1997, Zhang *et al.* 1997a).

As mentioned above, ABA fluxes can be interpreted as signals of different stresses. They can be modified by soil moisture or air humidity (*e.g.* Hartung and Radin 1989, Thompson *et al.* 1997, Sauter *et al.* 2001). Delivery of ABA to the leaf varies greatly as a function of both the concentration of ABA in the xylem and the transpiration rate of the plant (Trejo *et al.* 1995, Jarvis and Davies 1997). For example, the ABA fluxes in water-stressed *Pinus sylvestris* and *Picea sitchensis* in the middle of the day were usually no greater than those of the controls, as a result of the very low sap flow rate. However, the ABA flux in the water-stressed plants was greater than in the controls in the morning, and the stomata responded to these morning doses (Jackson *et al.* 1995). ABA concentration in leaves can be affected by leaf age. For example, under water stress young leaves of cassava and willow accumulated more ABA than mature or old leaves (Alves and Setter 2000, Liu *et al.* 2001).

To simulate effects of water stress, feeding shoots with ABA has often been used. For example, in white lupin, a similar depression of g_s was observed under moderate water stress and in excised leaves of well-watered plants fed with ABA at the concentration corresponding to that in xylem of moderately stressed plants. In contrast, feeding a similar concentration of ABA failed to reproduce the depression in g_s observed in severely stressed plants (Correia and Pereira 1995). In water-stressed grapevine the maximal g_s in mid-morning was closely correlated with xylem ABA concentration and similar g_s could be reached by the application of exogenous ABA. However, further decline of g_s during the day could not be mimicked by ABA application (Correia *et al.* 1995).

After rehydration the leaf ABA content usually rapidly decreases to the level observed in unstressed control plants (Alves and Setter 2000). However, in severely stressed white lupin the full recovery of stomatal conductance was not achieved immediately, in spite of xylem ABA concentration and predawn leaf water potential returning to pre-stress levels (Correia and Pereira 1995). Similarly, in detached *Vicia faba* leaflets (Harris and Outlaw 1991) and in intact leaves of *Acacia confusa* and *Leucaena leucocephala* (Liang and Zhang 1999), ABA content after stress relief rapidly returned to the control value, whereas the reopening of stomata showed an obvious lag time. This suggests the participation of other factors in after-effects of stress on stomata. In intact sunflower plants, recovery of g_s after feeding with ABA depended on ABA concentration, duration of feeding and irradiance of leaves (Heckenberger *et al.* 1996).

For the regulation of stomatal opening, ABA concentration in the vicinity of guard cells is of vital importance. This ABA concentration can be increased by redistribution of pre-existing ABA within the leaf, by ABA synthesis by guard cells themselves, and by synthesis in other leaf compartments and subsequent redistribution to guard cells. Alternatively, ABA may be imported in the xylem as a signal from stressed roots (*e.g.* Hartung *et al.* 1998, Popova *et al.* 2000, Zhang and Outlaw 2001c, Zhang *et al.* 2001c). In addition, water evaporation from guard cell walls causes increase in ABA concentration in the guard cell apoplast (Zhang *et al.* 2001c, Zhang and Outlaw 2001a,b). The concentration of free ABA in the vicinity of the guard cells also depends on β-glucosidase activity which releases ABA from the physiologically inactive ABA-glucose conjugate pool (Dietz *et al.* 2000).

Responses of stomata to ABA

Involvement of ABA in the regulation of stomatal opening is generally accepted. There are probably two sites of ABA perception, extracellular and intracellular (Leung and Giraudat 1998, Ng *et al.* 2001, Zhang and Outlaw 2001c). Stomatal closure can be triggered by extracellular ABA, but the protonated form (ABAH) readily permeates the lipid bilayer of the cell membrane (Assmann and Armstrong 1999). In addition, guard cells appear to have a significant carrier-mediated uptake of ABA (Leung and Giraudat 1998). The nature of guard cell ABA receptors still remains elusive.

ABA can regulate stomatal aperture by promoting stomatal closure and/or inhibiting stomatal opening induced by changes in *1*) osmotic potential of guard cells, *2*) mechanical properties of guard cells, and *3*) gene expression (*e.g.* Hetherington 2001).

1) The ABA-induced decrease in stomatal opening involves both an inhibition of channels facilitating K^+ entry and activation of channels controlling efflux of K^+ and of anions. Ca^{2+} is a second messenger in some, but not all, ABA-induced changes in guard cell ion channels; ABA-induced inactivation of the plasmalemma inward K^+ channel is usually Ca^{2+} mediated, whereas ABA-induced activation of the plasmalemma outward K^+ channel is Ca^{2+} independent (MacRobbie 1997, Allen *et al.* 1998, Leung and Giraudat 1998, Assmann and Shimazaki 1999, Lemtiri-Chlieh *et al.* 2000). In the later case pH changes are probably important (Allen *et al.* 1998, Leung and Giraudat 1998, Blatt 2000). However, Ca^{2+}-independent inhibition of inward K^+ currents by ABA was also proved (Romano *et al.* 2000). ABA enhances Ca^{2+} calcium concentration in cytosol by stimulation of both Ca^{2+} entry across the plasma membrane and the release from intracellular stores by Ca^{2+} channels sensitive to inositol-1,4,5-triphosphate or cyclic ADP-ribose (Leung and Giraudat 1998, Blatt 2000, Schroeder *et al.* 2001). Protein kinases and phosphatases may also participate in ABA signal transduction (Mori and Muto 1997, Pei *et al.*

1997, Roelfsema *et al.* 1998, Assmann and Shimazaki 1999, Luan 2002). Zhang *et al.* (2001d,e) also suggested H_2O_2 mediated ABA-induced inhibition of inward K^+ currents. ABA also inhibits blue-light dependent H^+ pumping activity in *Arabidopsis thaliana* (Roelfsema *et al.* 1998, Schroeder *et al.* 2001). In *Mesembryanthemum crystallinum*, ABA increased vacuolar ATPase activity in adult leaves but not in young ones (Barkla *et al.* 1999).

2) Eun and Lee (1997) observed that ABA treatment caused reorganization of the actin structure of guard cells from a radial pattern to a randomly oriented and short-fragmented pattern. ABA also disrupted cortical microtubules in *Vicia faba* guard cells, but not in epidermal cells (Jiang *et al.* 1996). This effect was reversible and arrays of microtubules reappeared within 1 h after removal of ABA. Cytoskeleton reorganization is probably involved also in the ABA-independent osmosensing pathway of stomatal opening regulation under water stress (Leun 2002).

3) The ABA signal can also be relayed to the nucleus of guard cell to bring about alterations in the pattern of gene expression leading to changes in content of water-transport proteins, ion-transport proteins, or proteins involved in carbon metabolism (Webb *et al.* 2001).

Long-term ABA treatment of *Tradescantia virginiana* plants led to increased stomatal density, smaller stomatal dimensions, and lower g_s for any given guard cell pressure potential (Franks and Farquhar 2001). On the leaf blade, stomata do not react homogeneously and stomatal patchiness has been often observed after exogenous ABA application (for review see Pospíšilová and Šantrůček 1994, Mott and Buckley 1998).

Sensitivity of stomata to ABA varies in different species and cultivars, with age of leaf, time of day, temperature, irradiance, air humidity, nutritional status, ionic composition of the xylem sap, and particularly the leaf water status (Borel *et al.* 1997, Correia *et al.* 1997, 1999, Niinemets *et al.* 1999, Augé *et al.* 2000, Wilkinson and Davies 2002). In *Vicia faba* the stomata of previously water-stressed plants were more sensitive to ABA applied through the petiole or sprayed onto leaf surfaces than stomata of well watered plants (Davies 1978). Similarly, stomata of *Trifolium subterraneum* were more sensitive to xylem ABA content in water-stressed than irrigated plants (Socias *et al.* 1997). In sunflower, g_s was greater in the phytotron-grown plants than in the outdoor plants at a given concentration of applied ABA and at a given leaf water potential (Hirasawa *et al.* 1995).

ABA concentration in plants grown *in vitro* is low and conditions that increase the endogenous ABA content (ventilation or ABA addition to the medium) improve the control of leaf water loss and plant vigour, and help in *ex vitro* transplantation (Pospíšilová 1996, Aguilar *et al.* 2000, Talavera *et al.* 2001). The success of *ex vitro* transfer can also be improved by ABA application immediately after the transfer (Pospíšilová *et al.* 1998). In the presence of ABA an increased sensitivity of stomata to a decrease in CO_2 partial pressure was also observed. This allowed plants to limit photoinhibition (Leymarie *et al.* 1998). Stomatal sensitivity to ABA may also be affected by temperature (*e.g.* in white lupin; Correia *et al.* 1999).

However, drought-induced changes in ABA concentration as well as stomatal sensitivity to ABA are not always correlated with plant drought resistance as, *e.g.*, Cellier *et al.* (1998) showed in different sunflower lines. In addition, stomatal sensitivity to ABA concentration in the leaf xylem sap is not always correlated with ABA biosynthesis ability; this was proved by comparison of wild type and an ABA-deficient mutant of *Nicotiana plumbaginifolia* (Borel *et al.* 2001).

Exogenous ABA can serve as antitranspirant. In addition to lowering stomatal conductance, the application of ABA results in the accumulation of proline and total saccharides (Hose *et al.* 2000), or in promotion of wax deposition on the leaf surface (Xu *et al.* 1994).

Cytokinin synthesis, degradation and changes during water stress

Cytokinins (CKs) promote cell division and, acting both in synergy and in antagonism with other plant hormones, influence a wide range of events during plant growth. Most naturally occurring CKs are N^6-substituted adenine molecules with a branched 5-carbon side chain. The most abundant of these is trans-zeatin (Z), but the less abundant isopentenyladenine (iP) is also very active. Riboside and ribotide derivatives are less active than the free bases, and *N*- and *O*-linked glucosides are mostly inactive (*e.g.* Zažímalová *et al.* 1999, Hooley 2001). The patways of CK biosynthesis have not yet been completely solved. The important step is probably the formation of N^6-(Δ^2-isopentenyl) adenosine-5′-monophosphate from Δ^2-isopentenyl pyrophosphate and adenosine-5′-monophosphate catalyzed by isopentenyltransferase (Mok and Mok 2001). Another possibility is the degradation of tRNA and the isomerization of *cis*-zeatin to *trans*-zeatin by *cis-trans* isomerase (Mok and Mok 2001). The biosynthetic pathway of aromatic CKs is not known. The major portion of the CKs in plants are produced in the meristematic regions of the roots and transported via xylem to the shoots where they act together with the locally synthesized CKs. CK metabolism is very complex and reflects the existence of many of the above mentioned compounds with different activities (for recent review see Emery and Atkins 2002). Irreversible degradation of CKs by N^6 side chain cleavage is catalyzed by cytokinin oxidase (according to new findings this enzyme might be cytokinin dehydrogenase; Galuszka *et al.* 2001). Endogenous CK contents are also regulated by other plant hormones, in particular by auxins (*e.g.* Kamínek *et al.* 1997, Zažímalová *et al.* 1999).

CKs play important regulatory role in plant growth and development. They promote accumulation of chlorophyll and conversion of etioplasts into chloroplasts, and delay leaf senescence. Their possible involvement in responses to adverse environmental conditions is also suggested (Hare *et al.* 1997, Brault and Maldiney 1999). The cellular site and molecular mechanism of CK action are poorly understood. They probably act at the plasma membrane in concert with other signals for the control of biological responses (Brault and Maldiney 1999, Hooley 2001). Some evidence points to a regulation of calcium flux (Hooley 2001).

In water stressed plants, CK synthesis in the roots and delivery to the leaves is usually decreased. In addition, CKs degradation might be increased. In consequence, decreased CK content in leaves was observed (for reviews see, Naqvi 1994, 1995, 1999, Pospíšilová *et al.* 2000). Recently, a decreased content of CKs under drought was found in alfalfa (Goicoechea *et al.* 1995, 1997) and grapevine (Stoll *et al.* 2000). The contents of Z, zeatin riboside (ZR), iP, and isopentenyladenosine (iPA) in rice substantially decreased with the decrease in soil moisture and they only slightly increased after rewatering (Bano *et al.* 1993). During dehydration of wheat seedlings a decline in the content of zeatin nucleotide and the accumulation of zeatin 9-N-glucoside was observed, but the total content of Z derivatives as well as the content of free base of Z remained almost constant (Mustafina *et al.* 1997/98). In contrast, decreased content of Z in wheat under water stress was observed by Teplova *et al.* (1999). CK concentration was not significantly changed in the apoplastic solution of water-stressed cotton and sunflower (Hartung *et al.* 1992, Masia *et al.* 1994). The concentration of CKs in the xylem sap of *Prunus dulcis* was also not related to tree water status (Fusseder *et al.* 1992). The xylem delivery rate of ZR from roots to shoots in sunflower decreased under both mild and severe water stress while the concentration of ZR in xylem sap decreased only under severe water stress (Shashidhar *et al.* 1996). The concentrations of Z, ZR, iP, and iPA decreased significantly in shoots and roots of barley cultivars after exposure to increased concentration of NaCl (Kuiper *et al.* 1990). A decreased rate of CK delivery into the xylem sap was observed in pea under NaCl stress (Zdunek and Lips 2001). In contrast, an increased CK content in pea roots under salt stress was found by Atanassova *et al.* (1999). In callus culture of *Anastatica hierochuntica* the increased concentration of salts in the medium decreased the CK content in callus (Abou-Mandour and Hartung 1995). Even if the content of CKs often declines under stress, this does not necessarily mean the less effect, because stress might increase cellular sensitivity to CK (Hare *et al.* 1997).

CKs may partially ameliorate negative effects of water stress, *e.g.*, by stimulating osmotic adjustment. This was observed in *Cicer* after benzyladenine (BA) application (Yadav *et al.* 1997) and in *Vigna* after kinetin (Kin) application (Agarwal and Gupta 1995). In tobacco and *Mesembryanthemum*, the addition of BA, Z, or iP induced accumulation of proline and osmotin (Tomas *et al.* 1992, 1995). However, disturbed water relations have been observed in transgenic plants with markedly elevated content of endogenous CKs (for review see Synková *et al.* 1997b).

Responses of stomata to cytokinins

The responses of stomata to exogenous CKs are species-specific and depend on CK type and concentration. The increase in transpiration of excised leaves of *Anthephora, Avena, Brassica, Helianthus, Hordeum,* and *Triticum* by Kin, BA, or Z was mentioned in the review of Incoll and Jewer (1987). They also mentioned increase in stomatal aperture induced by Kin in isolated epidermis of *Anthephora* and *Kalanchoë* but not in *Commelina, Pisum, Tridax, Vicia,* and *Zea.* Increase in g_s with increased ZR delivery to leaves was observed in sugarcane (Meinzer *et al.* 1991). Stomatal aperture in *Tradescantia* leaves and transpiration rate (E) in *Vigna* were markedly increased by Kin application (Pharmawati *et al.* 1998, Gupta *et al.* 1999). In *Melampyrum arvense,* the largest effect on stomatal opening was caused by application of ZR and dihydrozeatin riboside, followed by dihydrozeatin, Z, iPA, and BA; iP was almost inactive (Lechowski 1997). In *Commelina* the largest stomatal aperture was induced by Z, followed by Kin and BA (Santakumari and Fletcher 1987). Application of BA, Z, ZR, dihydrozeatin, and dihydrozeatin riboside increased E in *Avena* but not in *Triticum* (Badenoch-Jones *et al.* 1996). In tobacco and *Digitalis* plantlets growing *in vitro* the addition of BA stimulated opening of stomata and transpiration only in low concentrations (Diettrich *et al.* 1992, Pospíšilová *et al.* 1993). In *Phaseolus vulgaris* low concentrations of BA slightly stimulated g_s and E but higher concentration mostly inhibited them (Pospíšilová *et al.* 2001, Rulcová *et al.* 2001). The consistent stimulation of g_s or E was not observed by application of Kin in cotton (Radin *et al.* 1982, Radin and Hendrix 1988), by Z in flax (Drüge and Schönbeck 1992), by BA or N^6-(*m*-hydroxylbenzyl)adenosine in sugar beet (Čatský *et al.* 1996, Pospíšilová *et al.* 2001, Vomáčka and Pospíšilová 2003), and by Z and Kin in young maize leaves, but a stimulation of g_s was observed in old maize leaves (Blackman and Davies 1983, 1984). Stomatal aperture in *Vicia faba* was stimulated by adenosine, kinetin riboside and Kin in darkness and by adenosine and kinetin riboside also in light, but in light Kin itself had no effect or, at higher concentrations, inhibited stomatal aperture (Morsucci *et al.* 1991, 1992). In epidermal strips or leaf fragments of *Commelina*, Z or Kin decreased stomatal opening (Blackman and Davies 1983).

Fusseder *et al.* (1992) found promotion of g_s at increased content of endogenous CKs only when soil moisture was high. The increase in content of endogenous CKs was accompanied by an increase in g_s or E in *zmp*-transgenic tobacco plants (Pospíšilová *et al.* 1995, 1997/98), in transgenic tobacco plants with heat-inducible expression of *ipt*-gene (Kudoyarova *et al.* 1999), and in transgenic tobacco with *ipt* gene controlled by a chalcone synthase promoter (Wang *et al.* 1997a,b), but not in transgenic tobacco with *ipt* gene under control of light inducible promoter of a small unit of ribulose-1,6-bisphosphate carboxylase/oxygenase (Synková *et al.* 1995, 1999).

CKs are often considered as ABA antagonists. CKs delay leaf senescence, reverse leaf and fruit abscission induced by ABA or water stress, or release seed dormancy. This is in contrast with ABA inhibition of germination. In water-stressed rice and soybean, ABA content increased and at the same time CK content decreased (Thimann 1992). In maize, CKs reversed ABA mediated stomatal closure in both young and old leaves (Blackman and Davies 1984). In flax Z decreased stomatal response to ABA (Drüge and Schönbeck 1992). In cotton, Kin had little effect on stomatal response to ABA in control plants, but it decreased stomatal response to ABA in plants grown under nitrogen deficiency (Radin *et al.* 1982, Radin and Hendrix 1988).

The mechanism of CK action on guard cells might involve direct induction of membrane hyperpolarization by stimulation of electrogenic H^+-pump; stimulation of adenylate cyclase activity which could lead to an increase in intracellular adenosine 3′,5′-cyclic monophosphate content; stimulation of guanylate cyclase activity; or interaction with a calcium-calmodulin system (Incoll *et al.* 1990, Morsucci *et al.* 1991, Pharmawati *et al.* 1998). The internal calcium concentration might be a candidate for mediating interactions between CKs and ABA (Hare *et al.* 1997). The antagonism between CKs and ABA may be the result of metabolic interactions: CKs share, at least in part, a common biosynthetic origin with ABA (Cowan *et al.* 1999).

In desert-grown almond trees CKs showed peak contents in the morning and a rapid decrease in the afternoon; these daily variations preceded daily variation in g_s. Hence CKs may affect stomatal behaviour on a short-term basis, while ABA content reflects long-term water deficit (Fusseder *et al.* 1992). High content of CKs can override the effects of ABA on stomata; thus reduction in CK supply as soil dries might amplify shoot responses to an increasing concentration of ABA (Davies and Zhang 1991).

Auxins

Indole-3-acetic acid (IAA) was the first auxin and the first phytohormone to be described. In plants there are also other substances of an indole or non-indole nature and some of them show an intrinsic auxin activity. The most important seems to be indole-3-butyric acid (IBA) and phenoxyacetic acid. In contrast to ABA and CKs, auxins are mainly synthesized in shoots. The precursor of IAA is mostly tryptophan and biosynthesis follows several pathways. Plants store most of their IAA in a conjugated, probably inactive, form. The conjugates are either ester conjugates (predominately in monocotyledonous plants) or amide conjugates (predominately in dicotyledonous plants) (for review see, Slovin *et al.* 1999). Auxin contents are highest in regions of active cell division: the apical meristems, the cambium, the developing fruit, embryo and endosperm, and in young leaves. Many synthetic auxin analogues were derived and some of them (*e.g.* α-naphthaleneacetic acid, NAA, or 2,4-dichlorophenoxyacetic acid) are practically important.

Auxins affect wide spectrum of processes such as cell division, cell enlargement, vascular tissue differentiation, root initiation, flowering, fruit setting, gravitropism. IAA induces rapid events at the plasma membrane by binding to a population of the auxin-binding protein ABP1. Binding of auxin causes a conformational change affecting the C-terminus of ABP1 and this change probably activates the receptor at plasma membrane. The signal transduction pathway may involve activation of phospholipase and plasma membrane ATPase (for review see, MacDonald 1997).

In comparison with huge information on auxin content during plant growth and development, relatively little information is available on the changes in auxin content induced by water stress. After exposure to NaCl the IAA content in tomato roots markedly declines, but the IAA content in leaves remains unchanged (Dunlap and Binzel 1996). In callus culture of *Anastatica hierochuntica* the increased concentration of salts in the medium decreased

IAA content in callus (Abou-Mandour and Hartung 1995). In cotton leaves subjected to overpressure which simulated water stress, IAA content remained unchanged (Hartung *et al.* 1992).

Responses of stomata to auxins

In the literature, the information on the effects of auxins on stomatal opening is often confusing, mainly because the effects of IAA are totally different from those of synthetic auxins (Mansfield and Atkinson 1990). In addition, a concentration-dependent effect of IAA was found: stomatal opening at low concentrations and stomatal closure at higher concentrations (Assmann and Armstrong 1999). IAA promoted stomatal opening only on adaxial epidermis of *Commelina communis* and thus changed the ratio of apertures on adaxial and abaxial epidermes (Pemadasa 1982a). In this plant species, treatment with IAA promoted stomatal opening during the night but not to a level equivalent to that in the day (Snaith and Mansfield 1985). In *Pisum sativum* and *Phaseolus vulgaris* IAA increased g_s in the presence of CO_2 but not in absence of CO_2 (Eamus 1986). However, in *Commelina communis* IAA reversed the closing effect of high CO_2 concentration (Snaith and Mansfield 1982). In *Vicia faba* IAA also inhibited the closing effects of CO_2 and darkness (Říčánek and Vicherková 1992). Foliar spray with IAA partially counteracted the effect of water deficit on g_s, net photosynthetic rate (P_N), and E in cotton (Kumar *et al.* 2001).

IAA alleviated the closing effect of ABA in *Commelina communis* (Snaith and Mansfield 1982). In epidermal peels of *Vicia faba*, IAA stimulated stomatal opening and when both IAA and ABA were present, stomatal aperture was dependent on the relative concentration of each (Říčánek and Vicherková 1992, Dunleavy and Ladley 1995). In *Solanum melongena* IAA increased g_s in control and ABA-sprayed leaves, but not in previously water-stressed leaves (Eamus and Narayan 1989). In an auxin-hypersensitive mutant of *Arabidopsis thaliana* increased sensitivity to both auxins and ABA was observed (Ephritikhine *et al.* 1999).

In *Commelina communis*, phenylacetic acid (PAA) in low concentration promoted opening of stomata on adaxial epidermis but reduced stomatal opening on abaxial epidermis. However, PAA in high concentration suppressed stomatal opening on both leaf sides. PAA reduced the closing effect of ABA and *vice versa* ABA reduced PAA-induced abaxial stomata closure (Pemadasa 1982b). IBA did not affect E and P_N in either wild type or ABA-deficient mutants of tomato (Herde *et al.* 1997). However, treatment of stomata with NAA induced stomatal closure (Snaith and Mansfield 1984).

Stomatal opening is driven by H^+ extrusion through plasma membrane H^+-ATPase activated by red or blue radiation and probably also by auxins (Schroeder *et al.* 2001). Stomatal opening induced by IAA in epidermal strips of *Paphiopedilum tonsum* was preceded by a reduction of cytoplasmic pH (Gehring *et al.* 1998). Exogenous auxins (IAA and NAA) affect inwardly and outwardly rectifying K^+ currents in a dose-dependent and pH-dependent manner (Blatt and Thiel 1994, Grabov and Blatt 1998, Bauly *et al.* 2000). Low concentration of auxins promotes inward movement of K^+, while higher concentrations inhibit this activity (Estelle 1999). The effect is mediated by second messengers: changes in concentration of Ca^{2+} or pH (Gehring *et al.* 1998, Grabov and Blatt 1998). Cyclic GMP as the mediator within the Ca^{2+} signalling cascade was suggested for IBA signal transduction in *Commelina communis* (Cousson and Vavasseur 1998, Cousson 2001). Auxins can also induce a shift of the voltage dependence of anion channels (Lohse and Hedrich 1995). The extent of this shift depends on which auxin is applied (IAA or NAA) and its concentration (Assmann and Armstrong 1999). Huang *et al.* (2000) showed participation of changes in polymerization of microtubules and microfilaments in IAA induced stomatal opening in *Vicia faba*.

Other phytohormones

Gibberellins (GAs) are diterpenes constituted of four isoprene units. Nearly 70 gibberellins have already been isolated from natural sources. A relatively large content of gibberellins is found in apical internodes, developing young leaves, and ripening fruits. They are transported in both xylem and phloem. Cleavage of the ring system results in loss of activity. GAs composition and contents are usually connected with plant growth and development. In relation to environmental effects, irradiance and low temperature induced changes in GA metabolism were reviewed by Hedden (1999), but little is known about changes induced by water stress. Water stress reduced accumulation of GAs in lettuce (Aharoni *et al.* 1977), cottonwood saplings (Rood *et al.* 2000) and in rice grains in the early grain filling stage (Yang *et al.* 2001). No changes in GA content were observed in drought-stressed sunflower (Hubick *et al.* 1986).

Application of gibberellic acid (GA_3) to peanut increased g_s in control plants and partially relieved the effect of waterlogging, which induced a decrease of g_s (Bishnoi *et al.* 1992). A retardation of stomatal closure in water-stressed leaves following treatment with GA_3 was observed in lettuce (Aharoni *et al.* 1977). In *Commelina benghalensis* GA_3 increased stomatal aperture and reversed triazole-induced stomatal closure (Santakumari and Fletcher 1987). In *Vicia faba* and *Fritillaria imperialis* GA_3 treatment induced a transient opening of stomata in the dark, but not substantial accumulation of potassium in guard cells (Göring *et al.* 1990). In broad bean GA_3 increased not only g_s, but also P_N and ribulose-1,6-bisphosphate carboxylase/oxygenase activity (Yuan and Xu 2001). However, in *Triticum aestivum* GA_3 had no consistent effect on g_s and E in control or NaCl-treated plants (Ashraf *et al.* 2002), and in *Mentha spicata* GA_3 even decreased g_s and E (Singh *et al.* 1999). Nevertheless, treatment with GA_3 ameliorate negative effects of salinity on wheat growth (Ashraf *et al.* 2002).

Jasmonates are represented by jasmonic acid [JA; 3-oxo-2-(2-cis-pentenylcyclopentane-1-acetic acid)] and its methyl ester (MeJA). JA is formed from linoleic acid, the first step being catalyzed by lipoxygenase (*e.g.* Cleland 1999). They inhibit growth and seed germination and promote senescence, abscission, tuber formation, and ripening. MeJA-mediated signalling pathway might be involved in ozone tolerance (Koch *et al.* 1998) or in response to wounding stress (Liu *et al.* 2002).

Exogenous JA induced stomatal closure in broad bean (Liu *et al.* 2002) and barley (Tsonev *et al.* 1998). However, pretreatment of barley with JA before application of NaCl ameliorated inhibitory effect of NaCl on g_s and E (Tsonev *et al.* 1998). JA also reduced E in the wild-type and to a minor extent also in the ABA-deficient tomato plants (Herde *et al.* 1997). JA inhibits carbon dioxide fixation independently of ABA or stomatal closure.

Exogenously supplied MeJA caused accumulation of proline, and increased photorespiration rate and CO_2 compensation concentration similarly as water stress (Fedina and Tsonev 1997). MeJA caused closure of stomata, and decrease in E and P_N in *Commelina benghalensis* (Raghavendra and Reddy 1987), wheat (Leshem *et al.* 1994, Beltrano *et al.* 1998), pea (Fedina and Tsonev 1997), and olive detached leaves (Sanz *et al.* 1993). It also reduced the opening of stomata in chilled rice seedlings (Lee *et al.* 1996). In strawberry plants, MeJA reduced E and ameliorated effect of water stress on oxygen-scavenging enzymes and on lipid peroxidation (Wang 1999). Pretreatment with MeJA alleviated the inhibitory effect of NaCl on P_N in pea leaves, but not on g_s, E, and chlorophyll content (Fedina and Tsonev 1997). However, in other experiments, MeJA did not affect g_s and P_N in pea leaves (Lazova *et al.* 1999).

The possible mechanism of JA a MeJA action on stomatal opening is probably similar to that of ABA in suppression of H^+ efflux and K^+ influx (Raghavendra and Reddy 1987). In *Paphiopedilum*, JA and MeJA caused intracellular alkalization which preceded stomatal closure (Gehring *et al.* 1997).

Brassinosteroids have been isolated from various plants. Exogenous application of brassinosteroids (BRs) induces a broad spectrum of responses, including increased rate of stem elongation, pollen tube growth, leaf movements, proton pump activation, reorientation of cellulose microtubules, and xylogenesis (for review see, Yokota 1999). Nothing is known about changes in BR content during water stress. As concerns their effects on leaf gas exchange, epibrassinolide decreased stomatal opening and E in sorghum leaves and when used in combination with ABA it enhanced the effect of ABA (Xu *et al.* 1994). Pretreatment of jack pine seedlings with homobrassinolide delayed stomatal closure induced by water stress (Rajasekaran and Blake 1999).

Ethylene has two major effects on plants. The first is to induce a programmed series of events leading to senescence, and the second is to alter the direction of cell enlargement causing, *e.g.*, inhibition of stem elongation and promotion of stem width (Cleland 1999). In higher plants, most tissues produce more or less ethylene depending on their developmental stage and environmental conditions. Enhanced ethylene biosynthesis was induced by extreme temperatures, wounding, and mechanical and chemical stresses (Naqvi 1999). This promotion might be dependent on activity of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, ACC content and activity of ACC oxidase (Ievinsh *et al.* 2001).

However, considerable controversy surrounds the role of ethylene in the response to drought: increase as well as decrease in ethylene production was found (Cleland 1999). In detached leaves of *Brassica*, *Capsicum*, *Citrus*, *Phaseolus*, and *Ricinus* exposed to dry air continuous increase in ethylene content was observed, but only a transient increase in detached leaves of *Beta*, *Cucurbita*, *Lactuca*, and *Nicotiana* (Aharoni 1978). Decrease in ethylene production was observed, *e.g.*, in *Gerbera jamesonii* (Olivella *et al.* 1998).

Promotion of stomatal opening or closure, or lack of effect of ethylene has also been observed. Ethylene did nor regulate stomatal closure in response of *Rosmarinus officinalis* to drought (Munne-Bosch *et al.* 2002). Ethylene inhibited gas exchange in *Glycine max* (Gunderson and Taylor 1991). Application of etherel to *Mentha spicata* decreased g_s and E (Singh *et al.* 1999). According to Merrit *et al.* (2001) auxin-induced stomatal opening might be mediated through auxin-induced ethylene production by guard cells.

Conclusions

The activities of phytohormones depend on their contents and activities, as well as on their interactions. Water stress triggers a change in hormonal balance, including an increase in leaf content of ABA and/or a possible decline in contents of CKs, auxins, and GAs (Table 1).

Table 1. The most often mentioned changes in leaf contents of main groups of phytohormones during water stress and the responses of stomata to application of growth regulators.

	Leaf content	Stomatal conductance
Abscisic acid	increased	decrease
Cytokinins	mostly decreased	increase or no change
Auxins	decreased or no change	increase or decrease
Gibberellins	decreased or no change	increase or decrease
Jasmonates	??	decrease
Ethylene	decreased or increased	??

Plant responses to phytohormones are often judged from their responses to exogenously applied natural or synthetic phytohormones. However, when we apply the phytohormones and follow the plant response, it is necessary to consider that the applied phytohormones can change the contents of endogenous phytohormones by their uptake, by promotion of endogenous phytohormone biosynthesis, or stimulation of their degradation (for review concerning CKs see, *e.g.*, Hare *et al.* 1997, Kamínek *et al.* 1997). Thus, the composition and concentration of phytohormones in the site of action might be different from the site of application.

Another complication is the fact that application of one phytohormone can stimulate or inhibit synthesis of other phytohormones; interactions between auxins and CKs are well known. In addition, the response of plant to the application of exogenous hormone does not necessarily mean that endogenous hormone is involved in the natural regulation of that system.

The position of ABA as the most important stress hormone is an undisputed fact. In addition, recent investigations have contributed significantly to the elucidation of the signalling pathways that participate in the regulation of stomatal opening by ABA. However, our knowledge about the participation of other phytohormones in the stomatal regulation of gas exchange during water stress is still far from clear. From the above survey (Table 1), the most probable candidates for alleviation of ABA effects seems to be CKs and auxins and for stimulation of ABA effects JA and MeJA. Moreover, plant hormones play a role in the transformation of stress-related signals into changes in gene expression needed for adaptation to suboptimal environmental conditions (Hare *et al.* 1997).

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