

The evolution of abscisic acid (ABA) and ABA function in lower plants, fungi and lichen

Wolfram Hartung

Lehrstuhl Botanik I, der Universität Würzburg, Julius von Sachsplatz 2, D 97082 Würzburg, Germany.

Email: hartung@botanik.uni-wuerzburg.de

This paper is part of an ongoing series: 'The Evolution of Plant Functions'.

Abstract. Abscisic acid (ABA) – the universal stress hormone of cormophytes – was detected in very low concentrations in almost all organisms tested from a range of cyanobacteria, algae, bryophytes, fungi and lichens and higher plants (Fig. 1). There are a few reports only on stress-induced ABA biosynthesis in cyanobacteria and algae. This extra ABA is released to the external medium. Application of external ABA has been shown to produce weak and contradicting effects on development and metabolism of algae. In most studies, extremely high concentrations of external ABA have been applied, those being far beyond any physiological concentration range. It is, therefore, extremely difficult to discuss those data satisfactorily. When organisms start to colonise terrestrial habitats (e.g. aquatic liverworts, mosses), endogenous ABA is increased even under mild drought stress, then desiccation protecting mechanisms are stimulated and the formation of terrestrial organs is induced. The same can be observed in water ferns (*Marsilea*) and in a range of heterophyllous angiosperms. Sporophytes of hornwort and mosses that bear true stomata, have particularly high ABA levels and their stomata respond to ABA as is the case in cormophytes, although a significant regulatory function of these stomata does not exist. Fungi produce large amounts of ABA that are released into the external medium and do not seem to have a function for the fungus. Fungal ABA, however, may be significant in associations of fungi with cyanophytes and algae (lichens), in mycorrhizal associations and in the rhizosphere of higher plants.

Additional keywords: algae, bacteria, cyanophytes, desiccation, landform, rhizosphere, soil, stomata, stress.

Introduction

In 1880, Charles Darwin postulated that endogenous substances of plants ('matter') were formed in the tips of the coleoptiles of *Phalaris canariensis* in response to external influences and were then transported to a target tissue where they induce tropistic movements¹ (Darwin 1880). From this, research into one of the most exciting fields of botanical sciences – the physiology of plant hormones – was initiated. Starting from Darwin's 'matter', the five classical groups of phytohormones, auxins, gibberellins, cytokinins, abscisic acid and ethylene have been detected and investigated. Later on abscisic acid was shown to be such a 'matter' in tropistic movements of root tips.

Darwin was not greatly interested in stress effects on plants, or in external stresses that disturb the water balance of plants, otherwise he may have also postulated the existence of a stress hormone. In cormophytes, the phytohormone abscisic acid has been proved to be the universal stress hormone, with a stress dependent biosynthesis, transport to target cells (predominantly stomata) and an action that enables the plant to cope better with the stress situation (e.g. reduction of water loss,

induction of desiccation tolerance). Such can be seen in the relevant chapter in any textbook of botany and plant sciences.

In lower plants and prokaryotes the situation is more complex and contradictory. Although ABA and ABA-like substances, detected by bioassays, have been found since the late 1960s in cyanophytes and algae, no clear physiological functions of ABA could be demonstrated. Without a function, however, such substances only can be regarded as marginal compounds of the secondary metabolism without any significance for the development and metabolism in the organism.

In the following, I intend to show the evolution of ABA from a compound of secondary metabolism without a physiological function to a true stress hormone, the biosynthesis of which is stimulated under stress with beneficial effect on the organism, which enables it to survive the stress situation.

ABA in bacteria

Until recently it was well accepted that bacteria do not synthesise ABA. Hirsch *et al.* (1989) and Müller *et al.* (1989) investigated 22 bacteria species, many of them soil bacteria, including *Azospirillum brasiliense*, using extremely sensitive

¹The results seem to imply the presence of 'some matter' in the upper part which is acted on by light and which transmits its effect to the lower part.

immunological methods. They could not find ABA. Recently, however, Forchetti *et al.* (2007) detected ABA in isolated strains of endophytic bacteria in roots of *Helianthus annuus* and Cohen *et al.* (2009) found ABA in *Azospirillum brasilense*. When the rhizosphere of *Zea mays* was enriched with this bacterium, ABA was taken up by the roots and contributed there to an increased ABA.

Nothing is known about the biochemistry of ABA (biosynthesis and metabolism) or about a possible function of ABA for bacteria. The situation for bacteria is entirely unclear – considerable research is required in this field.

ABA in cyanobacteria

ABA was detected in 11 species of cyanobacteria (Hirsch *et al.* 1989; Zahradnickova *et al.* 1991; Marsalek *et al.* 1992a; Manickavelu *et al.* 2006). Four of them showed an increase of ABA biosynthesis under salt stress. (*Trichormis variabilis*; Zahradnickova *et al.* 1991; *Nostoc muscorum*, *Synechococcus leopoliensis*; Marsalek *et al.* 1992a; and *Plectonema* sp. from paddy fields, Manickavelu *et al.* 2006). In all these cases the extra ABA was released into the external medium, consequently, we do not have to expect significant stress-dependent increases of internal ABA.

A physiological role remains obscure. In response to external ABA application, Ahmad *et al.* (1978) observed an ABA induced growth of *Anacystis nidulans*, Huang (1991) a reduction of plasmamembrane permeability and Marsalek *et al.* a stimulation of nitrogenase activity (Marsalek and Simek 1992; *Trichormis variabilis*; Marsalek *et al.* 1992c; *Nostoc muscorum*; Simek and Marsalek 1992, 1993; *Trichormis variabilis*). In all cases, very high concentrations ($>10^{-4}$ M) have been applied: concentrations that are well above physiological concentration ranges.

ABA in algae

Until now ~100 species of algae have been tested for ABA, 96% of which contained ABA (e.g. Hirsch *et al.* 1989; Jameson 1993; Hartung and Gimmler 1994).

The studies included the following algal divisions: Rhodophyta, Heterokontophyta, Haptophyta, Cryptophyta, Dinophyta, Euglenophyta, Chlorophyta and Streptophyta (Fig. 1). The the rare cases in which ABA could not be detected, the negative result is likely due to insufficiencies in the analytical methods applied (*Enteromorpha compressa*, Niemann and Dörffling 1980; *Caulerpa paspaloides*, Jacobs 1985; *Fritschiella tuberosa*, Tietz and Kasprk 1986; *Porphyra*, Zhang *et al.* 1993). For positive reports on ABA in Rhodophyta, including *Porphyra*, see Hirsch *et al.* (1989) and Yokoya *et al.* (2009) (12 Brazilian species).

ABA contents in algal cells vary between 7 and 34 nmol ABA kg⁻¹ FW. These numbers are similar as those of liverwort growing under water (Hartung and Gimmler 1994) but significantly lower than those of unstressed terrestrial plants.

Only limited data are available about stress effects on algal ABA concentrations. Mostly salt stress has been applied to *Dunaliella* species (Hirsch *et al.* 1989; Cowan and Rose 1991; Cowan *et al.* 1992) and *Chlorella vulgaris* (Marsalek *et al.* 1992b). In all cases, salt stress increased ABA formation.

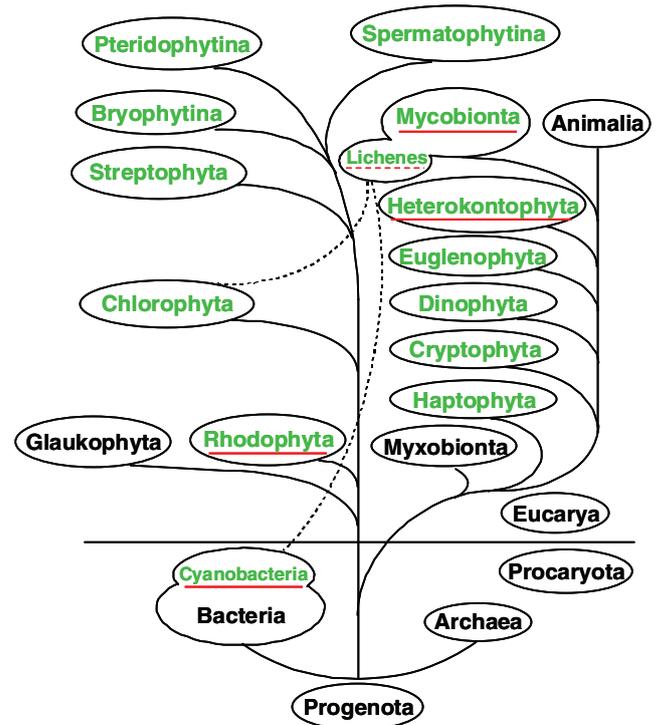


Fig. 1. Phylogenetic tree of plants and fungi. Grey (green in the online version) letters show those organisms that biosynthesise abscisic acid. For bacteria there are very few contradicting data; for the other organisms (black letters) no published data are available. The few reports on ABA in animals are not discussed in this review. Underlining (red in the online version) indicates that ABA is synthesised directly via farnesyl-diphosphate (see Fig. 2). In lichens, part of the ABA also may be formed from 9'-cis-neoxanthin in the algal partner. Adapted and modified after Bresinski and Kadereit (2002).

ABA production was stimulated by nitrogen deficiency in *Dunaliella* sp. (Tominaga *et al.* 1993), heat stress in *Chlorella vulgaris* (Bajguz 2009) drought and acid stress in *Stichococcus bacillaris* and *Chlorella vulgaris* (Marsalek *et al.* 1992b), oxidative stress in *Haematococcus pluvialis* (Kobayashi *et al.* 1997, 1998), light stress in *Chlorella minutissima* (Stirk *et al.* 2005) and alkaline shock in *Dunaliella acidophila* (Hirsch *et al.* 1989). Compared with cormophytes (10–20-fold increase), the stress-dependent increase of ABA biosynthesis of cyanophytes and algae is much weaker (2–5-fold increase). In all cases, stress ABA appears to be released across the plasmamembrane to the surrounding medium and often it has been analysed only there. Because of the strong stress-dependent ABA efflux, cellular ABA may not be increased significantly. An effect of ABA that has been released from the algae to the surrounding media on aquatic organisms in the neighbourhood, as suggested by Hussain and Boney (1973), seems to be extremely unlikely, since it is extremely diluted.

A stress physiological function may exist in aerial terrestrial algae, such as *Trentepohlia*, *Apatococcus* and *Desmococcus*, especially with respect to drought stress. However, such investigations are absent.

ABA biosynthesis and metabolism in algae

Bopp-Buhler *et al.* (1991) and Cowan and Rose (1991) have observed incorporation of mevalonolactone into ABA of *Dunaliella parva*. This incorporation was increased by salt stress. They have also performed inhibitor experiments with fluridone, norflurazon and AMO 1618; compounds that clearly inhibit the formation of those carotenoids that are believed to be important precursors of ABA. From a relatively weak reduction of ABA biosynthesis, these authors conclude that at least a significant part of ABA is not formed from carotenoids.

In contrast, 9'-*cis*-neoxanthin, a suitable substrate for ABA synthesis, was found in green algae that contain chlorophyll *a* and *b*. It was not found in other algal divisions such as Heterokontophyta, Rhodophyta and photoautotrophic prokaryotes. However, all these organisms form ABA. Therefore, different from cormophytes, the latter may synthesise ABA on the direct pathway via farnesyl-diphosphate (Figs 1, 2).

ABA effects on algae

There have been several attempts to elucidate the physiological function of ABA in algae by treatment of the cells with external ABA. Most of these experiments have been performed in a situation of extremely poor knowledge of the physiology of ABA in algae (e.g. occurrence, internal concentration, uptake and metabolism, permeabilities of membranes for ABA). Further, in most cases, extremely high external ABA concentration have been applied; these greatly exceeding any physiological situation and, therefore, producing pharmacological effects of only

marginal significance. From this, contradicting data have been observed and they do not give a consistent picture (see reviews by Jameson 1993; Hartung and Gimmler 1994). For example, it has been shown that permeability of membranes to different solutes was either stimulated (Chara, Wanless *et al.* 1973; Ord *et al.* 1977) or reduced (*Dunaliella*, Hirsch *et al.* 1989). Ion uptake was stimulated (Wanless *et al.* 1973, Na⁺, K⁺, Cl⁻; Ullrich and Kunz 1984, nitrate) and inhibited, respectively (Hirsch *et al.* 1989, K⁺). Photosynthesis was not affected in most cases. Concerning respiration, Ullrich and Kunz (1984) observed stimulation, Huang (1991), however, inhibition.

Algal differentiation has been shown to be affected (gametogenesis in *Chlamydomonas*, Ishiura 1976; abscission of oospores in *Chara*, Vanden Driessche *et al.* 1997). ABA promotes growth in the cyanobacteria *Nostoc* and *Anacystis*, (Ahmad *et al.* 1978) and inhibits growth in *Coscinodiscus* (Kentzer and Mazur 1991). Hirsch *et al.* (1989) speculated that within algae, a positive correlation may exist between ABA content and the organisation level.

Tanaka *et al.* (2004) have shown that halotolerant *Chlamydomonas* strains express LEA genes (designated *cw80 Lea3*), which could be induced by salt and cold stresses, but not by ABA. This indicates that although ABA is present and may be stimulated under stress, a clear physiological function (e.g. in gene expression regulation) could not be established until now.

Recently it has been suggested several times that ABA may protect algal cells against photoinhibition in *Chlamydomonas reinhardtii* (Saradhi *et al.* 2000). Yoshida (2005) and Yoshida *et al.* (2003, 2004) found, in the same species, a protective effect of ABA against oxidative damage caused by salt and osmotic stress. Catalase and ascorbate peroxidase activities were shown to be significantly higher in ABA treated cells (Yoshida *et al.* 2003). Kobayashi *et al.* (1997, 1998) suggest that ABA protects *Haematococcus pluvialis* against oxidative stress. ABA may be important in mitigation of oxidative damage in stressed algae. Again, more research is required in this field.

ABA in bryophytes

ABA has been detected in Hepaticae, especially in the Marchantiopsida (Hartung and Gimmler 1994), in a few species of Anthocerotopsida (Hartung *et al.* 1987) and in a few mosses (Ergün *et al.* 2002, nine moss species) including the gametophytes of *Funaria* (Werner *et al.* 1991). In the Marchantiopsida, a large variability could be observed, ranging from 30 nmol g⁻¹ FW in the extremely desiccation tolerant *Exormothea* species to 1–10 pmol g⁻¹ FW in the submerged living thallus of *Riccia fluitans* (Hartung and Gimmler 1994).

ABA biosynthesis and metabolism bryophytes

Very few, partly indirect, data are available regarding biosynthesis and metabolism of ABA. According to Takaichi and Mimuro (1998) the 9'-*cis*-neoxanthin is present in bryophytes, showing that an important precursor of the indirect biosynthetic pathway exists in bryophytes. Hellwege and Hartung (1997) detected phaseic acid, dihydrophaseic acid and the glucose ester of ABA in *Riccia fluitans*,

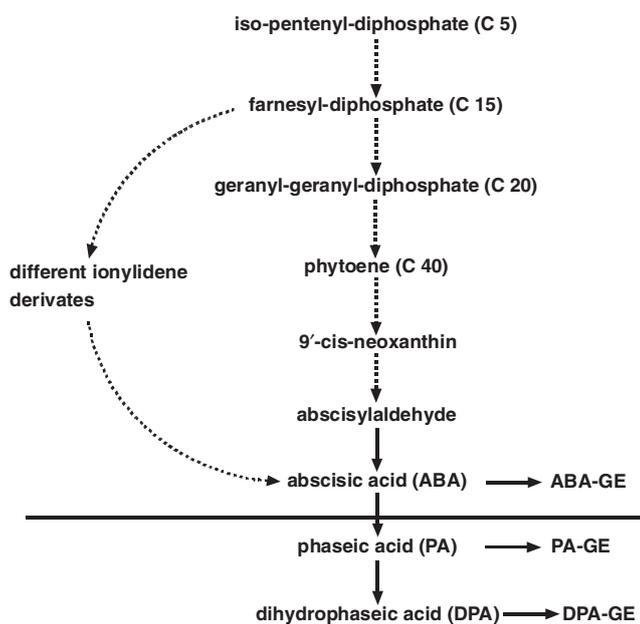


Fig. 2. A simplified diagram of the biosynthesis and degradation of abscisic acid. Fungi, cyanobacteria and algae that lack 9'-*cis*-neoxanthin form ABA directly via farnesyl-diphosphate and different ionylidene derivatives. When 9'-*cis*-neoxanthin is present a C-15-intermediate is released from 9'-*cis*-neoxanthin which is converted to abscisyl aldehyde and ABA. ABA is degraded to phaseic acid (PA) and dihydrophaseic acid (DPA). Glucose esters exist from ABA, PA and DPA (ABA-GE, PA-GE, DPA-GE).

suggesting that degradation of ABA occurs by similar reactions as known for cormophytes (Fig. 2).

ABA functions in bryophytes

The induction of land form characteristics

Some members of Marchantiopsida live submerged (*Riccia fluitans*) or on the surface of the water (*Ricciocarpus natans*) and experience developmental changes (e.g. increased lateral growth, formation of rhizoids and pores) when the thallus becomes terrestrial – as happens when a pond is drying out. During this period ABA increases 20–30-fold. Treatment of the submerged thallus with external ABA also induces the formation of landform characteristics, even when the thallus is forced to stay under water (Hellwege *et al.* 1992). This process is accompanied by changes of the pattern of proteins, including dehydrins and LEA proteins, which are believed to have an important function in the induction of desiccation tolerance (Hellwege *et al.* 1996). In submerged liverworts, ABA enables the organism to occupy the terrestrial environment. This resembles the induction of terrestrial leaves in the heterophyllous water fern (*Marsilea quadrifolia*, Lin *et al.* 2005) and angiosperms (*Proserpinaca intermedia*, Kane and Albert 1982; *Ranunculus flabellaris*, Young *et al.* 1987; *Potamogeton nodosus*, Gee and Anderson 1998; *Hippuris vulgaris*, Goliber 1989; *Ludwigia arcuata*, Kuwabara *et al.* 2003) that occurs under the control of ABA.

Other developmental changes induced by external ABA include inhibition of callus and protonema growth and gemmae formation (for references see Hartung and Gimmler 1994).

Desiccation tolerance

Those tissues of bryophytes (thallus of *Exormotheca* species, tubers of *Anthoceros dichotomus*) that have the highest endogenous ABA concentrations, also when fully hydrated, belong to those organisms or organs with the highest desiccation tolerance. ABA-treatment of mesophytic thalli of different species that are not desiccation tolerant (protonemata of *Funaria hygrometrica*, Olaf Werner *et al.* 1991; *Marchantia polymorpha*, *Riccia fluitans*, Hellwege *et al.* 1994, 1996; *Pallavicinia lyellii*, Pence *et al.* 2005) and of non-hardened thalli of *Exormotheca* (Hellwege *et al.* 1994) increases desiccation tolerance significantly.

Stoma-bearing bryophytes

The sporophyte of Anthocerotopsida bears highly differentiated stomata of the *Amaryllis* type, whereas gametophyte thallus is extremely primitive. Hartung *et al.* (1987) found particularly high ABA concentrations in the sporophyte, which could be further increased under stress. The stomata reacted normally to increases in ABA (closing) and to fusicoccin (opening). The physiological function of ABA-responding stomata in *Anthoceros* is unclear. They cannot have a function comparable to those of cormophytes, because the *Anthoceros*-sporophyte is a only few mm high with stomata that mostly do not have a substomatal intercellular space and that are not connected to a xylem like water transport system. Thus, a role in gas exchange and water transport can be only negligible.

Hence, a stress physiological system including stomata that respond to ABA was developed at very early stage of evolution of land plants.

Garner and Paolillo (1973) have shown that stomata of the sporogone of *Funaria* respond in a similar way to ABA.

ABA in fungi

Assante *et al.* (1977) showed that *Cercospora rosicola* produces large amounts of ABA. Since then ABA has been detected in many species of ascomycetes, fungi imperfecti and basidiomycetes. A review on phytohormones in fungi including ABA has been published by Tudzynski and Sharon (2002) including a list of ABA producing fungi.

The fungal biosynthesis of ABA has been investigated in detail in different *Cercospora* species (*C. rosicola*, *C. cruenta*, *C. pini-densiflori*). All these investigations showed that ABA is formed directly via farnesyl-diphosphate, different ionylidene derivatives and deoxyABA (Fig. 2; for references see Tudzynski and Sharon 2002). Kettner (1991), Kettner and Dörffling (1987) and Hartung and Eggeling (1984) were unable to find conversion of ABA to phaseic acid and dihydrophaseic acid, as was the case in autotrophic organisms including algae and liverworts (Fig. 2). The endogenous content is very likely regulated by release of ABA to the external medium.

Hartung and Eggeling (1984) have performed pH-dependent uptake experiments with radioactive ABA and *C. cruenta* and in contrast with cells from higher plants, observed high uptake rates at pH 8.0 when ABA is present predominantly as ABA⁻ anion, thus showing that fungal cells do not function as an anion trap. They have also determined ABA efflux rates from the mycelium of *C. cruenta* and found them to be at least 10 times higher than in root tissues of *Hordeum vulgare* L. (barley). They concluded that the fungal plasma membrane exhibits a high permeability for ABA⁻, which causes a continuous release of newly synthesised ABA.

ABA biosynthesis in fungi

Norman *et al.* (1981) investigated the effects of the composition of external media on fungal ABA production. Compounds that can be used as carbon or nitrogen sources stimulate both growth and ABA production. The same is true for polyols such as sorbitol (Hartung and Eggeling 1984) and mannitol (Kitagawa *et al.* 1995), which are often used to create osmotic stress. In fungal cultures, polyols can be taken up by the mycelium and used as a carbon source. Consequently, polyols are not suitable as osmotica for fungi or for investigation of stress effects on fungal ABA formation. It remains unclear whether fungi exhibit a stress dependent ABA biosynthesis.

ABA functions in fungi

Only few published data are available on the effects of external ABA on fungi. There are two examples of weak stimulations on mycelium growth by external ABA (Stopinska and Michniewicz 1988). Growth of *C. rosicola* and *C. cruenta* was not affected by ABA (W. Hartung and S. Eggeling, unpubl. data).

Although ABA does not seem to have any function in fungi, fungal ABA maybe of some importance for plants infected

with ABA-producing phytopathogenic fungi, in mycorrhizal associations and in lichens, respectively.

Leaves, infected by pathogenic fungi, often have increased ABA levels, which seem to be partly due to fungal ABA (Kettner 1991; Schmidt *et al.* 2008). Also, mycorrhizal fungi appear to be able to release ABA to roots (Murakami-Mizukami *et al.* 1991; Danneberg *et al.* 1992). In these cases, increases in ABA in plant tissues are mostly too weak (compared with stress-dependent increases) to trigger a stress physiological response. It also should be mentioned that the glomeromycote fungi involved in arbuscular mycorrhizas cannot be cultured in the absence of the host, which makes the investigation of the ABA relation of such a fungus very difficult.

ABA in lichens

Only a few studies have been published on ABA in lichens. Dietz and Hartung (1997, 1998) found ABA in 26 lichen species, Schroeter *et al.* (2000) detected ABA in 10 Antarctic species, Ott *et al.* (2000) in five and Ergün *et al.* (2002) in nine species.

In contrast with higher plants and liverworts, the ABA levels of lichens were increased transiently when dry thalli were moistened, but decreased significantly afterwards (*Hypogymnia physoides*, *Leptogium* sp., *Parmelia sulcata*, *Peltigera praetextata*, *Usnea filipendula*; Dietz and Hartung 1998). Biosynthesis of ABA in freshly hydrated thalli might be essential before the next desiccation because of the often short periods of thallus water saturation. The fungal partner is, most likely, the major site of ABA synthesis. Fungal ABA may be important to induce the formation of protective factors in the algae, to improve their desiccation tolerance.

Xanthoria parietina and *Peltigera praetextata* suffer less from excess of water when pre-treated with ABA or sprayed with ABA solutions (Dietz and Hartung 1999).

Conclusions

At present, we are a long way from understanding the function of ABA in bacteria, cyanophytes and algae. ABA seems to be ubiquitously distributed in cyanobacteria and algae. In many groups, where 9'-*cis*-neoxanthin is missing, ABA is likely to be synthesised directly via farnesyldiphosphate. Here, comparison of genome sequences, if available, with that from flowering plants might be useful in determining the biosynthetic pathways of ABA in cyanobacteria and algae that lack 9'-*cis*-neoxanthin. Degradation occurs similarly as in higher plants. In a few examples, salt stress was shown to induce ABA biosynthesis. However, this extra stress-ABA is released into the medium, resulting in a slight increase of internal ABA only. In bacteria the situation is even more obscure. Two positive reports conflict with 20 negative attempts to find ABA in bacteria. Nothing is known about ABA biosynthesis, degradation and function in bacteria.

No clear stress physiological functions of ABA in algae have been determined, although several recent reports suggest that algal ABA may have protective role against oxidative stress.

It cannot be excluded that early in evolution the complete biochemical equipment to form and metabolise ABA was invented in bacteria, cyanophytes and algae, although it may not have been essential for fitness of the organism. With the

progress of evolution, when organisms such as submerged living liverworts started to occupy terrestrial habitats, ABA gained an important function as a stress hormone. In liverworts, ABA induces developmental changes resulting in terrestrial organs and tissues and it induces desiccation tolerance by forming protective proteins such as LEA proteins or dehydrins. Early in evolution, ABA proved to be effective in closing stomata of sporophytes of hornworts, although stomata seem to have no stress physiological function there that is comparable to that of cormophytes. In cormophytes, stomata proved to be the most important target cells of the stress hormone ABA in short-term regulation of water relations.

The situation for fungal ABA is similar. There is no clear significant function for the fungus itself. Fungal ABA that is synthesised in high amounts is released easily into the surrounding medium. It may positively affect stress physiological processes of plant partners such as algae in lichens or plant roots, which are surrounded by ABA-containing soil solution or associated to mycorrhizal fungi.

ABA released from soil microorganisms (bacteria, cyanobacteria, algae, fungi) to the soil solution and the rhizosphere has been shown to be important for plant ABA relations (Hartung *et al.* 1996) and very likely also for stress physiology of roots (Jiang and Hartung 2008).

In the case of algae and cyanobacteria it would be worth investigating aerial algae such as *Trentepohlia* or cyanobacteria on temporarily moistened and dry habitats such as rocks on land or seashores where desiccation stress is combined with salt stress.

Acknowledgements

The constructive comments of Professor Hermann Heilmeyer (Technical University, Freiberg, Germany) and the help of Dr Jiang Fan (Beijing Normal University, Beijing) with the figures are gratefully acknowledged.

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Manuscript received 16 March 2010, accepted 27 May 2010