Journal of Experimental Botany, Vol. 59, No. 1, pp. 37–43, 2008
Transport of Plant Growth Regulators Special Issue
doi:10.1093/jxb/erm127 Advance Access publication 26 June, 2007

Journal of Experimental Botany
www.jxb.oxfordjournals.org

SPECIAL ISSUE REVIEW PAPER

Long-distance signalling of abscisic acid (ABA): the factors regulating the intensity of the ABA signal

Fan Jiang[1] and Wolfram Hartung[2,*]

[1] *College of Life Science, BeiJing Normal University, Xin Jie Kou Wai Da Jie 19, 100875 BeiJing, China*

[2] *Lehrstuhl Botanik I der Universität Würzburg, Julius von Sachs Platz 2, D 97082 Würzburg, Germany*

Received 14 March 2007; Revised 15 May 2007; Accepted 15 May 2007

Abstract

Abscisic acid (ABA) is a stress signal, which moves in the xylem from the roots to the aerial parts of the plant, where it regulates stomatal movement and the activity of shoot meristems. Root growth-promoting micro-organisms in the rhizosphere, lateral ABA flows in the root cortex across apoplastic barriers, ABA redistribution in the stem, leaf apoplastic pH values, and the action of β-glucosidases, both in the apoplast and the cytosol of the mesophyll, play an important role in the regulation of signal intensity. The significance of abscisic acid glucose ester as a long-distance stress signal is discussed.

Key words: Abscisic acid glucose ester, apoplast, β-glucosidases, pH, rhizosphere, xylem.

Introduction

The role of abscisic acid (ABA) as a universal plant stress hormone is well established. Under conditions of mild stress as the soil starts to dry, when the water potential of the leaves is not or only slightly affected, ABA is accumulated in root tissues, released to the xylem vessels, and transported to the shoot where stomatal and meristematic activities are regulated to help the plant cope with the stress situation. Such reactions have often been discussed and reviewed in the past, especially as far as stomatal reactions are concerned (Zhang and Davies, 1990; Davies *et al*., 2005). Loveys (1984) and Wartinger *et al*. (1990) were the first to show the relationship between xylem ABA concentration (ABA_{xyl}) and leaf conductance (G) and the maximal leaf conductance (G_{max}), respectively, under natural climatic fluctuations in the field. Recently, more than 60 publications were analysed to investigate this relationship for a wide range of plants of different habitats, life forms, and ecotypes (Heilmeier *et al*., 2007). It turned out that in nearly all cases the same typical relationship can be observed; with a narrow range of ABA_{xyl} within-leaf conductance reacts very sensitively but with a wide range of ABA_{xyl} even dramatic changes of ABA_{xyl} have only a small impact on G_{max} (Fig. 1). Furthermore, stomatal reactions are always much better correlated with ABA_{xyl} than with leaf bulk ABA, pointing to the importance of ABA as a hormonal long-distance signal in the xylem.

ABA signalling can be intensified in many crops, for instance grapevine, by applying modern irrigation techniques, such as partial root drying (PRD; Davies *et al*., 2005). PRD is an irrigation technique where water is distributed unevenly to the root system with an irrigated and a dry part. With PRD grapevines, Stoll *et al*. (2000) showed that ABA signalling is diminished after prolonged drying of one compartment. To sustain the effect of PRD it was necessary to alternate wet and dry parts regularly (PRD-A). PRD-A was shown by Dodd *et al*. (2006) to intensify ABA signalling with positive consequences for water saving and improvement of the quality of the crops.

The factors that regulate the intensity of the ABA signal in the xylem, on its way from the root to the target cells, are therefore of particular interest and will be discussed in this contribution.

The intensity of the ABA signal in the xylem

When discussing the intensity of the ABA signal in the xylem, internal and external sources of ABA have to be considered. External ABA originates from root exudation and from ABA-producing soil organisms (predominantly fungi), whereas internal ABA comes from biosynthesis in

* To whom correspondence should be addressed. E-mail: hartung@botanik.uni-wuerzburg.de

the roots and from phloem import of ABA, which has been synthesized previously in the shoot, into the root (Fig. 2).

External factors affecting ABA formation and accumulation in roots

Dry soils of habitats in arid climates are often nutrient-deficient, alkaline, loaded with salt, and compacted. In agricultural areas, large amounts of ammonium fertilizers may be applied to plants. In natural environments, dissolved organic nitrogen (predominantly glycine; Hartung and Ratcliffe, 2002) is often the only form of nitrogen. In Table 1 the impact of such external factors on ABA formation, accumulation, lateral transport in roots, and long-distance flows is summarized. Salt stress, ammonium nutrition, and phosphate and potassium deficiency increase ABA formation in the roots. In the case of phosphorus and potassium deficiencies, only small amounts are deposited in the roots, a high percentage being released quickly and effectively to the xylem. Particularly strong ABA synthesis and accumulation in the roots can be observed in hemiparasites such as *Rhinanthus minor*. They release ABA in substantial amounts to the soil solution (Jiang *et al*., 2004). ABA accumulation also can be increased when ABA degradation is inhibited by tetcyclacis, a compound that prevents the formation of phaseic acid. In maize seedlings this results in a 4-fold increase of ABA in the xylem (Fig. 2; Table 1).

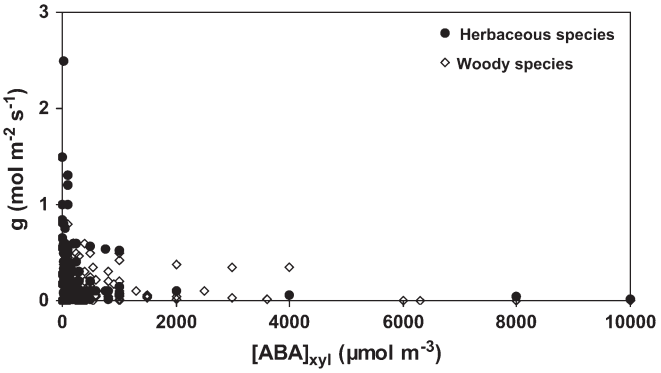

Fig. 1. The relationship between ABA_{xyl} and leaf conductance in woody and herbaceous species of different life forms and originating from different habitats (based on an analysis of more than 60 publications by Heilmeier *et al*., 2007).

A possible role for growth-promoting rhizobacteria

Recently it has been shown that growth-promoting rhizobacteria have an impact on ABA flows in plants. Arkhipova *et al*. (2005) detected substantially increased amounts of ABA in the shoots of lettuce that were treated with the cytokinin-producing bacterium *Bacillus subtilis*. The authors concluded that locally high cytokinin concentrations induced ABA biosynthesis in the roots. The

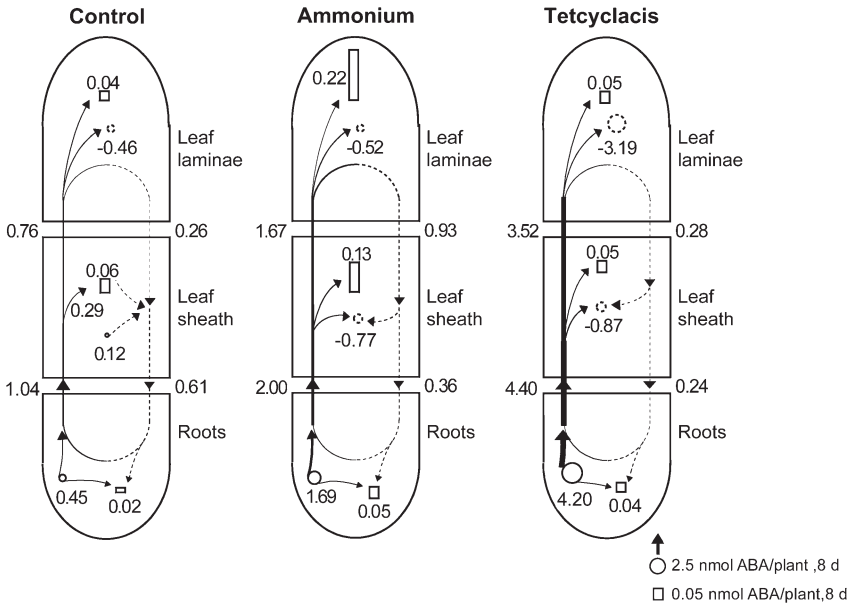

Fig. 2. Flow profiles for metabolism, transport, and deposition of abscisic acid (ABA) in maize plants (*Zea mays* L.) supplied with 1 mM NO_3^- (as control), treated with 1 mM NH_4^+ or tetcyclacis over 8 d of the study period starting 6 d after planting. The age of the plants at the end of the experiment=18 d (n=5). Based on the assumption that mass flow occurs both in xylem and phloem the net K flows (obtained as described by Jeschke *et al*., 1995) and the ratios of ABA:K in the transport fluids were used to estimate the net flows of ABA in the two transport pathways over the study period. The increments of ABA in the maize tissues were calculated from two harvests (6 d and 14 d after planting). The metabolism of ABA in maize tissue was calculated according to Jiang *et al*. (2004). Dotted arrows indicate flows in the phloem, black arrows flows in the xylem. The width of the arrows (flows), the areas of the squares (deposition), and of the circles (complete circles, net synthesis; dotted circles, net degradation) are drawn in relation to the rates of flows. The numbers beneath the arrows, squares, and circles indicate the net flows in nmol $plant^{-1}$ 8 d^{-1}.

Table 1. *Summary of external effects on net ABA biosynthesis, metabolism, deposition, and long-distance flows in different plants*

External stress factors such as soil matric potential, soil strength, alkaline pH, and flooding are not included because detailed analyses of long-distance flows between plant organs are not available. ↑, Stimulation, ↓, inhibition, ↔, no effect. Empty fields are due to missing data.

Treatment[a]	Net ABA synthesis in roots	Net ABA metabolism in roots	ABA deposition in roots	Lateral ABA flow in roots	ABA flow in the xylem	Net ABA synthesis in shoots	Net ABA metabolism in shoots	ABA deposition in shoots	ABA flow in the phloem	ABA retranslocation phloem to xylem
Salt										
Lupinus[1]	↑ (×20)	↔	↑ (×30)	↑	↑ (×10)		↑	↑	↑	↑
Ricinus[2]	↑ (×3)			↑	↑ (×22)				↑	
N deficiency[3]	↓		↓	↓	↓		↑	↓	↓	
NH_4^+										
Ricinus[4]	↑		↑	↑	↑		↑	↑	↑ (×3)	↑
Zea mays[5]	↑		↑	↑	↑(×2)					
P deficiency[2]	↑		↔	↑	↑		↑ (×3)	↓	↔	↔
K deficiency[6]	↑ (×4)		↔	↑	↑ (×5)		↑	↔	↑ (×3)	↑
Tetcyclacis[5]	↑ (×9)		↑ (×2)		↑ (×4)		↑ (×7)	↔	↔	↓
Ethephon[7]	↑ (×1.5)		↓		↑ (×2.4)	↑ (in sheath)	↑ (in laminae)	↓	↑ (×2)	↑ (×4)
Variovorax paradoxus[7]	↓		↑ (×3)		↓		↔	↓	↓	↓
Bacillus subtilis[8]	↔			↑	↑			↑		
Parasitizing *Rhinanthus*[9]	↑ (×l6)	↔	↑	↑	↑		↑	↑	↑	↑

[a] References: [1] Wolf *et al*., 1990; [2] Jeschke *et al*., 1997; [3,4] Peuke *et al*., 1994; [5] F Jiang, unpublished results 1; [6] Peuke *et al*., 2002; [7] F Jiang *et al*., unpublished results 2; [8] Arkhipova *et al*., 2005; [9] Jiang *et al*., 2004.

newly formed ABA would then be loaded quickly to the xylem vessels without a significant deposition in the root tissues, a situation that resembles that of phosphorus- and potassium-deficient castor bean plants (see above).

Another widespread rhizobacterium is *Variovorax paradoxus* which contains ACC-deaminase. *Variovorax* is believed to degrade the precursor of ethylene, ACC (aminocyclopropane-carboxylic acid) resulting in strongly reduced ethylene formation in roots (Penrose and Glick, 2001). Ethylene, on the other hand, has repeatedly been shown to induce ABA biosynthesis (Grossmann and Hansen, 2001; Chiwocha *et al*., 2005). Indeed, the ethylene generator ethephon increases long-distance ABA signalling in the xylem and ABA formation in the roots (Table 1). Plants treated with *Variovorax* showed a tendency of slightly lower ABA synthesis in roots and xylem transport and a clearly reduced ABA transport of ABA in the phloem back to the roots (Table 1; F Jiang *et al*., unpublished results). Auxin-producing rhizobacteria should also be able to affect ABA flows. Since IAA is known to induce the biosynthesis of ethylene, again an impact of auxin-producing rhizobacteria on ABA production and flows may be expected (Fig. 3). Additionally, microorganisms that are able to degrade ABA in the rhizosphere should be able to influence ABA flows. Indeed, several bacterial colonies that use ABA as a carbon source have been isolated successfully (W Hartung and F Jiang, unpublished results). Whether it is possible for such soil micro-organisms to influence ABA signalling in plants remains to be shown.

Lateral transport of ABA

As shown above, root-synthesized ABA of phosphate- and potassium-deficient castor bean plants can be loaded very effectively to the xylem without a significant deposition in the roots. One explanation is an effective lateral transport under transpiring conditions with an apoplastic bypass flow of ABA directly into the xylem vessels. When an apoplastic bypass flow exists, solutes in the xylem are not diluted when lateral water flow is increased under transpiring conditions. For maize it has been shown that ABA can be transported with the water directly into the xylem. Freundl *et al*. (1998) have determined the apparent reflection coefficient σ for ABA in maize and sunflower roots. When σ is 1, all ABA molecules are reflected at the endodermis. They are then forced to enter the symplast. Increased lateral water flows would then dilute ABA_{xyl}. In the case of maize (Fig. 4), σ is always less than 1, showing that ABA can be dragged directly to the xylem. It is concluded that the chemical composition of the Casparian bands is important for σ. External conditions may have an impact on their chemical composition (Hose *et al*., 2001) and it is therefore concluded that the chemical properties of the Casparian bands in the endodermis allow an apoplastic bypass flow, a high ABA_{xyl}, and a small deposition in the roots (Freundl *et al*., 1998).

Except for Fabaceae, the roots of nearly all plants form Casparian bands in the hypodermis (=exodermis), especially when growing in well-aerated soil. By contrast to the Casparian bands of the endodermis, those of the

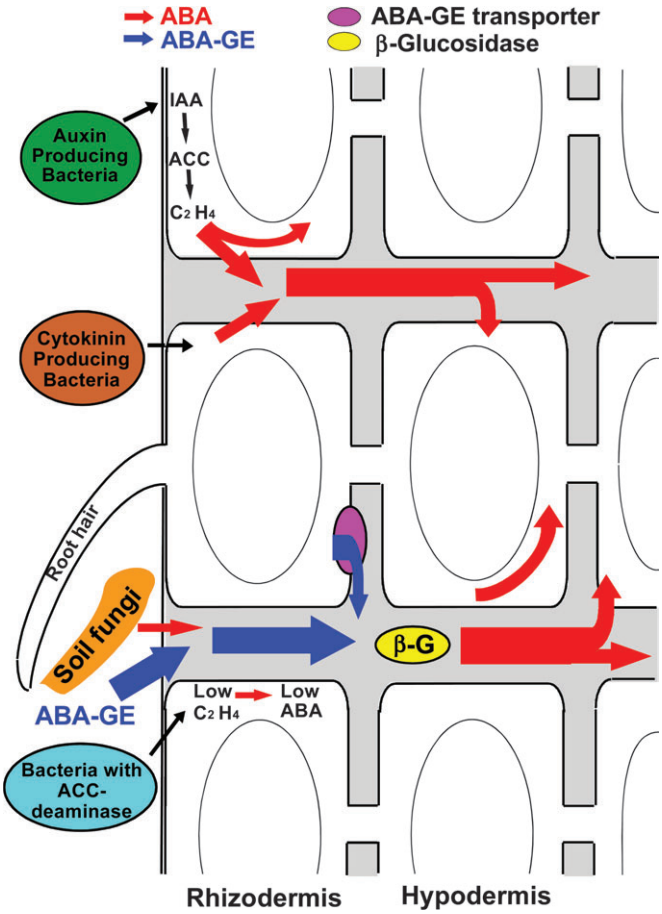

Fig. 3. Schematic presentation of the origin and the flows of ABA (red arrows) and ABA-GE (blue arrows) in the root cortex. A possible role of auxin (IAA) and cytokinin-producing rhizobacteria (Arkhipova *et al*., 2005), and of bacteria exhibiting 1-aminocyclopropane-1-carboxylate deaminase (ACC-deaminase; Belimov *et al*., 2007) is shown. Soil fungi produce and release large amounts of ABA (for references see Frankenberger and Arshad, 1995). The width of the arrows symbolizes the intensity of the flows. Arrows originating in the cytosol symbolize the cytosolic ABA biosynthesis in the root cortex.

exodermis are much more effective apoplastic barriers for ABA, preventing ABA loss to the soil solution, especially under non-transpiring conditions (Hose *et al*., 2001). The role of the exodermis is illustrated in Fig. 5.

Abscisic acid glucose ester as a long-distance hormonal signal

Sauter and Hartung (2000) and Sauter *et al*. (2002) have shown that the glucose ester of ABA (ABA-GE) also occurs in the soil solution, often in higher concentrations than ABA. The Casparian bands of the exodermis and endodermis are perfect barriers for ABA-GE. When an exodermis is absent (Fabaceae and plants cultivated hydroponically), external ABA-GE is dragged into the apoplast of the root cortex, apoplastic β-glucosidases can cleave the conjugate and release free ABA, which can be

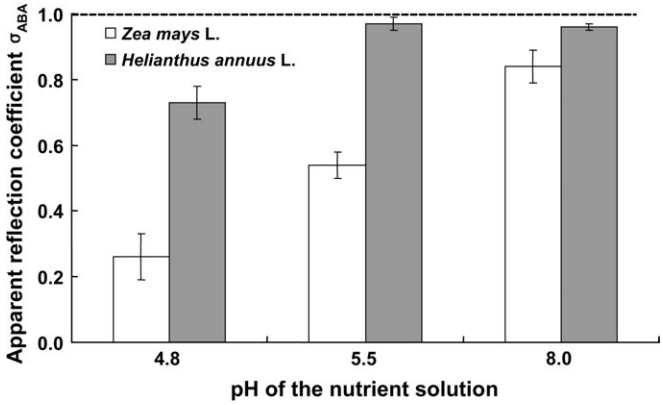

Fig. 4. Apparent reflection coefficent of abscisic acid (σ_{ABA}) for young root systems of maize and sunflower. Water flow was induced by the application of a pressure difference of 0.06 MPa to the cut surface of decapitated plants. ABA concentration of the nutrient solution was 100 nM. [After Freundl *et al*. (1998); for a more detailed explanation see this publication.]

redistributed to the symplast and/or dragged across the endodermis into the xylem (Hartung *et al*., 2002) (Fig. 3). Release of ABA-GE that has been synthesized in the cytoplasm of the cortex cells across the plasma membrane of xylem parenchyma cells into the xylem is a rate-limiting process because of the extremely low permeability of plant plasma membranes (Baier *et al*., 1990). Here the action of an ABA-GE transporter is postulated that releases substantial amounts of the ABA conjugate to the xylem, especially under stress conditions (Fig. 6).

ABA-GE is a perfect long-distance signal

When 10–15-cm-long bean internodes or etiolated maize mesocotyls were perfused with ABA in a concentration typical of stressed plants, ABA was redistributed to the stem tissue and ABA of the surrounding stem tissue was released to the xylem when ABA_{xyl} was low (Sauter and Hartung, 2002). This redistribution was quite rapid (10–20 min) pointing to a high permeability coefficient of the plasma membranes of the surrounding stem parenchyma cells for ABA (Hartung *et al*., 2002). ABA_{xyl} consequently does not remain constant during its transport. Especially under unstressed conditions, when the xylem sap is acid (with a high portion of the easily permeating undissociated species ABAH), substantial amounts of ABA could be lost during transport through the xylem over a longer distance. It has also been shown (Sauter and Hartung, 2002) that ABA can be fed into the xylem when it is high in the stem parenchyma and when xylem sap pH is increased. The concentration of $ABA\text{-}GE_{xyl}$, however, remains unchanged, also over long distances under all conditions, because of the extremely low permeability of biomembranes for this conjugate (Sauter and Hartung, 2002). Over long distances, ABA-GE is the best candidate for a hormonal stress signal (Fig. 6).

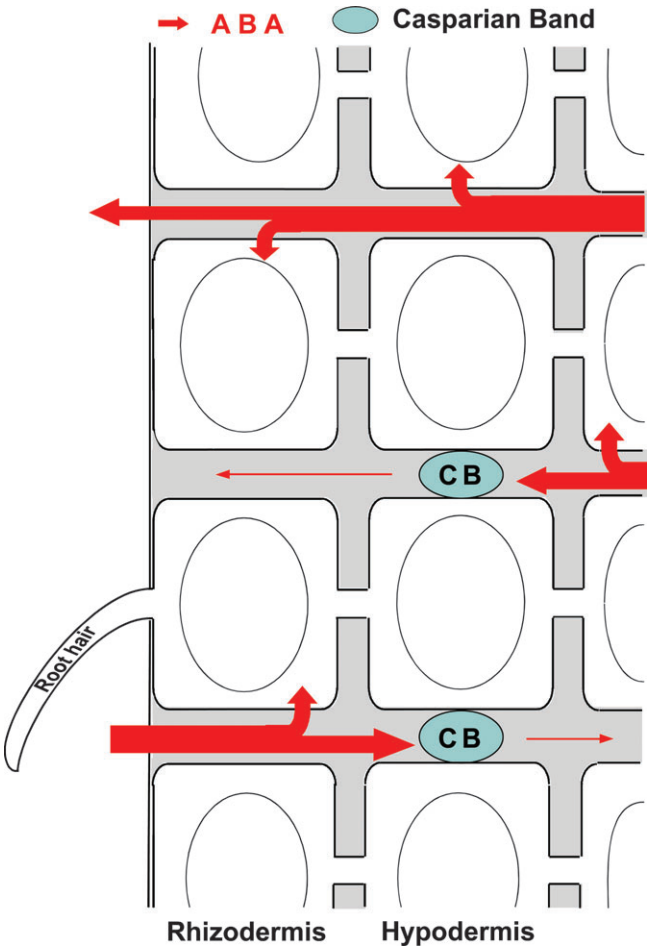

Fig. 5. The impact of Casparian bands (CBs) in the hypodermis of roots on apoplastic ABA transport. CBs strongly reduce ABA exudation under non-transpiring conditions (middle row of cells) and cause an accumulation in the apoplast of the cortex and force the uptake into the symplast (especially under transpiring conditions; bottom). The absence of CBs allows ABA exudation to the rhizosphere, predominantly under non-transpiring conditions. The widths of the red arrows symbolize the intensity of the ABA flows.

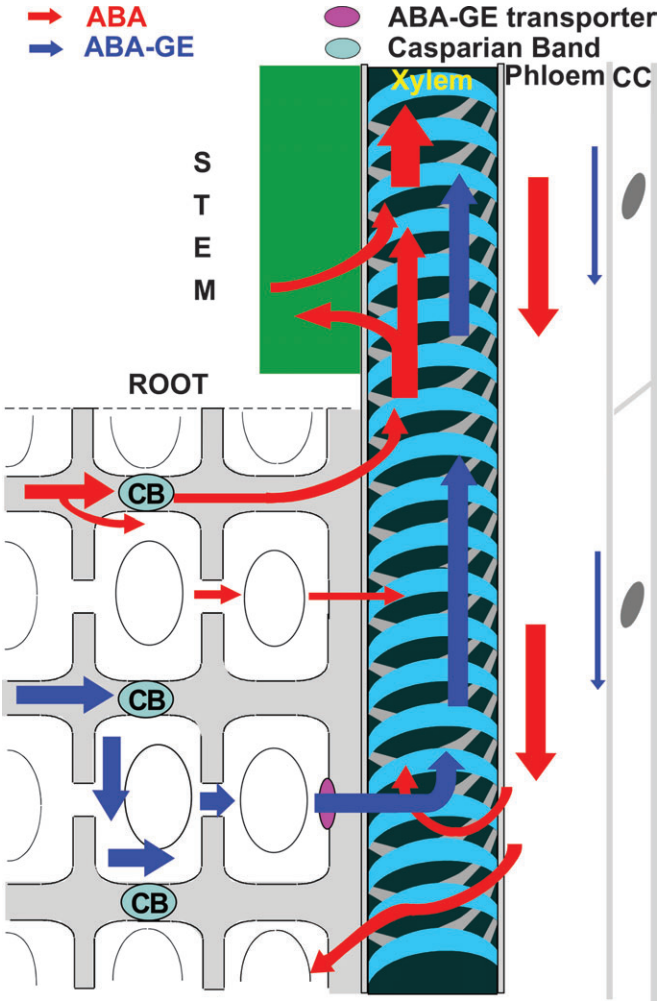

Fig. 6. Schematic presentation of ABA and ABA-GE flows from the root cortex into the xylem of the vascular system of the stem. ABA passes the Casparian bands (CBs) of the endodermis in significant quantities. Only a small amount is diverted into the cortex symplast. For apoplastic ABA-GE (originating from external sources) the CBs are perfect barriers. Release of ABA-GE, synthesized in the cytosol of cortical cells, requires a transporter. With ABA-GE, signal transport in the xylem without loss to the surrounding living cells is possible. The recirculation of ABA from the phloem vessels to the xylem is also illustrated. The width of the arrows represents the intensity of the flows of ABA and ABA-GE.

The fate of free and conjugated ABA in the leaf

ABA biosynthesis is increased significantly in leaves only when turgor approaches zero. Stomatal closure, however, is already observed when Ψ_{leaf} is still unaffected as the soil starts drying. Under such mild stress conditions, import of ABA delivered from the xylem is necessary. This ABA is not necessarily accumulated in the leaf. After having acted on the stomata it can be rapidly metabolized without being deposited. This has been observed earlier for phosphorus- and potassium-deficient castor bean plants (Jeschke *et al*., 1997; Peuke *et al*., 2002).

Redistribution within the leaf can lower ABA_{xyl}, especially when the xylem sap is acid. Then ABA may redistribute to the cytoplasm of the mesophyll cells according to the anion trap concept (Slovik *et al*., 1995). Such a redistribution is prevented when, as described by Wilkinson (Wilkinson, 1999; Davies *et al*., 2002), the apoplast is alkalized under stress. Thus redistribution of ABA is strongly reduced and the intensity of the ABA signal remains high. Release of ABA to the apoplast has also been shown (Hartung *et al*., 1988) (Fig. 7).

Sauter *et al*. (2002) pointed out that ABA-GE, which is physiologically inactive, can act as a signal only when it is cleaved in the leaf apoplast and when the released physiologically active free ABA can reach the target cells. They have also shown that an apoplastic β-glucosidase (β-G) specific to the substrate ABA-GE exists and that the activity of this enzyme is increased 7-fold under salt stress in barley leaves (Dietz *et al*., 2000).

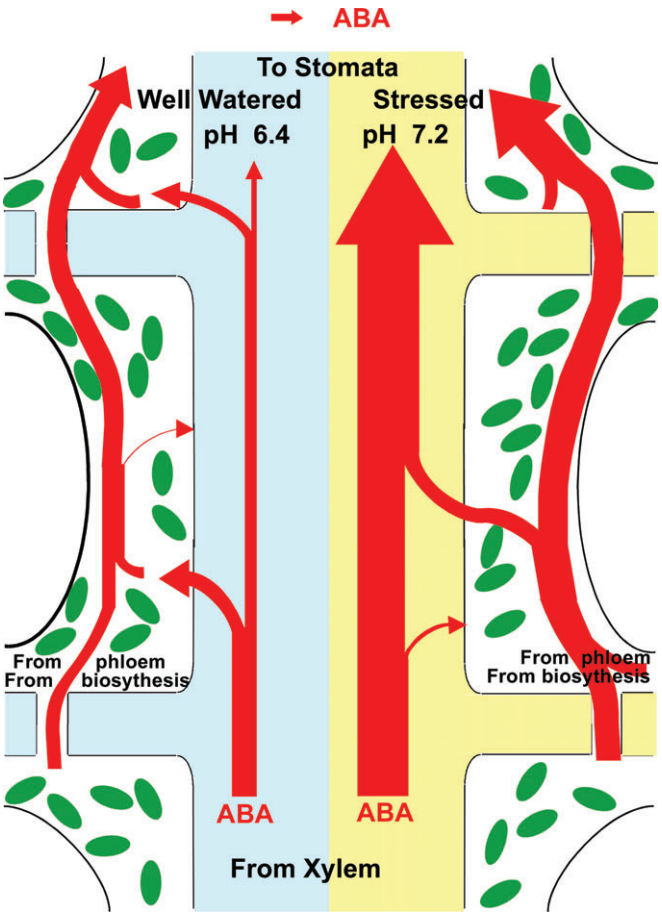

Fig. 7. Schematic presentation of the origin and the flows of ABA within a well-watered (left half) and stressed (right half) plant leaf. The impact of apoplastic pH for ABA redistribution between mesophyll cells and xylem is shown. The width of the arrows represents the intensity of the ABA flows.

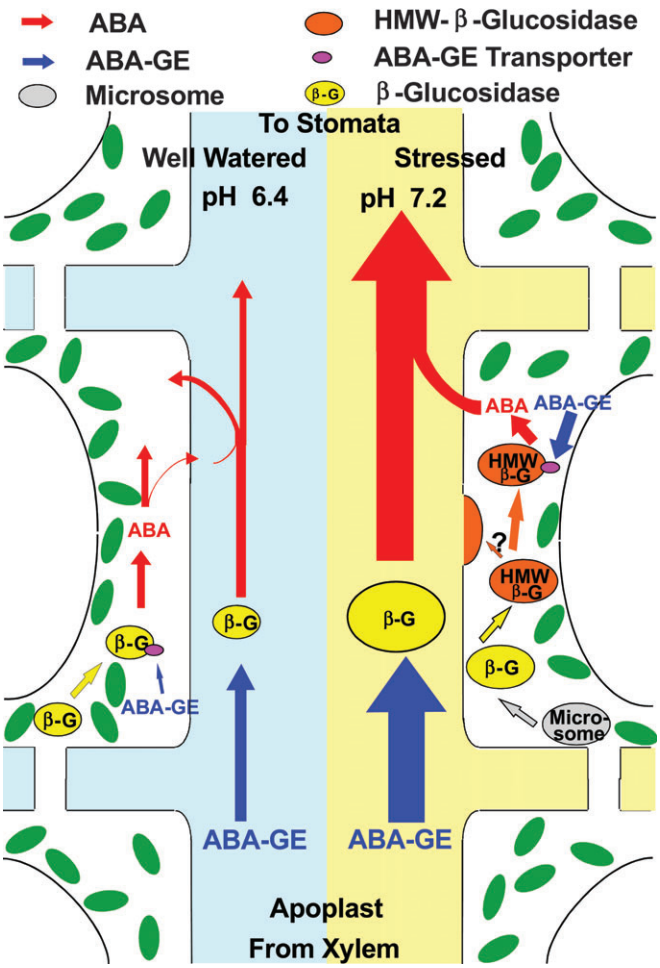

Fig. 8. A diagram illustrating the origin and flows of ABA-GE in a well-watered (left half) and a stressed (right half) plant leaf. β-G, β-Glucosidase; HMW-β-G, high molecular weight β-G. The width of the arrows (ABA-GE, blue; ABA, red) symbolizes the intensity of the flows of the hormonal signals.

Recently, Lee *et al*. (2006) have shown that *Arabidopsis* plants, deficient in β-G, exhibit lower ABA levels in leaves and produce stress-sensitive phenotypes. Dehydration caused rapid polymerization of β-G in microsomes of wild-type *Arabidopsis* leaves with a four times higher activity than in unstressed controls. ABA-GE was cleaved with much higher rates and ABA could be released from the microsomes to the cytosol. Further release to the apoplast would be facilitated because of flattened pH gradients across the mesophyll plasma membrane and thus intensify the ABA signal. Similar to the plasma membrane of xylem parenchyma cells, the action of an ABA-GE transporter again has to be postulated to load the microsomes with ABA-GE. Transport of vesicles loaded with the high-molecular-weight β-G to the plasma membrane of mesophyll and subsequent release to the apoplast cannot be excluded. Additionally, it could contribute to increased β-G activity in the apoplast (Fig. 8). The latter step, however, is hypothetical. Here more research is required. ABA and ABA-GE, both from the roots and the leaves, act harmoniously together to create and intensify an effective and specific stress signal for plants growing in drying soils.

Conclusion

The intensity of the root to shoot ABA signal is regulated on four different anatomical levels: (i) the rhizosphere, (ii) the root cortex, (iii) the stem, and (iv) the leaves. Accordingly four processes have to be considered: (i) interactions between growth-promoting rhizobacteria and the root; (ii) anatomical features of the root cortex (Casparian bands); (iii) apoplastic pH values in the stem and the leaf; and (iv) the action of apoplastic and cytosolic β-glucosidases in the leaves. The conjugate ABA-GE is a perfect long-distance signal because it is translocated without loss to the surrounding tissues. Virgin areas of research are predominantly the impact of soil conditions and rhizospheric micro-organisms on ABA signalling and the physiology and biochemistry of transporters that allow

the passage of ABA-GE across biomembranes into the apoplast or microsomes.

Acknowledgement

The work reviewed above was possible because of the generous financial support of Deutsche Forschungsgemeinschaft.

References

Arkhipova TN, Veselov SU, Melentiev AI, Martynenko EV, Kudoyarova GR. 2005. Ability of bacterium *Bacillis subtilis* to produce cytokinins and to influence the growth and endogenous hormone content of lettuce plants. *Plant and Soil* **272,** 201–209.

Baier M, Gimmler H, Hartung W. 1990. Permeability of the guard cell plasma-membrane and tonoplast. *Journal of Experimental Botany* **41,** 351–358.

Belimov AA, Dodd IC, Safranova VI, Hontzeas N, Davies WJ. 2007. *Pseudomonas brassicacarum* strain AM3 containing 1-aminocyclopropane-1-carboxylate deaminase can show both pathogenic and growth-promoting properties in its interaction with tomato. *Journal of Experimental Botany* **58,** 1485–1495.

Chiwocha SDS, Cutler AJ, Abrams SR, Ambrose SJ, Yang J, Ross ARS, Kermode AR. 2005. The *etr1-2* mutation in *Arabidopsis thaliana* affects the abscisic acid, auxin, cytokinin and gibberellin metabolic pathways during maintainance of seed dormancy, moist-chilling and germination. *The Plant Journal* **42,** 35–48.

Davies WJ, Kudoyarova G, Hartung W. 2005. Long-distance ABA signalling and its relation to other signalling pathways in the detection of soil drying and the mediation of the plant's response to drought. *Journal of Plant Growth Regulation* **24,** 285–295.

Davies WJ, Wilkinson S, Loveys B. 2002. Stomatal control by chemical signalling and the exploitation of this mechanism to increase the water use efficiency in agriculture. *New Phytologist* **153,** 449–460.

Dietz KJ, Sauter A, Wichert K, Messdaghi D, Hartung W. 2000. Extracellular β-glucosidase activity in barley involved in the hydrolysis of ABA glucose conjugate in leaves. *Journal of Experimental Botany* **51,** 937–944.

Dodd IC, Theobald JC, Bacon MA, Davies WJ. 2006. Alternation of wet and dry sides during partial rootzone drying irrigation alters root to shoot signalling of ABA. *Functional Plant Biology* **33,** 1081–1089.

Frankenberger WT, Arshad M. 1995. *Phytohormones in soils*. New York, NY: Marcel Dekker.

Freundl E, Steudle E, Hartung W. 1998. Water uptake by roots of maize and sunflower affects the radial transport of abscisic acid and the ABA concentration in the xylem. *Planta* **207,** 8–19.

Grossmann K, Hansen H. 2001. Ethylene triggered abscisic acid: a principle in plant growth regulation? *Physiologia Plantarum* **113,** 9–14.

Hartung W, Radin JW, Hendrix DL. 1988. Abscisic acid movement into the apoplastic solution of water-stressed cotton leaves: role of apoplastic pH. *Plant Physiology* **86,** 908–913.

Hartung W, Ratcliffe RG. 2002. The utilization of glycine and serine as nitrogen sources in roots of *Zea mays* and *Chamaegigas intrepidus*. *Journal of Experimental Botany* **53,** 2305–2314.

Hartung W, Sauter A, Hose E. 2002. Abscisic acid in the xylem: where does it come from, where does it go to? *Journal of Experimental Botany* **53,** 27–33.

Heilmeier H, Schulze ED, Jiang F, Hartung W. 2007. General relations of stomatal responses to xylem sap abscisic acid under stress in the rooting zone: a global perspective. *Flora* **202,** (in press).

Hose E, Clarkson DT, Steudle E, Schreiber L, Hartung W. 2001. The exodermis: a variable apoplastic barrier. *Journal of Experimental Botany* **52,** 2245–2254.

Jeschke WD, Klagges S, Hilpert A, Bhatti AS, Sarwar G. 1995. Partitioning and flows of ions and nutrients in salt-treated plants of *Leptochloa fusca* L. Kunth. I. Cations and chloride. *New Phytologist* **130,** 23–35.

Jeschke WD, Peuke AD, Pate JS, Hartung W. 1997. Transport, synthesis, and catabolism of abscisic acid (ABA) in intact plants of castor bean (*Ricinus communis* L.) under phosphate deficiency and moderate salinity. *Journal of Experimental Botany* **48,** 1737–1747.

Jiang F, Jeschke WD, Hartung W. 2004. Abscisic acid (ABA) flows from *Hordeum vulgare* to the hemiparasite *Rhinanthus minor* and the influence of infection on host and parasite abscisic acid relations. *Journal of Experimental Botany* **55,** 2323–2329.

Lee KH, Piao HL, Kim HY, Choi SM, Jiang F, Hartung W, Hwang Ildoo, Kwak JM, Lee IJ, Hwang Inhwan. 2006. Activation of glucosidase via stress-induced polymerization rapidly increases active pools of abscisic acid. *Cell* **126,** 1109–1120.

Loveys BR. 1984. Diurnal changes in water relations and abscisic acid in field-grown *Vitis vinifera* cultivars. III. The influence of xylem-derived abscisic acid on leaf gas exchange. *New Phytologist* **98,** 563–573.

Penrose DM, Glick BR. 2001. Levels of ACC and related compounds in exudates and extracts of canola seeds treated with ACC-deaminase-containing plant growth promoting bacteria. *Canadian Journal of Micobiology* **47,** 368–372.

Peuke AD, Jeschke WD, Hartung W. 1994. The uptake and flow of C, N and ions between roots and shoots in *Ricinus communis* L. III. Long-distance transport of abscisic acid depending on nitrogen nutrition and salt stress. *Journal of Experimental Botany* **45,** 741–747.

Peuke AD, Jeschke WD, Hartung W. 2002. Flows of elements, ions and abscisic acid in *Ricinus communis* under potassium limitation. *Journal of Experimental Botany* **53,** 241–250.

Sauter A, Dietz KJ, Hartung W. 2002. A possible stress physiological role of abscisic acid conjugates in root to shoot signalling. *Plant, Cell and Environment* **25,** 223–228.

Sauter A, Hartung W. 2000. Radial transport of abscisic acid conjugates in maize roots and its implication for long-distance stress signals. *Journal of Experimental Botany* **51,** 929–935.

Sauter A, Hartung W. 2002. The contribution of internode and mesocotyl tissues to root-to-shoot signalling of abscisic acid. *Journal of Experimental Botany* **53,** 297–302.

Slovik S, Daeter W, Hartung W. 1995. Compartmental distribution and redistribution of abscisic acid (ABA) in roots as influenced by environmental changes: a biomathematical model. *Journal of Experimental Botany* **46,** 881–894.

Stoll M, Loveys B, Dry P. 2000. Hormonal changes induced by partial rootzone drying of irrigated grapevine. *Journal of Experimental Botany* **51,** 1627–1634.

Wartinger A, Heilmeier H, Hartung W, Schulze ED. 1990. Daily and seasonal courses of leaf conductance and abscisic acid in the xylem sap of almond trees [*Prunus dulcis* (Miller) D.A.Webb] under desert conditions. *New Phytologist* **116,** 581–587.

Wilkinson S. 1999. pH as a stress signal. *Plant Growth Regulation* **29,** 87–99.

Wolf O, Jeschke WD, Hartung W. 1990. Long-distance transport of abscisic acid in salt-stressed *Lupinus albus* plants. *Journal of Experimental Botany* **41,** 593–600.

Zhang J, Davies WJ. 1990. Changes of ABA in xylem sap as a function of changing water status can account for changes in leaf conductance and growth. *Plant, Cell and Environment* **13,** 277–285.