Review Article

Hormonal regulation in green plant lineage families

M.M. Johri

Formerly from Department of Biological Sciences, TIFR, Mumbai
Present Address : 32 New Cosmos, Juhu Versova Link Road, Andheri (W), Mumbai - 400 053, India

---

ABSTRACT

The patterns of phytohormones distribution, their native function and possible origin of hormonal regulation across the green plant lineages (chlorophytes, charophytes, bryophytes and tracheophytes) are discussed. The five classical phytohormones – auxins, cytokinins, gibberellins (GA), abscisic acid (ABA) and ethylene occur ubiquitously in green plants. They are produced as secondary metabolites by microorganisms. Some of the bacterial species use phytohormones to interact with the plant as a part of their colonization strategy. Phytohormone biosynthetic pathways in plants seem to be of microbial origin and furthermore, the origin of high affinity perception mechanism could have preceded the recruitment of a metabolite as a hormone. The bryophytes represent the earliest land plants which respond to the phytohormones with the exception of gibberellins. The regulation by auxin and ABA may have evolved before the separation of green algal lineage. Auxin enhances rhizoid and caulonemal differentiation while cytokinins enhance shoot bud formation in mosses. Ethylene retards cell division but seems to promote cell elongation. The presence of responses specific to cytokinins and ethylene strongly suggest the origin of their regulation in bryophytes. The hormonal role of GAs could have evolved in some of the ferns where antheridiogens (compounds related to GAs) and GAs themselves regulate the formation of antheridia.

During migration of life forms to land, the tolerance to desiccation may have evolved and is now observed in some of the microorganisms, animals and plants. Besides plants, sequences coding for late embryogenesis abundant-like proteins occur in the genomes of other anhydrobiotic species of microorganisms and nematodes. ABA acts as a stress signal and increases rapidly upon desiccation or in response to some of the abiotic stresses in green plants. As the salt stress also increases ABA release in the culture medium of cyanobacterium *Trichormus variabilis*, the recruitment of ABA in the regulation of stress responses could have been derived from prokaryotes and present at the level of common ancestor of green plants. The overall hormonal action mechanisms in mosses are remarkably similar to that of the higher plants. As plants are thought to be monophyletic in origin, the existence of remarkably similar hormonal mechanisms in the mosses and higher plants, suggests that some of the basic elements of regulation cascade could have also evolved at the level of common ancestor of plants. The networking of various steps in a cascade or the crosstalk between different cascades is variable and reflects the dynamic interaction between a species and its specific environment. **[Physiol. Mol. Biol. Plants 2008; 14(1&2) : 23-38]** *E-mail : mmjohri@mailhost.tifr.res.in*

Key words : *Green plant families; Bryophytes; Abscisic acid; Auxin; Cytokinin; Ethylene; Antheridiogens; miRNA; Origin of hormonal regulation*

During their growth, plants interact dynamically not only with the edaphic factors but also with gravity, environmental factors and a variety of microorganisms. This interaction involves a continuous dialogue or cross-talk between a plant and its immediate environment. The phytohormones are of prime importance in this dynamic interaction to regulate and integrate the overall growth, development and reproduction. Among the various phytohormones, auxin was the first to be discovered and subsequently gibberellins, cytokinins, abscisic acid and ethylene were identified. These five hormones are often referred to as the classical five and additional ones such as salicylic acid, jasmonates, brassenosteroids, nitric oxide and systemin have been added to the list. The bryophytes constitute the first group of green plants to have adapted to the land habitat. The mosses are among the most ancient lineage of plants that respond to phytohormones. Hormonal regulation could have evolved utilizing the elements or modules pre-existing in the haploid, unicellular ancestor of green plants. This topic has been reviewed earlier (Johri, 2004). In this paper, the hormonal responses in the green plant families, especially in the bryophytes, are updated and recent information on the novel genes or gene families in mosses is also included. Information on the

---

Correspondence and Reprint requests : M.M. Johri phytohormones in heterotrophic organisms will also be discussed in order to examine the origin of hormonal regulation in a wider perspective.

Green plant lineage families

The green plant lineage includes the chlorophytes, charophytes, bryophytes and tracheophytes (Baldauf *et al*., 2000). This lineage is believed to be monophyletic in origin (Graham, 1996). The phylogenetic relationships of different lineages of land plants - the embryophytes represented by green algae, bryophytes, pteridophytes and seed plants have been reviewed extensively (Karol *et al*., 2001; Kendric and Crane, 1997; Mishler *et al*., 1994; Renzaglia *et al*., 2000). Here, only the salient features of the most widely accepted viewpoint will be discussed. The stoneworts (Charales) are the closest living relatives of the land plants; the hornworts seem to represent a group that is basal to the land plants while moss/liverwort clade is sister to the tracheophytes. Whether the mosses or liverworts are paraphylous to tracheophytes is debatable. A few reports strongly suggest the monophyly of mosses with tracheophytes but clearly more studies are needed. The analysis of DNA sequences encoding the cytosolic small heat shock proteins (sHSPs) suggests a basal position of the moss *F. hygrometrica* with seed plants (Waters and Vierling, 1999). Likewise, the analysis of the mitochondrial nad7 gene by Hashimoto and Sato (2001) also suggests the monophyly of mosses and tracheophytes and the paraphyly of liverworts to these two taxa.

During the origin of land plants, as the ancestral forms migrated from an aqueous to terrestrial habitat, major changes in metabolism and structural diversity occurred to cope up with the gaseous atmosphere and periodic arid conditions on the land. The transition is estimated to have occurred about 430 million years ago and the diversification into various groups of green plant families occurred after this process. Several important metabolic pathways are believed to have originated during the transition including those for plant hormones (Kendrick and Crane, 1997). It is worth mentioning that rhizoid production by exogenous auxin in the green alga *Chara* is thought to be a very ancient response that may have evolved before the separation of mosses from the common ancestor of green plant lineage (Cooke *et al*., 2002).

Bryophytes as an ancient lineage may have retained many novel genes

The bryophytes represent the most ancient lineage of the embryophytes that have been independent all along during the evolution of vascular plants. The genomes of bryophytes have been suggested to be a rich source of novel genes (Matsunaga *et al.,* 2004; Proctor, 2001; Rensing *et al.,* 2002; Wood *et al.,* 1999). Mention may be made of a novel phytochrome gene in the moss *Ceratodon purpureus* which actually encodes a light regulated protein kinase of 140 kDa (Thummler *et al.,* 1992). Because of the highest ratio of homologous recombination to nonhomologous recombination (Schaefer and Zrÿd, 1997), the moss *Physcomitrella patens* has become highly amenable to a genetic analysis of genes at a level comparable to the yeast. A high degree of conservation between moss and seed plant sequences has been observed. The intron-exon structure and the codon usage in mosses (*P. patens* and *Tortula ruralis*) are very similar to the dicotyledenous plants (Reski *et al*., 1998, Wood *et al*., 1999).

The ESTs in the moss *P. patens* have been extensively analyzed (Nishiyama *et al.,* 2003). It is estimated that over 15,883 transcripts are expressed in *P. patens* and at least 66% of *A. thaliana* genes had homologues in the moss. As the moss ESTs are still not saturated, the proportion of *A. thaliana* homologous genes could even be higher. Using the putative moss transcripts as the query, 9,942 (62.6%) sequences shared significant similarities to *A. thaliana* proteins while 10,757 (76.7%) transcripts had significant similarities to the nonredundant amino acid sequence data in the GenBank. Of these, 9,907 transcripts had highest levels of similarity to genes in vascular plants, while the remaining 850 showed high levels of similarity to other organisms (Nishiyama *et al.,* 2003). From the latter, 300 putative transcripts were selected that seemed highly unlikely to be present in vascular plants but were present in mosses. These transcripts termed as MST's (moss transcripts absent in vascular plants) probably correspond to new genes in land plants. Their absence has been attributed to the possible gene loss or rapid evolution in vascular plant lineages, or due to a horizontal transfer of genes from other organisms to the moss. The 300 MSTs corresponded to 244 genes and, in principle, should include the genes that are required for the moss to survive and reproduce. The identification of genes such as those for DNA damage repair, e.g. the P011933 gene for the DNA repair hydrolase, the P002718 gene for RecA, and the P009868 gene for *Eso1* among the putative transcripts, is an important and noteworthy result that can explain very high level of homologous recombination in *P. patens* (Nishiyama *et al*., 2003). Another example of genes in *P. patens* that are absent in vascular plants is the presence of putative transcripts P001256 and P005876 which are highly similar to the *cab* homologue L1818r-1 of *Chlamydomonas reinhardtii*. This class of *cab* genes has been found in other land plants and may have been lost from the lineage of spermatophytes (Nishiyama *et al.,* 2003). These authors have further provided strong evidence for the presence of bacterial type glutathione S-transferase in *P. patens* and is an example of horizontal transfer of bacterial gene to moss genome.

Two ENA-type Na^+-ATPases (PpENA1 and PpENA2) have been identified in *P. patens* (Bentito and Rodriguez-Navarro, 2003). PpENA1 acts as a Na^+ pump during the normal growth of moss under moderate salt stress by regulating sodium levels (Lunde *et al.*, 2007). The functional role of PpENA2 is still unknown and its expression is lower than PpENA1. In vascular plants, typically the sodium levels are maintained solely by Na^+/H^+ antiporters and Na^+-ATPases are absent. These results suggest that the moss has either gained the Na^+-ATPase gene or the vascular plants have lost this gene.

Several families of microRNAs (miRNAs) have been found in green plants ranging from algae, mosses, ferns, gymnosperms and angiosperms (Floyd and Bowman, 2004; Arazi *et al*., 2005; Axtell and Bartel, 2005; Molnár *et al*., 2007; Zhang *et al.,* 2006; Zhao *et al.,* 2007) suggesting that the regulation by miRNA is ancient in origin. At least 88 annotated miRNA families have been identified in the moss *P. patens* and 44 in the lycopod *Selaginella moellendorffii* (Axtell *et al.,* 2007; Fattash *et al*., 2007). The target analysis indicates that in *P. patens* several miRNAs regulate overall development and are involved in signal transduction, cell wall biosynthesis and defense pathways. A small number of families are highly conserved in mosses, lycopods and angiosperms; these are abundantly expressed, are involved in the regulation of developmental processes and have generally retained homologous target interactions during the diversification of land plants. Majority of the miRNAs in mosses and lycopods are lineage specific and expressed at a level lower than the conserved miRNAs. An instance of convergent miRNA function has also been found where two lineage specific miRNAs originating independently (one in bryophytes and the other in angiosperms) were found to perform a common function (Axtell *et al.,* 2007). Some of the miRNAs have been found to be developmentally regulated or upregulated by auxin (Arazi *et al.,* 2005). In *P. patens* a miRNA has also been found to be involved in the cleavage of auxin response factor mRNA. The miRNA based posttranscriptional regulation may have played a major role during the diversification of land plant lineages (Axtell *et al*., 2007).

Occurrence of Phytohormones in Bacteria and Fungi

The bacteria and fungi produce a variety of secondary metabolites including the phytohormones (reviewed by Bopp, 1990; Johri, 2004). The production of phytohormones is now well-documented by the free living and pathogenic bacterial species. Recently, it has also been suggested that IAA could also be a native signalling molecule in bacteria (Spaepen *et al*., 2007). The fact that several bacteria can catabolize IAA and use it as a sole source of carbon, nitrogen and energy (Leveau and Lindow, 2005), more information is needed about its possible role as signalling agent in bacteria. The GAs were first identified from the fungus *Gibberella fujikuroi* and are now known to occur in several species of bacteria, fungi, ferns and seed plants (reviewed by Johri, 2004). ABA and ethylene have been found to be produced by some of the bacteria and fungi (Zahradnicková *et al.,* 1991). The pathogenic bacterial species and fungi use phytohormones to modulate the physiology of host plant as a part of their colonization strategy.

Growth Substances in Algae and their possible function

In algae, phytohormones and several morphogenetic substances have been found (Johri, 2004). Exogenous IAA enhances rhizoid production in the excised segments of thalli in the green alga *Chara* (Sievers and Schröter, 1971). The *Chara* rhizoids seem to have naphthylphthalmic acid-sensitive IAA efflux carrier and capacity for polar transport (see Cooke *et al*., 2002). Among more recent reports, several cytokinins have been found in the axenic strains of *Protococcus, Chlorella* and *Scenedesmus* (Chlorophyta) and in seaweeds; the predominant cytokinins were isopentenyladenine (IP) derivatives, zeatins and aromatic cytokinins such as benzyladenine and topolin derivatives (Stirk *et al*., 2003; Ordog *et al*., 2004). ABA seems to be involved in the acquisition of desiccation tolerance and a polypeptide of 60 kDa has been suggested to be a dehydrin in the stress tolerant green alga *Dunaliella parva* (see Hartung *et al.,* 1994). It is worth mentioning that ABA increase in the culture medium upon salt stress has earlier been observed in the cultures of *Draparaldia* and *Dunaliella* (Tietz *et al.,* 1987). However, much remains to be learnt about the possible native role of phytohormones in algae.

Specific morphogenetic substances are also present in algae. These range chemically from glutamic acid to glycoproteins and even volatile hydrocarbons (reviewed by Johri, 2004). These substances tend to be species-specific, act at very low concentrations and function as pheromones. Thus, chemical communication through the specific pheromones had evolved early and is already well established in algal species. In the simplest situation, a metabolite such as glutamic acid itself acts as a morphogenetic or a regulatory substance. Such metabolites act at concentrations that are far lower than the substrate levels. *In order for a metabolite to acquire a regulatory function in signalling, high affinity specific recognition systems (presumably based on receptor systems) must be in place.*

Hormonal responses in cryptogams

As already mentioned, hormonal responses remarkably similar to those of the higher plants are now well-documented in bryophytes (Johri, 2004). The responses to abiotic stresses and adaptation to them are also mediated by ABA in several bryophytes. The only exception seems to be the situation about gibberellins; the evidence for their presence and specific effects in bryophytes is not very strong. There are several reports describing the pharmacological effects of exogenously applied GAs, but these do not support the role of GAs as a native hormone in bryophytes. The regulatory role of gibberellins as antheridiogens is well documented in some of the ferns of the Schizaeaceae (Bopp, 1990; Johri, 1990).

The Moss Protonemal System

The gametophytic phase in mosses such as *Funaria hygrometrica* and *P. patens* is represented by a filamentous protonema and a leafy moss plant, the gametophore. The protonema shows a highly ordered development which is regulated by phytohormones (Bopp and Atzorn, 1992a; Johri, 1978). The hormonal responses are rapid and discernible either in single cells or in a group of a few cells and are thus more or less cell autonomous. The protonema development involves the chloronemal and the caulonemal phases and, developmentally, the chloronema represents the default state of differentiation. Basically three phyhormones – auxin, cytokinin and ABA are of major importance in regulating the protonemal development and adaptation to abiotic stresses.

Auxin Regulation of Caulonema and Protonemal Rhizoid Differentiation

The caulonema differentiation is regulated by inoculum size, auxin and nutrient levels. It is a developmental switch, which is turned on only by biologically active auxins (Johri and Desai, 1973; Johri and D'Souza, 1990). Endogenous auxin has been shown to be involved in caulonema formation (Atzorn *et al.*, 1989a; 1989b). Exogenous IAA regulates caulonema by inhibiting chloronema production and stimulating the caulonema differentiation. Both basipetal transport and IAA-binding sites seem to be involved during caulonema differentiation and chloronema inhibition (Johri, 2004).

In liquid cultures as nutrients get depleted, protonemal rhizoids differentiate. Auxin also markedly stimulates the formation of rhizoids in liverworts and mosses (reviewed by Cove and Ashton, 1984). Their development is also auxin-regulated and during differentiation expression of homeodomain-leucine zipper I gene *Pphb7* is induced (Sakakibara *et al.,* 2003). As rhizoids and caulonema are similar structures and products of the same differentiation process (Knoop, 1984), there must also be a relationship between starvation stress and caulonema differentiation. This aspect has been investigated by Johri and D'Souza (1990) and these studies quite unexpectedly indicated that the responsiveness of cells to auxin can be modulated by medium pH and nutrient level. A similar role of auxin, pH and stress in the formation of embryogenic cell type has since been found in the leguminous plant *Medicago sativa* (Pasternak *et al.,* 2002).

Stimulation of Chloronema Differentiation by 3',5'-Cyclic AMP

The inhibitory effect of auxins is specifically antagonized by exogenous 3',5'-cAMP (Handa and Johri, 1976; 1979) and endogenous 3',5'-cAMP is involved in chloronema proliferation. Cyclic AMP and cyclic AMP-specific phosphodiesterases have been demonstrated in the chloronemal cells (Handa and Johri, 1977; Sharma and Johri, 1982). A far higher level of intracellular cAMP in chloronema than in caulonema and the stimulation of chloronema formation by the inhibitors of cyclic nucleotide phosphodiesterase are consistent with the role of endogenous cAMP (Handa and Johri, 1979).

Interestingly, cAMP-mediated regulation, well known in fungi and bacteria, still seems to operate in algae and mosses and selected higher plants (*see* Assmann, 1995; Minorsky, 2003). For instance, 3',5'-cAMP and 3',5'-cGMP are present in the duckweed *Lemna paucicostata* and have been implicated in the flowering response and circadian rhythmicity (Gangwani *et al.*, 1991, Hasunuma *et al.*, 1988). With the cloning of a functional cyclic nucleotide gated cation channel from *Arabidopsis* (Leng *et al.*, 1999), the physiological basis for the pharmacological effects of cAMP can be explained. However, it is still not possible to assign an *in vivo* role of cAMP in higher plants and genes for adenyl cyclase and cAMP-specific phosphodiesterase have not been found in *Arabidopsis* and rice genomes. The mechanism of cAMP synthesis in the moss or duckweed is also unknown. 3',5'-cGMP is now accepted as an important second messenger in plants and a functional guanylyl cyclase from *Arabidopsis* has also been characterized (Ludidi and Gehring, 2003). As pointed out by Assmann (1995), future studies on systems such as the growth of incompatible pollen tubes, which is stimulated by exogenous cAMP, or on etiolated grass protoplasts, where the swelling response may be cAMP regulated, will help in unravelling the *in vivo* role of cAMP in some of the higher plants.

Patterns of Auxin Metabolism in Bryophytes and Green Algae

The evolutionary pattern of auxin metabolism across the different lineages of green plants has been extensively investigated (Sztein *et al.,* 1999; 2000; 2002; Cooke *et al.,* 2002). The trend suggests that excised plant tissues, cell cultures or cell free extracts synthesize auxin via the tryptophan-dependent (TD) pathways. The auxin can be produced by tryptophan-independent (TI) pathways also (Wright *et al.,* 1991; Normanly *et al.,* 1993). Depending on the state of growth and rate of cell proliferation, cells can switch from the TI to the TD pathway. In the intact plants, the TI pathways are the predominant ones that produce low levels of IAA in a steady and sustained manner. The TD pathway results in far higher IAA levels required for rapid cell proliferation as is the case during embryo development and in wounding response (Michalczuk *et al.*, 1992, Sztein *et al.,* 2002). The endogenous levels of free IAA are regulated basically by a net balance between the rates of biosynthesis, conjugation and degradation.

The Charophyte *Nitella* tips synthesize IAA but maintain rather low steady-state level of free IAA and IAA conjugates. The synthesis of conjugates is also very slow and IAA levels in this alga seem to be regulated by a balance between biosynthesis and degradation. The exact pathway of auxin production in *Nitella* is yet to be established. Among liverworts, the five species that were tested synthesized IAA via the TI pathway and also showed slow conjugation rates indicating a regulation similar to *Nitella* (Sztein *et al.,* 2000). The apical regions of the hornwort *Phaeoceros* thalli showed high levels of free IAA and IAA-amide conjugates under steady-state conditions and auxin levels seem to be regulated by the conjugation/hydrolysis pathway. Interestingly, a similar trend is also shared by the tracheophytes. The vegetative shoot tips of four moss species investigated biosynthesized auxin via the TI pathway and maintained far lower levels of free IAA. Of the total IAA, about 10% was in the free form while the rest as amide conjugates (Sztein *et al.*, 2000). The amides were synthesized at intermediate to rapid rates suggesting that the moss gametophores also employ the conjugation/hydrolysis strategy. Thus, the thalli or vegetative shoot tips throughout the green plant lineages synthesize auxin employing the TI pathway. In the charophytes and liverworts, IAA levels seem to be regulated at macro level through the synthesis-degradation pathways, while in the mosses and tracheophytes the regulation is precisely tuned employing the strategy of IAA-conjugate synthesis and hydrolysis.

Some information about the evolutionary patterns of IAA transport is also available (Cooke *et al*. 2002). As already stated, in the gametophytic structures there is strong evidence for the presence of polar basipetal transport and efflux carriers in the liverwort thalli and moss rhizoids (Maravolo, 1976; Rose and Bopp, 1983). Auxin is involved in regulating the axial growth of sporophytes which have been found to show a transition of auxin movement from simple diffusion to polar transport (Poli *et al*., 2003).

Regulation of bud formation by cytokinins

The cytokinins induce the formation of bud initials, which arise as side branches from caulonemal cells (Gorton and Eakin, 1957). At least 20 native cytokinins have been identified in the moss *Physcomitrella patens* and some of them are also released into the culture medium (von Schwartzenberg *et al*., 2007). In the sporophyte cultures of the moss hybrid *Physcomitrium pyriforme* x *F. hygrometrica*, presence of a kinetin-like substance termed bryokinin, was first reported by Bauer (1966). This cytokinin was later identified as isopentenyladenine (iP) in the culture medium as well as the sporophytic callus (Beutelmann and Bauer, 1977). Cytokinin over-producing mutants of *P. patens* form buds constitutively (Ashton *et al*., 1979); these exhibit an up-regulated cytokinin biosynthesis and a far higher conversion of isopentenyladenosine ([9R]iP) into iP as compared to the wild type (Schulz *et al*., 2001). *P. patens* contains a prokaryote-type t-RNA-isopentenyl-transferase gene (IPT) which catalyses cytokinin formation by modifying the side chain of adenine next to anticodon and degradation of tRNA liberates cytokinin nucleotides (Yevdakova and von Schwartzenberg, 2007). Cytokinin oxidase EST's have been found in *P. patens* and similar to higher plants, the cytokinin levels could be regulated by the degradation pathway (Nishiyama *et al*., 2003).

Role of Calcium in Bryophytes

Calcium is a ubiquitous second messenger in eukaryotes and of especial interest are the calcium-dependent protein kinases (CDPKs) which occur only in the plant kingdom and some protozoans (Cheng *et al.,* 2002). Among mosses, the role of calcium is well-documented in auxin enhanced caulonema differentiation, cytokinin induced bud formation and responses to physical stimuli such as cold shock and touch (Conrad and Hepler, 1988; Russell *et al*., 1996; Schumaker and Gizinski 1996). In bryophytes, the calcium sensing elements and the subsequent signalling cascades are remarkably similar to that of angiosperms. In the chloronemal cells of *F. hygrometrica*, five CDPKs and one calcium-regulated calmodulin (CaM) dependent PK (CCaMK) have been found. Calcium is required for the autophosphorylation as well as substrate phosphorylation by the CDPKs of Mr 44, 48, 63 and 70 kDa (D'Souza and Johri, 1999). Characterization of a partial genomic clone of the fifth CDPK shows that this FhCDPK gene encodes a transcript of about 2.6 kb which is up-regulated by nutritional deprivation. The genomic clone shows the canonical autoinhibitory region and the four EF hands (Mitra and Johri, 2000). The deduced amino acid sequence shows extensive homology with CDPKs from higher plants. It shared 73 % identity with the *Fragaria* CDPK and 71 % homology with CDPK isoform-7 of *Arabidopsis*. The homology to the liverwort *Marchantia* or the moss *Tortula* CDPKs was lower (59-64 %). The 70 kDa moss CCaMK belongs to another very important class of the calcium-regulated PKs that have a kinase domain followed by a CaM-binding domain homologous to neural visinin-like molecules (Harmon *et al*., 2000). The purified moss 70 kDa PK prefers lysine-rich histone as substrate and is fully active in the presence of 50 mM free calcium (D'Souza and Johri, 2003). At sub-optimal levels of free calcium (23 µM), the enzyme is completely inactive but is activated by the moss CaM (5-100 nM). The activity of the moss CCaMK is thus CaM-dependent at low levels of calcium, a response which is likely to have a physiological significance.

Occurrence of ABA in Bryophytes and its Role in Desiccation Tolerance

ABA inhibits the protonemal growth and cytokinin-induced bud formation in *Funaria* (Valdon and Mummery, 1971), closure of stomata in the sporophytes of the moss *Funaria* and the hornwort *Anthoceros* (Garner and Paolillo, 1973, Hartung, *et al*., 1987). In the presence of ABA, the side branches on the protonema remain short, inhibited which resemble the brood cells (Johri, 1988). Brood cell formation with ABA has also been found in the moss *Physcomitrella patens* (Schipper *et al*., 2002); these cells withstand rapid drying and could conceivably play a role in the desiccation response. There is overwhelming evidence for the presence of ABA in the bryophytes. It is involved in the adaptation to desiccation (Hartung *et al*., 1987; 1994). While surveying several species of Marchantiales, Hartung *et al.* (1987) described the presence of far higher level of ABA-like material in the desiccation tolerant species such as *Exormotheca bulbosa* and *Plagiochasma rupestre* than the hygrophytic species such as *Conocephalum conicum*, *Marchantia polymorpha* and *Riccia albovestata*. In the same study, the tubers of *Anothoceros dichotomus* also showed relatively higher amounts of ABA-like material than the sporophytic or the gametophytic tissues suggesting a possible correlation between the endogenous high level of ABA and desiccation tolerance.

A strong support for the role of ABA as a stress hormone derives from the physiology of liverworts such as *Riccia fluitans* and *Ricciocarpus natans* which exist in two forms, the submerged or floating waterform and a landform. In both species, ABA transforms the waterform into the landform (Hellwege *et al*., 1992). A similar role of ABA has been found in regulating the development of several terrestrial characteristics in many aquatic plants exhibiting the phenomenon of heterophylly (reviewed by Lin, 2002; Minorsky, 2003). The formation of aerial leaves is ABA-regulated in plants ranging from the fern *Marsilea* (Liu, 1984) to angiosperms such as *Potamogeton* (Anderson, 1978), *Limnophila* (Mohan Ram and Rao, 1982) and *Rananculus* (Young and Horton, 1985).

A comparative analysis of the polypeptides synthesized by submerged, terrestrial and ABA-treated submerged thalli of *R. fluitans* showed that ABA regulates the expression of several genes (Hellwege *et al*., 1996). Each of these types of thalli showed a specific pattern of polypeptides; of the 17 landform-specific polypeptides, 12 were induced by ABA and were also detected in the ABA-treated submerged thalli. A cDNA clone, corresponding to the *Ric 1* gene, was finally identified which encoded a 30 kDa landform specific hydrophobic protein. It was found to share homology with the group 3 of LEA proteins, was not expressed in the submerged thalli and but was induced at high level by ABA. A single copy of the group 1 LEA gene designated as PpLEA-1 is present in the moss *P. patens.* Its transcription is up-regulated in response to osmotic stress and ABA (Kamisugi and Cuming, 2005) and possibly involved in the acquisition of desiccation tolerance (see also Gillesa *et al.,* 2007). Additional evidence for the regulation of desiccation tolerance by ABA comes from the studies on the extremely xerophilic liverwort *Exormotheca holstii*. This species is highly drought tolerant and ABA induces the formation of proteins that are immunologically related to dehydrins from corn and desiccation tolerant resurrection plant *Craterostigma plantagineum* (Hellwege *et al.*, 1994). The ability to accumulate stress-dependent ABA to a high level to confer drought tolerance seems to be a species-specific trait, because the hygrophilic species *Marchantia polymorpha* although accumulated ABA upon slow desiccation, but not sufficiently high to confer drought tolerance.

Among mosses, ABA has been detected in the protonema of *F. hygrometrica*. Upon slow drying, there is an increase in endogenous ABA and the protonema survives desiccation (Werner *et al.*, 1991; Bopp and Atzorn, 1992b). The *Funaria* protonema can be hardened similar to the liverwort *Exormotheca* and furthermore, the exogenous ABA treatment also restores desiccation tolerance in the non-hardened protonema. The desiccated and the ABA-treated protonema synthesize several new polypeptides and on the basis of cross reactivity, there is strong evidence for the presence of dehydrins (Bopp and Werner, 1993; Werner and Bopp, 1993). A dehydrin gene in *P. patens* has been found to exert a protective role against dehydration tolerance (Saavedra *et al.,* 2006). The ABA- and osmotic stress-inducible promoter elements from the wheat *Em* gene are fully functional in the moss *P. patens* (Knight *et al.*, 1995). Thus, stress responses seem to be remarkably similar and well conserved between higher plants and bryophytes. Besides the regulation of gene expression discussed above, ABA also evokes rapid responses and activates a 38 kDa myelin-basic protein (MBP) kinase in the chloronema cells of the moss *F. hygrometrica* within minutes of treatment (D'Souza and Johri, 2002). The activation is transient, independent of calcium, specific to ABA and is also evoked by salt stress but not by other abiotic stresses. The effects of ABA and NaCl are additive and thus perceived independently such that the signals converge at the level of MBP kinase. Since ABA is also involved in conferring resistance against desiccation in moss, the activation of MBP kinase by salt and ABA seems to be a part of a signalling network.

Effect of Ethylene in Bryophytes

Similar to higher plants, IAA application stimulates ethylene production in the leafy liverwort *Plagiochila arctica* (Law *et al.*, 1985). Ethylene in general retards cell division but seems to promote cell elongation. It suppresses the ventral row of leaves in *P. arctica* (Basile and Basile, 1983). The elongation of seta in the sporophyte of the thallose liverwort *Pellia epiphylla* involves a dual regulation by auxin and ethylene (Thomas *et al.*, 1983). Among mosses, as the *Funaria* protonemal cultures become old and senescent they produce ethylene. IAA also stimulates ethylene production. In the presence of external ACC (1-amino-cyclopropane-1-carboxylic acid), ethylene production is slightly promoted but methionine or glutamate have no effect. With ACC, the young protonema produces tmema cells, a cell type characteristic of old and aging cultures. The formation of tmema cells normally in old cultures could be related to ethylene production (Rohwer and Bopp, 1985).

Phytohormones in Pteridophytes and Their Role

All the major groups of phytohormones have been found in pteridophytes. The role of auxin in the determination of angle meristems in *Selaginella* and the development of fronds in the fern *Osmunda* is well established. The polarity of auxin transport shows that the outgrowths referred to as rhizophores are indeed roots (Wochok and Sussex, 1974). By exogenously applying auxin or by culturing the dorsal meristem on auxin-containing medium, the fate of meristems can be changed and dorsal meristem also develops into roots (Webster, 1969; Wochok and Sussex, 1975). Another characteristic response of auxin is the regulation of uncoiling of the crozier and the development of frond in ferns. The developing fronds in ferns produce auxin and the influence of pinnae can be replaced by exogenous auxin (Briggs *et al.*, 1955, Briggs and Steeves 1959; Schneider and Wightman, 1986). In the rachis, auxin is transported in a polar and basipetal manner and is also required for the differentiation of xylem and sclerenchyma in the maturing zone (Briggs *et al.*, 1955). The shoot tips of *Selaginella* and *Ceratopteris* synthesized IAA via the TI pathway, maintained a low level of free IAA and rapidly synthesized IAA conjugates. In seed plants and pteridophytes, the predominant conjugated forms have been identified as IAA-asparate/IAA-glutamate and/or IAA-glucose (Sztein *et al.,* 2000). In general, the tracheophytes show very rapid rates of conjugate biosynthesis and the regulation of free IAA levels seems to be mainly at the level of conjugate biosynthesis and conjugate hydrolysis (Sztein *et al.*, 2000, Cooke *et al.*, 2002).

By and large 2iP based cytokinins are characteristic of bryophytes and pteridophytes and zeatin and its riboside were not detected in the sporophytic tissues from *Dryopteris* and *Equisetum*. Likewise, no cytokinin was detected in the sporangial fronds of *Lygodium*

(Yamane *et al*., 1983). Similar to mosses, the major effect of cytokinin in ferns is to enhance cell division and shoot bud formation (Peterson, 1967).

As mentioned earlier, gibberellins are of special significance for their hormonal role in the pteridophytes. GA_{36} has been identified from the most primitive extant pteridophyte the *Psilotum nudum*. The situation in the tree fern *Cyathaea australis* is as complex as in the angiosperms and 10 different GAs have been found in the croziers. Methyl ester of the GA_9 (GA_9-Me) has been found in the conditioned medium of *Lygodium japonicum* cultures (Yamane *et al*., 1979). It is produced by the prothalli, secreted in the medium and has been identified as antheridiogen A_{Ly}. It induces antheridia prematurely but inhibits archegonium formation. Regulatory substances referred to as antheridiogens were first demonstrated by Döpp (1950) and at present three other antheridiogens A_{An}, A_{Pt} and A_{Ce} are known. Chemically A_{An} is a GA-related diterpenoid and its chemical structure proposed by Nakanishi *et al.* (1971) was revised later by Corey and Myers (1985). The antheridiogens show a narrow activity spectrum and can also substitute for light and induce spore germination in dark. GA_3, GA_4 and GA_9 and their methyl esters induce both dark germination and antheridium formation in *Lygodium*, while only the gibberellins are active in *Anemia* (Sugai *et al*., 1987). The antheridiogens play a very important ecological role. It has been suggested that the different responses evoked by antheridiogens ultimately result in lowering the chances of intragametophytic self-fertilization and, at the same time, enhance the intersporophytic crossing (Schraudolf, 1985; Takeno and Furuya, 1987).

Ethylene is produced by axenic cultures of several species of algae, liverworts, mosses and ferns (Elmore and Whittier, 1973; Elmore and Whittier, 1975). The promotion of megasporangium formation in *Selaginella* also involves ethylene effects at the level of cell division. The differentiation of a microsporangium or a megasporangium is controlled by the number of times the sporogenous tissue cells divide. It is conceivable that ethylene suppresses the final cell division of the sporogenous tissue cells (Brooks, 1973), and the absence of partitioning of the cytoplasm may be an important factor to establish conditions making for femaleness (Bell, 1979). In the semiaquatic fern *Regnellidium diphyllum*, upon submergence the petiole or leaf rachis rapidly elongates and this response is initiated by the endogenously accumulated ethylene (Musgrave and Walter 1974; Cookson and Osborne, 1979). Ethylene seems to be synthesized in ferns from a pathway different from that of higher plants as ACC has not been found to be a precursor of ethylene (Chernys and Kende, 1996; Osborne *et al.* 1996). As already pointed out by Kim *et al.* (2000), ACC-dependent ethylene synthesis could have evolved after the divergence of ferns.

In a survey of various plant groups, Hiron (1974) reported an increase of putative ABA content in several ferns after wilting (see Table 5 in Johri, 1990). ABA is present in the gametophytic tissues such as spores and filamentous gametophytes of *Anemia phyllitidis* (Bürcky, 1977; Cheng and Schraudolf, 1974). ABA inhibits the elongation of protonema in *Mohria caffrorum*, the formation of adventitious gametophytes from non-meristematic explants of *A. phyllitidis* and antheridiogen-induced antheridia formation in *Ceratopteris richardii* (Chia and Raghavan, 1982; Hickok, 1983; Reynolds, 1981). ABA induces the land form of morphological characteristics in the plants of *Marsilea quadrifolia* (Lin, 1984). ABA is also involved in the regulation of dehydrins in the desiccation tolerant fern *Polypodium virginianum* (Reynolds and Bewley, 1993) and thus the relationship between water-stress and ABA content in ferns seems to be similar to that in the higher plants and undoubtedly the endogenous ABA plays a role in the acclimation response to stress.

Origin of Hormonal Response in Plants

Were the pathways for the biosynthesis of phytohormones in green plants derived from prokaryotes?

Among the living organisms, only plants and microbes are capable of synthesizing literally thousands of metabolic products due to the secondary metabolism. It is of considerable interest and importance to unravel if plants invented the pathways specific to them or alternatively such pathways evolved utilizing the genetic information from prokaryotes. Several observations indicate that a reciprocal horizontal exchange of genes has been occurring between the plant material and microorganisms and therefore microbial origin of phytohormone synthesis genes cannot be ruled out (Johri, 2004). First of all, many microorganisms grow in close association with plant material and this would enhance chances of DNA uptake (Bode and Müller, 2003). *While discussing the origin of land plants, Pirozynski and Mallloch (1975) concluded "land plants never had an independence (from fungi); for if they had they could never have colonized land" (italics intentional by Johri for emphasis).* The fossil records seem to support this hypothesis (Redecker *et al.,* 2000). Based on the above suggestions and advances in our understanding of metabolic pathways and horizontal gene transfer, it is therefore tempting to suggest that the pathways of phytohormone biosynthesis in green plants are of prokaryotic origin (author's suggestion). The basic elements for the biosynthesis of phytohomones would have to be in place in the common unicellular ancestor of plants, while it was still in the aquatic habitat; later the pathways could evolve and diversify independently in the various lineages of green plants.

Possible acquisition of hormonal function by secondary metabolites

Chemical signalling in plants is extensively used through pheromone- and or hormone-based mechanisms. The studies in algae and fungi show that chemical signalling through pheromones had already evolved in the sexual reproduction and somatic cell repair (Waaland, 1986; Al-Hasani and Jaenicke, 1992). According to Kochert (1978), the pheromones of unicellular eucarionts could be the ancestors of hormones for all multicellular eucarionts. The action of secondary metabolites (present in ancestral forms) as hormones could have acquired a regulatory role during the diversification of multicellular organisms. Although Kochert had visualized the pheromones of unicellular eukaryotes (termed as eucarionts by him) to be the ancestors of hormones in multicellular eukaryotes, there is no evidence to support it. The notion of hormonal mechanisms being present in the unicellular common eukaryote is certainly a viable one if the biosynthesis of hormones was in place at the level of common ancestor of plants.

Whereas the pheromones-based regulation represents the earliest form of signalling, the phytohormonal regulation seems to have evolved independently early during the origin of plants. *Unlike a pheromone, which has a species-specific signature, the phytohormones have a more general role and a particular hormone evokes the same generalized function across the green plants (italics intentional for emphasis).* As argued in this review, the auxin, cytokinin and ABA regulate respectively the root formation, shoot bud formation and the desiccation responses in plants. Thus, it is not a question of pheromones functioning as hormones but rather the two types of signalling systems have originated independently during the evolution of multicellular organisms.

Possible origin of specific receptors

Following Kochert's general idea about the possible origin of hormones, Schraudolf (1985; 1986) has compared the similarities between the pheromone system of Schizaeaceae and the gibberellin responses in angiosperms. According to him, "the reaction of antheridiogens in Schizaeaceous ferns represents the "moment of becoming a hormone for gibberellin-like molecules in phanerograms" (Schraudolf, 1985). He further argues that "In contrast to animal evolution, the phylogeny of plants seems to be characterized by a post-evolution of hormone-receptor molecule. This event was a prerequisite for a common and ubiquitously distributed metabolic product to take over the function of a regulatory molecule. The phylogeny of phytohormones therefore has to be written as a phylogeny of their receptors'' (Schraudolf, 1985). It is not difficult to visualize the acquisition of high-affinity perception mechanisms including the receptors either at the level of common ancestor of land plants or even later after the separation of algal or the bryophytic lineage. It is reasonable to assume that the high affinity perception mechanism preceded the recruitment of a metabolite as a hormone.

In *Arabidopsis* the receptors for ethylene and cytokinin have been identified to be the sensory hybrid-type histidine kinases and the two-component systems are involved in the signal transduction (Urao *et al*., 2000; Hwang and Sheen, 2001). The two-component histidine receptors seem to have been derived from the cyanobacterial genome as a result of horizontal transfer of genes during the origin of the ancestor of plants (Urao *et al*., 2000; Mount and Cheng, 2002). As bryophytes represent the earliest group of land plants with demonstrable responses to phytohormones, the histidine kinase receptors are expected to be present in them and EST clones homologous with receptor-like kinases and ethylene responsive element binding protein (EREBP)-like transcription factors have been found in the gametophytic transcriptome of *P. patens* (Nishiytama *et al*., 2003). Their detailed characterization is awaited.

Based on the foregoing discussion, at least the ethylene and cytokinins receptors in the extant plants had their origin from the elements in the microbial organisms. As pointed out by Schraudolf (1985), the crux of the issue in phytohormonal regulation is the problem of the origin of specific receptors.

When did the response to various hormones evolve?

An analysis of the distribution of phytohormones and their native function across different groups indicates several trends. Auxins, cytokinins, abscisic acid and ethylene are produced ubiquitously but their demonstrable native hormonal role seems to have evolved later during the origin of various lineages (Fig. 1). Except for bryophytes, gibberellins are present in bacteria, fungi and tracheophytes. In bryophytes, the presence and function of gibberellins needs a reinvestigation because at present there is no creditable evidence for their role as a native hormone. Likewise, the role of GAs in green algae also needs to be clarified.

In the green alga *Chara*, the presence of auxin efflux carrier and polar transport on one hand and the formation of rhizoids by exogenous auxin on the other hand indicate that the hormonal role of auxin is ancient and may have evolved even before the evolution of land plants (Cooke *et al.,* 2002). As already discussed, the hormonal role of native auxin in the differentiation of rhizoid and caulonema is well established in bryophytes and rhizoids. With regard to auxin movement, the bryophytes show a transition from simple diffusion to polar transport. In the young sporophytes of the hornwort *Phaeoceros*, auxin movement lacks polarity and moves by simple diffusion. The young sporophytes of the liverwort *Pellia epiphylla* showed movement sensitive to auxin-transport inhibitors but also lacked polarity. The sporophytes of the moss *Polytrichum ohioense* showed strong bidirectional polar transport; which was basipetal in the young sporophytes but acropetal in the older ones. Thus different groups of bryophytes employ different strategies of auxin movement and the moss sporophytes transport auxin in a manner remarkably similar to vascular plants (Poli *et al*., 2003). Though the data are limited, the emerging trend strongly indicates the existence of polar auxin transport in *Chara* rhizoids and moss sporophytes. Thus the bipolar auxin movement may have evolved gradually building on the elements present in the common ancestor before the separation of Charales. At present, the available data strongly suggest

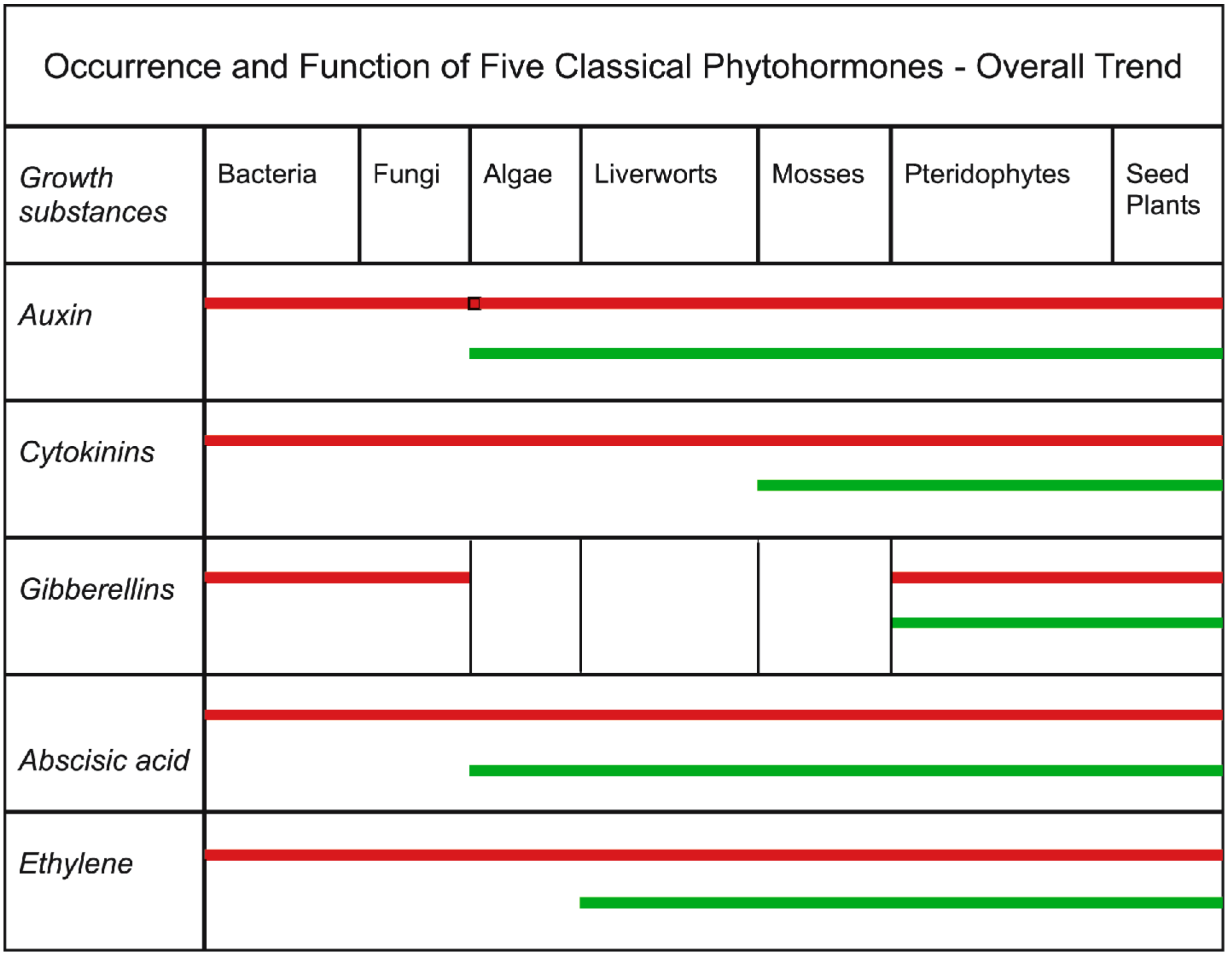

Fig. 1. Occurrence and native function of the classical five phytohormones in bacteria, fungi and green plant lineage groups. Green line indicates the presence of endogenous phytohormone in a group and red line indicates that the native phytohormone has a well-documented function in that group (After Johri, 2004).

the origin of cytokinin response at the level of bryophytes as no well-defined role of native cytokinins has been found in algae. Cytokinins regulate the differentiation of shoot bud initials in mosses. As pointed out earlier, the cytokinin receptors seem to have been derived from the histidine kinases of prokaryotic origin and more information about these receptors in mosses is awaited.

The desiccation tolerance is wide spread in living organisms and has been found in microorganisms, animals and plants (see Proctor, 2001). Besides green plants, sequences coding for LEA-like proteins are present in the genomes of other anhydrobiotic species including microorganisms (*Deinococcus radiodurans*) and nematodes (*Aphelenchus avenae*) (see Browne *et al*., 2002). Thus, during adaptation to land habit, protective mechanisms evolved very early as a common strategy against periodic drought conditions. As ABA accumulates rapidly upon desiccation in plants, it could it be a far more efficient communicating agent to link the desiccation signal with the expression of genes for the acquisition of tolerance. The relationship between ABA and stress signal is also very ancient and salt stress has been found to increase the release of ABA even in the culture medium of cyanobacterium *Trichormus variabilis* (syn. *Anabaena variabilis*) (Zahradnièková *et al.,* 1991). How salt regulates the release of ABA in the cyanobacterium remains to be understood? In green plants the expression of some of the LEA group of proteins is regulated by ABA while others are synthesized when cells experience abiotic stresses. The recruitment of ABA as a phytohormone in the regulation of stress responses could have been derived from prokaryotes and could also be present at the level of common ancestor of green plants (author's proposal). The presence of dehydrin-like proteins in the desiccation tolerant across all the families of green lineages is consistent with this suggestion.

CONCLUSIONS AND FUTURE PERSPECTIVES

The responses to phytohormones across the different lineages of green plants have been analysed to trace the possible origin regulation by each hormone. As the DNA sequence information on a larger number of prokaryotic and eukaryotic genomes is becoming available, one is beginning to gain fresh insight about the horizontal transfer of genes across different species. A reciprocal horizontal exchange of genetic information between the plant material and microorganisms seems to have been occurring continuously and the possibility that the pathways of phytohormone biosynthesis in green plants are of prokaryotic origin cannot be ruled out. As pointed out by Bode and Müller (2003), in contrast to the generally accepted hypothesis, several plant-specific metabolic pathways have in recent years also been found in prokaryotes. For instance cellulase synthase in vascular plants has been suggested to been transferred from cyanobacteria to plants (Nobles *et al*., 2001).

As rapid advances are being made in the genomics of green plant lineage families, an analysis of molecular characteristics that led to the successful colonization of land by bryophytes could be very instructive and might lead to a better understanding of their fuller development in the seed plants. It could also lead to the identification of genes and miRNAs families that led to the networking of developmental regulation during the colonization of land and ultimately culminated in the diversification of green plant lineages.

The response to desiccation is widespread and motifs similar to LEA group of proteins have been reported in bacterial and nematodes besides plants. This response may have evolved before the separation of plant and animal lineages. The widespread identification of dehydrins in algal, bryophytic and fern species is consistent with an ancient origin of tolerance against desiccation in green plants. The role of ABA in linking the stress signal with the physiology of the plant seems to have evolved later but before the separation of green algal lineage. As the cyanobacterium *Trichormus variabilis* (syn. *Anabaena variabilis*) releases ABA in the culture medium in response to salt stress, the recruitment of ABA in the regulation of stress responses could also be prokaryotic in origin.

Throughout the green plants, auxin evokes a rhizogenic response and regulates the formation of rhizoids and roots. Auxin movement seems to be polar in the rhizoids of the alga *Chara*, and ranges from simple diffusion to polar transport in the bryophytes. The moss sporophytes transport auxin in a bipolar manner remarkably similar to vascular plants (Poli *et al*. 2003). The trends of auxin movement, pharmacological effects and the role of endogenous auxin strongly support the evolution of auxin regulation prior to the separation of algal lineage. At present, as the responses specific to cytokinins and ethylene are clearly documented in liverworts and mosses, there is a strong case for the recruitment of cytokinins and ethylene as hormones in bryophytes. The fact that the receptors for ethylene and cytokinins are possibly of cyanobacterial origin, the basic elements of perception mechanisms based on receptors seem to have evolved early during the formation of the unicellular common ancestor of plants.

The role of gibberellins is also unclear in green algae and bryophytes. Gibberellins and GA-like compounds, the antheridiogens, have been found to regulate the antheridia formation in some of the ferns indicating that the hormonal role of GAs may have evolved at the level of pteridophytes.

ACKNOWLEDGEMENTS

I am glad that a special issue of Physiology and Molecular Biology of Plants is planned on the occasion of 60th birthday of Professor Sudhir K. Sopory. It has been a pleasure knowing him and interacting with him in many scientific forums. The studies on the protonema of the moss *Funaria* discussed in this review were carried out when the author was at the Tata Institute of Fundamental Resarch, Mumbai. I am grateful to over a dozen students and visitors whose published studies have been included in this review.

REFERENCES

Al-Hasani, H. and Jaenicke, L. (1992). Characterization of a sex-inducer glycoprotein of *Volvox certeri f. weismannia*; *Sex. Plant Reprod*., 5:8-12.

Anderson, L.W.J. (1978). Abscisic acid induces formation of floating leaves in the heterophyllous aquatic angiosperm *Potamogeton nodosus. Science*, 201:1135-1138.

Arazi, T., Talmor-Neiman, M., Stav, R., Riese, M., Huijser, P. and Baulcombe, D.C. (2005). Cloning and characterization of micro-RNAs from moss. *Plant J.*, 43:837-848.

Ashton, N.W., Cove, D.J. and Featherstone, D.R. (1979). The isolation and physiological analysis of mutants of the moss *Physcomitrella patens*. *Planta,* 144:437-442.

Assmann, S.M. (1995). Cyclic AMP as a second messenger in higher plants. Status and Future Prospects. *Plant Physiol.,* 108: 885-889.

Atzorn, R., Geier, U. and Sandberg, G. (1989a). The physiological role of indole acetic acid in the moss *Funaria hygrometrica* Hedw. I. Quantification of indole-3-acetic acid in tissue and protoplasts by enzyme immunoassay and gas chromatography-mass spectrometry. *J. Plant Physiol*., 135**:** 522-525.

Atzorn, R., Bopp, M. and Merdes, U. (1989b). The physiological role of indole acetic acid in the moss *Funaria hygrometrica* Hedw. II. Mutants of *Funaria hygrometrica* which exhibit enhanced catabolism of indole-3-acetic acid. *J Plant Physiol*., 135: 536-530.

Axtell, M.J. and Bartel, D.P. (2005). Antiquity of microRNAs and their targets in land plants. *Plant Cell,* 17: 1658-1673.

Axtell, M.J., Snyder, J.A. and Bartel, D.P. (2007). Common functions for diverse small RNAs of land plants. *Plant Cell,* 19: 1750-1769.

Baldauf, S.L., Roger, A.L., Wenk-Siefert, I. and Doolittle, W.F. (2000). A kingdom-level phylogeny of eukaryotes based on combined protein data. *Science,* 290:972-977.

Basile, D.V. and Basile, M.R. (1983). Desuppression of leaf primordia of *Plagiochila arctica* (Hepaticae) by ethylene antagonists. *Science,* 220:1051-1053.

Bauer, L. (1966). Isolierung und Testung einer kinetinartigen Substanz aus Kalluszellen von Laubmoossporophyten. *Z. PflPhysiol*., 54**:**241-253.

Bell, P.R. (1979). The contribution of the ferns to an understanding of the life cycles of vascular plants. In : *The Experimental Biology of Ferns* (Ed. Dyer, A.F.), Academic Press, London, pp. 58-85.

Benito, B. and Rodríguez-Navarro, A. (2003). Molecular cloning and characterization of a sodium-pump ATPase of the moss *Physcomitrella patens*. *Plant J.,* 36*:*382–389

Beutelmann, P. and Bauer, L. (1977). Purification and identification of a cytokinin from moss callus cells. *Planta,* 133:215-217.

Bode, H.B. and Müller, R. (2003). Possibility of bacterial recruitment of plant genes associated with the biosynthesis of secondary metabolites. *Plant Physiol.*,132:1153-1161.

Bopp, M. (1990). Plant Hormones in Lower Plants. In : *Plant Growth Substances 1988.* (Eds. Pharis, R.P. and Rood, S.), Springer-Verlag, Berlin, pp 1-10.

Bopp, M. and Atzorn, R. (1992a). The morphogenetic system of the moss protonema; Crypt. Bot., 3:3-10

Bopp, M. and Atzorn, R. (1992b). Hormonelle Regulation der Moosentwicklung. *Naturwissenschaften*, 79:337-346.

Bopp, M. and Werner, O. 1993. Abscisic acid and desiccation tolerance in mosses. *Bot. Acta,* 106:103-106.

Briggs, W.R. and Steeves, T.A. (1959) Morphogenetic studies on *Osmunda cinnamomea* L. The mechanism of crozier uncoiling. *Phytomorphology,* 9:134-137.

Briggs, W.R., Steeves, T.A., Sussex, I.M. and Wetmore, R.H. (1955). A comparison of auxin destruction by tissue extracts and intact tissues of the fern *Osmunda cinnamomea*. *Plant Physiol.,* 30:148-155.

Brooks, K.E. (1973). Reproductive biology of *Selaginella* I. Determination of megasporangia by 2-chloroethylphosphonic acid, an ethylene-releasing compound. *Plant Physiol*., 51:718-722.

Browne, J., Tunnacliffe, A. and Burnell, A. (2002). Plant desiccation gene found in a nematode. *Nature,* 416: 38.

Bürcky, K. (1977). The occurrence of abscisic acid in *Anemia phyllitidis* L. Sw. (Schizaeaceae) during ripening of spores. *Z. PflPhysiol*., 85**:**181-183.

Cheng, C.-Y. and Schraudolf, H. (1974). Nachweis von Abscisinsure in Sporen and jungen Prothallien von *Anemia phyllitidis* L. Sw.; *Z. PflPhysiol*., 71**:**366-369.

Cheng, S-H., Willmann, M.R., Chen, H-C. and Sheen, J. (2002) Calcium signalling through protein kinases. The Arabidopsis calcium-dependent protein kinase gene family; *Plant Physiol.,* 129:469-485.

Chernys, J. and Kende, H. (1996). Ethylene biosynthesis in *Regnellidium diphyllum* and *Marsilea quadrifolia. Planta,* 200:113-118.

Chia, S. E. and Raghavan, V. (1982). Abscisic acid effects on spore germination and protonemal growth in the fern *Mohria caffrorum. New Phytol*., 92:31-38.

Conrad, P. A. and Hepler, P. K. (1988). The effect of 1,4-dihydropyridines on the initiation and development of gametophore buds in the moss *Funaria. Plant Physiol.,* 86:984-687.

Cooke, T. J., Poli, D. B., Sztein, A. E. and Cohen, J. D. (2002). Evolutionary patterns in auxin action; *Plant Mol. Biol*., 49**:**319-338.

Cookson, C. and Osborne, D. J. (1979). The effect of ethylene and auxin on cell wall extensibility of the semi-aquatic fern *Regnellidium diphyllum. Planta*, 146**:**303-307.

Corey, E. J. and Meyers, A. G. (1985) Total synthesis of (I)-antheridium-inducing factor (A_{AN},2) of the fern *Anemia phyllitidis*. Clarification of stereochemistry, *J. Amer. Chem. Soc*., 107:5574-5576

Cove, D. J. and Ashton, N. W. (1984). The hormonal regulation of gametophytic development in bryophytes. In : *The Experimental Biology of Bryophytes*, (Eds. Dyer, A.F. and Duckett, J. G.), Academic Press, London, pp. 177-201.

Döpp, W. (1950). Eine die Antheridienbildung bei Farnen fordernde Substanz in den Prothallien von *Pteridium aquilinum*. *Ber. Deut. Bot. Des*., 63:139-147.

D'Souza, J.S. and Johri, M.M. (1999). Ca^{2+}dPKs from the protonema of the moss *Funaria hygrometrica*. Effect of indole-acetic acid and cultural parameters on the activity of a 44 kDa Ca^{2+}dPK. *Plant Science,* 145**:**23-32.

D'Souza, J.S. and Johri, M. M., (2002). ABA and NaCl activate myelin basic protein kinase in the chloronema cells of the moss *Funaria hygrometrica*; *Plant Physiol. Biochem*., 40**:**17-24.

D'Souza, J. S. and Johri, M. M., (2003). Purification and characterization of a Ca^{2+}-dependent/ calmodulin-stimulated protein kinase from moss chloronema cells. *J. of Biosciences,* 28: 223-233.

Elmore, H. W. and Whittier, D. F. (1973). The role of ethylene in the induction of apogamous buds in *Pteridium* gametophytes. *Planta,* 111:85-90.

Elmore, H. W. and Whittier, D. F. (1975). Ethylene production and ethylene-induced apogamous bud formation in nine gametophytic strains of *Pteridium aquilinum. Ann. Bot.,* 39**:**965-971.

Fattash, I., Voss, B., Reski, R., Hess, W. R. and Frank, W. (2007). Evidence for the rapid expansion of microRNA-mediated regulation in early land plant evolution. *BMC Plant Biology,* 7:13.

Floyd, S.K. and Bowman, J.L. (2004). Gene regulation: ancient microRNA target sequences in plants. *Nature*, 428:485-486.

Gangwani, L., Tamot, B. K., Khurana, J. P. and Maheshwari, S. C. (1991). Identification of 3'-5'-cyclic AMP in axenic cultures of *Lemna paucicostata* by higher-performance liquid chromato-graphy. *Biochem. Biophys. Res. Commun*., 178**:**1113-1119

Garner, L. B. and Paolillo, D. J. (1973). On the function of the stomata in *Funaria. Bryologist*, 76:423-427.

Gillesa, G. J., Hinesa, K. M,, Manfrea, A. J., Marcotte, Jr. W. R. (2007) A predicted N-terminal helical domain of a Group 1 LEA protein is required for protection of enzyme activity from drying. *Plant Physiol and Biochem*., 45:389-399.

Gorton, B. S, and Eakin, R. E. (1957). Development of the gametophyte in the moss *Tortella caespitosa*. *Bot. Gaz*., 119:31-38.

Graham, L.,G. (1996) Green algae to land plants: an evolutionary transition. *J. Plant Res*.,109: 7737-7742.

Handa, A.,K. and Johri, M.,M. (1976). Cell differentiation by 3',5'-cyclic AMP in a lower plant. *Nature*, 259:480-482.

Handa, A.,K. and Johri, M.,M. (1977). Cyclic adenosine 3',5'-monophosphate in moss protonema. A comparison of its levels by protein kinase and Gilman assays. *Plant Physiol*., 59:490-496.

Handa, A.,K. and Johri, M.,M. (1979). Involvement of cyclic adenosine 3':5'-monophosphate in chloronema differentiation in protonema cultures of *Funaria hygrometrica*. *Planta,* 144:317-324.

Harmon, A.,C., Yoo,,B-C. and Harper, J. (2000) CDPKs – a kinase for every Ca^{2+} signal. *Trends Plant Sci*., 5:154-159.

Hartung, W., Hellwege, E.,M. and Volk, O.,H. (1994). The function of abscisic acid in bryophytes. *J. Hattori Bot. Lab.,* No.76:59-65.

Hartung, W., Weiler, E.,W. and Volk, O.,H. (1987). Immunochemical evidence that abscisic acid produced by several species of Anothocerotae and Marchantiales, *Bryologist,* 90:393-400.

Hashimoto, K. and Sato, N. (2001). Characterization of the mitochondrial nad7 gene in *Physcomitrella patens*: similarity with angiosperm nad7 genes. *Plant Science*. 160:807-815.

Hasunuma, K., Funadera, K., Furukawa, K. and Miyamoto-Shinohara, Y. (1988) Rhythmic oscillation of cyclic 3',5'-AMP and –GMP concentration and stimulation of flowering by 3',5'-GMP in *Lemna paucicostata* 381. *Photochem. Photobiol*. 48:89-92.

Hellwege, E. M., Volk, O. H. and Hartung, W. (1992). A physiological role of abscisic acid in the liverwort *Riccia fluitans* L., *J. Plant Physiol*., 140:553-556.

Hellwege, E. M., Dietz, K-J. and Hartung, W. (1996). Abscisic acid causes changes in gene expression involved in the induction of landform of the liverwort *Riccia fluitans* L. *Planta*, 198:423-432.

Hellwege, E. M., Dietz, K-J., Volk, O. H. and Hartung, W. (1994). Abscisic acid and the induction of desiccation tolerance in the extremely xerophilic liverwort *Exomotheca holstii*. *Planta,* 194:525-531.

Hickok, L.G. (1983). Abscisic acid blocks antheridiogen-induced antheridium formation in gametophytes of the fern *Ceratopteris richardii*. *Can. J. Bot*., 61:888-892.

Hiron, R.W.P. (1974). Effects of physiological stress on natural growth inhibitor level in plants. Ph.D. Thesis, University of London.

Hwang, I. and Sheen, J. (2001). Two-component circuitry in *Arabidopsis* cytokinin signal transduction. *Nature*, 413:383-389.

Johri, M.M. (1978). Regulation of cell differentiation and morphogenesis in lower plants. In : *Frontiers of Plant Tissue Culture 1978* (Ed. Thorpe, T.A.), Univ. of Calgary Offset Printing Services, Calgary, Canada. pp 27-36.

Johri, M.M. (1990) Hormonal regulation of development and differentiation in lower plants. In *Proceedings International Congress of Plant Physiology*, (Eds. Sinha, S.K., Sane, P.V., Bhargava, S.C. and Agrawal, P.K.), InPrint Exclusives, New Delhi, India, pp. 760-775.

Johri, M. M. (2004). Possible origin of hormonal regulation in green plants. *Proc Indian Natl. Sci. Acad.,* B70(3):335-465.

Johri, M.M. and Desai, S. (1973). Auxin regulation of caulonema formation in moss protonema. *Nature New Biology,* 245:223-224.

Johri, M.M. and D'Souza, J.S. (1990). Auxin Regulation of Cell Differentiation in Moss Protonema. In *Plant Growth Substances 1988*, (Eds. Pharis, R.P. and Rood, S.), Springer-Verlag, Berlin, pp. 407-418.

Kamisugi, Y. and Cuming, A.C. (2005). The evolution of the abscisic acid-response in land plants: comparative analysis of group1 LEA gene expression in moss and cereal. *Plant Mol Biol.* 59:723-737.

Karol, K.G., McCourt, R.M., Climino, M.T. and Delwiche, C.F. (2001). The closest living relatives of land plants. *Science*, 294:2351-2353.

Kendrick, P. and Crane, P.R. (1997). The origin and early evolution of plants on land. *Nature,* 389:33-39.

Kim, J.H., Cho, H-T. and Kende, H. (2000) á-Expansins in the semiaquatic ferns *Marsilea quadrifolia* and *Regnellidium diphyllum*: evolutionary aspects and physiological role in rachis elongation. *Planta,* 212:85-92.

Knight, C.D., Sehgal, A., Atwal, K., Wallace, J. C., Cove, D. J., Coates, D., Quatrano, R.S., Bahadur, S., Stockley, P.G. and Cuming, A.C. (1995). Molecular responses to abscisic acid and stress are conserved between moss and cereals. *Plant Cell,* 7:499-506.

Knoop, B. (1984). Development in Bryophytes; in Experimental Biology of Bryophytes. (Eds. Dyer, A. F. and Duckett, J. G.), Academic Press, London, pp. 143-176.

Kochert, G. (1978). Sexual pheromones in algae and fungi. *Annu. Rev. Plant Physiol.,* 29:461-486.

Law, D.M,, Basile, D.V. and Basile, M.R, (1985). Determination of endogenous indoleacetic acid in *Plagiochila arctica* (Hepaticae), *Plant Physiol.,* 77:926-929.

Leng, Q., Mercier, R. W., Yao, W. and Berkowitz, G. A. (1999) Cloning and first functional characterization of a plant cyclic nucleotide-gated cation channel. *Plant Physiol.*, 121:753-761.

Leveau, J.H.J. and Lindow, S.E. (2005). Utilization of the plant hormone indole-3-acetic acid for growth by *Pseudomonas putida* strain 1290. *Applied and Environmental Microbiol.*, 71:2365-2371.

Lin, B.L. (2002), Heterophylly in Aquatic Plants, in Plant Physiology (Taiz, L. and Zeiger, E), Sinauer Associates Inc., Sunderland, MA, USA., Essay 23.1.

Liu, B.L.L. (1984). Abscisic induces land form characteristics in *Marsilia quadrifolia* L. *Amer. J. Bot.*, 71:638-644.

Ludidi, N. and Gehring, C. (2003). Identification of a novel protein with guanylyl cyclase activity in *Arabidopsis thaliana. J. Biol. Chem.,* 278:6490-6494.

Lunde, C., Drew, D.P., Jacobs, A. K. and Tester, M. (2007). Exclusion of Na^+ via sodium ATPase (PpENA1) ensures normal growth of *Physcomitrella patens* under moderate salt stress. *Plant Physiol.,* 144:1786-1796.

Maravolo, N.C. (1976). Polarity and localization of auxin movement in the hepatic *Marchantia polymorpha*. *American J. Bot.*, 63:529-531.

Matsunaga, T., Ishii, T., Matsumoto, S., Higuchi, M., Darvill, A., Albersheim, P. and O'Neill, M.A. (2004). Occurrence of the primary cell wall polysaccharide rhamnogalacturonan II in pteridophytes, lycophytes, and bryophytes. Implications for the evolution of vascular plants. *Plant Physiol.,* 134:339-351.

Michalczuk, L., Ribnicky, D.M., Cooke, T.J. and Cohen, J.D. (1992). Regulation of indole-3-acetic acid biosynthesis pathways in carrot cell cultures. *Plant Physiol.*, 100: 1346-1353.

Minorsky, P.V. (2003). Guanosine-3',5'-cyclic monophosphate (cGMP) in plants. *Plant Physiol.,* 131:1578-1579.

Minorsky, P. V. (2003). Heterophylly in aquatic plants. *Plant Physiol.,* 133:1671-1672.

Mishler, B. D., Lewis, L.A., Buchheim, M. A,, Renzaglia, K. S., Garbary, D. J., Delwiche,, C. F., Zechman, F. W., Kantz, T. S. and Chapman, R. L. (1994). Phylogenetic relationships of the "green algae" and the "bryophytes". *Ann. Mo. Bot. Gard.,* 81:451-483.

Mitra, D. and Johri, M.M. (2000). Enhanced expression of a calcium-dependent protein kinase from the moss *Funaria hygrometrica* under nutritional starvation. *J. Biosci.*, 25:331-338.

Mohan Ram, H.Y. and Rao, S. (1982). In-vitro induction of aerial leaves and of precocious flowering in submerged shoots of *Limnophila indica* by abscisic acid. Planta, *155*:521-523.

Molnár, A., Schwach, F., Studholme, D.J., Thuenemann, E.C. and Baulcombi, D.C. (2007). miRNAs control gene expression in the single-cell alga *Chlamydomonas reinhardtii.* Nature http://dx.doi.org/10.1038/nature05903.

Mount, S.M. and Cheng, C. (2002). Evidence for plastid origin of plant ethylene receptor genes. *Plant Physiol.,* 130:10-14.

Musgrave, A. and Walters, J. (1974). Ethylene and buoyancy control of rachis elongation of the semi-aquatic fern *Regnellidium diphyllum. Planta,* 121:51-56.

Nakanishi, K., Endo, N. and Näf, U. (1971). Structure of the antheridium-inducing factor of the fern *Anemia phyllitidis. J. Am. Chem. Soc*., 93**:**5579-5581.

Nishiyama, T., Fujita, T., Shin,-I T., Seki, M., Nishide, H., Uchiyama, I., Kamiya, A., Carninci, P., Hayashizaki, Y., Shinozaki, K., *et al*. (2003). Comparative genomics of *Physcomitrella patens* gametophytic transcriptome and *Arabidopsis thaliana*: implications for land plant evolution. *Proc. Natl. Acad. Sci., USA*, 100**:**8007–8012.

Nobles, D. R., Romanovicz, D. K. and Brown R. M. (2001). Cellulose in cyanobacteria. Origin of vascular plant cellulose synthase? *Plant Physiol.,* 127:529-542.

Normanly, J., Cohen, J. D. and Fink, G. D. (1993). Arabidopsis thaliana auxotrophs reveal a tryptophan-independent biosynthetic pathway for indole-3-acetic acid. *Proc. Natl. Acad. Sci., USA,* 90:10355-10359.

Ordog, V., Stirk, W. A., van Staden, J., Novak, O. and Strnad, M. (2004). Endogenous cytokinins in three genera of microalgae from the chlorophyta. *J. Phycol.,* 40:88-95.

Osborne, D.J., Walters, J., Milborrow, B.V., Norville, A. and Stange, L.M.C. (1996). Evidence for a non-ACC ethylene bio-synthesis pathway in lower plants. *Phytochemistry,* 42:51-60.

Pasternak, T. P., Prinsen, E., Ayaydin, F., Miskolczi, P., Potters, G., Asard, H., Van Onckelen, H. A., Dudits, D. and Feher, A. (2002). The role of auxin, pH, and stress in the activation of embryogenic cell division in leaf protoplasts-derived cells of Alfalfa. *Plant Physiol.,* 129:1807-1819.

Peterson, R. L. (1967). Callus induction in *Ophioglossum petiolatum* Hook. *Can. J. Bot.*, 45:2225-2227.

Pirozynski, K.A. and Malloch, D.W. (1975). The origin of land plants: a matter of mycotrophism. *BioSystems,* 6:153-164.

Poli, D.B., Jacobs, M. and Cooke, T.J. (2003). Auxin regulation of axial growth in bryophyte sporophytes: its potential significance for the evolution of early land plants. *American J. Bot*., 90:1405-1415.

Proctor, M. (2001). Patterns of desiccation tolerance and recovery in bryophytes. *Plant Growth Regulation,* 35:147-156.

Redecker, D., Kodner, R. and Graham, L.E. (2000). Glomalean fungi from the Ordovician; *Science,* 289:1920-1921.

Rensing, S. A., Rombauts, S., Van de Peer, Y. and Reski, R (2002). Moss transcriptome and beyond. *Trends in Pl. Sci.,* 7:535-538.

Renzaglia, K. S., Duff, R. J., Nickrent, D. L. and Garbary, D. J. (2000). Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. *Phil. Trans. R. Soc. Lond.,* B 355:769-793.

Reski, R., Reynolds, S., Wehe, M., Kleber-Janke, T. and Kruse, S. (1998). Moss (*Physcomitrella patens*) expressed sequence tags include several sequences which are novel for plants. *Bot. Acta*, 111:1-7.

Reynolds, T. L. (1981). Effects of auxin and abscisic acid on adventitious gametophyte formation by *Anemia phyllitidis*. *Z. PflPhysiol*., 103:9-14.

Reynolds, T.L. and Bewley, J.D. (1993). Characterization of protein synthetic changes in a desiccation-tolerant fern, *Polypodium virginianum*. Comparison of the effects of drying, rehydration and abscisic acid, *J. Exp. Bot.,* 44:921-928.

Rohwer, R. and Bopp, M. (1985). Ethylene synthesis in moss protonema. *J. Plant Physiol*., 117:331-338.

Rose, S. and Bopp, M. (1983). Uptake and polar transport of indoleacetic acid in moss rhizoids. *Physiol Plant*., 58: 57-61.

Russell, A. J., Knight, M. R., Cove, D. J., Knight, C. D., Trewavas, A. J. and Wang, T. L. (1996). The moss, *Physcomitrella patens*, transformed with apoaequorin cDNA responds to cold, shock, mechanical perturbation and pH transient increases in cytoplasmic calcium. *Transgenic Res*., 5:167-170.

Saavedra L., Svensson, J., Carbaffo, V., Izmendi, D., Wefin, B. and Vidal, S. (2006). A dehydrin gene in *Physcomitrella patens* is required for salt and osmotic stress tolerance. *Plant J.,* 45:237-249.

Sakakibara, K., Nishiyama, T., Sumikawa, N., Kofuji, R., Murata, T. and Hasebe, M. (2003). Involvement of auxin and homeodomain-leucine zipper I gene in rhizoid development of the moss *Physcomitrella patens*. *Development*, 130:4835-4846.

Schaefer, D.G., Zrÿd J.–P. (1997). Efficient gene targeting in the moss *Physcomitrella patens. Plant J*., 11:1195-1206.

Schneider, E. A. and Wightman, F. (1986). Auxins of non-flowering plants. I. Occurrence of IAA and phenylacetic acid in vegetative and fertile fronds of ostrich fern *(Matteucia struthiopteris)*. *Physiol. Plant*., 68:396-402.

Schipper, O., Schaefer, D., Reski, R and Fleming, A. (2002). Expansins in the bryophyte *Physcomitrella patens*. *Plant Mol. Biol*., 50:789-802.

Schraudolf, H. (1985). Action and phylogeny of antheridiogens. *Proc. Royal Soc. Edinb*., 86B:75-80.

Schraudolf, H. (1986). Phytohormones and Filicinae: chemical signals triggering morphogenesis in Schizaeaceae. In : *Plant Growth Substances 1985* (Ed. Bopp, M.), Springer-Verlag, Berlin, pp 270-274.

Schulz, P. A., Hofmann, A. H., Russo, V. E. A., Hartmann, E., Laloue, M. and Schwartzenberg, V.K. (2001). Cytokinin overproducing *ove* mutants of *Physcomitrella patens* show increased riboside to base conversion. *Plant Physiol.,* 126:1224-1231.

Schumaker, K. S. and Gizinski, M. J. (1996). G proteins regulate dihydropyridine binding sites in moss plasma membranes. *J. Biol. Chem*., 271 :21292- 21296.

Sharma, S. and Johri, M.M., (1982). Partial purification and characterization of cyclic AMP phosphodiesterase from *Funaria hygrometrica. Arch Biochem. Biophys.,* 21:87-97.

Sievers, A. and Schröter, K. (1971). Versuch einer Kausalanalyse der geotropischen Reaktionskette im *Chara*-Rhizoid. *Planta*, 96:339-353.

Spaepen, S., Vanderleyden, J. and Remans, R. (2007). Indole-3-acetic acid in microbial and microorganism-plant signalling. FEMS Microbiol Rev., 31:1-24.

Stirk, W.A., Novák, O., Strnad, M. And van Staden, J. (2003). Cytokinins in macroalgae. *Plant Growth Regulation,* 41:13-24.

Sugai, M., Nakamura, K., Yamane, H., Sato, Y. and Takahashi, N. (1987). Effects of gibberellins and their methyl esters on dark germination and antheridium formation in *Lygodium* and *Anemia phyllitidis. Plant Cell Physiol*., 28:199-202.

Sztein, A. E., Cohen, J. D. and Cooke, T. J. (2000). Evolutionary patterns in the auxin metabolism in green plants. *Int. J. Plant Sci*., 161:849-859.

Sztein, A. E., Cohen, J. D., de la Feuente, I. G. and Cooke, T. J. (1999). Auxin metabolism in mosses and liverworts. *American J. Bot.*, 86:1544-1555.

Sztein, A. E., Iliæ, N., Cohen, J. D. and Cooke, T. J. (2002) Indole-3-acetic acid biosynthesis in isolated axes from germinating bean seeds: The effect of wounding on the biosynthetic pathway. *Plant Growth Regulation*, 36:201-207.

Takeno, K. and Furuya, M. (1987). Sporophyte formation in experimentally induced unisexual female and bisexual gametophytes of *Lygodium japonicum*. *Bot. Mag.*, 100:37-41.

Thomas, R. J., Harrison, M. A., Taylor, J. and Kaufman. P. B. (1983). Endogenous auxin and ethylene in *Pellia* (Bryophyta). *Plant Physiol.*, 73:395-397.

Thummler, F., Dufner, M., Kreisl, P. and Dittrich, P. (1992). Molecular cloning of a novel phytochrome gene of the moss *Ceratodon purpureus* which encodes a putative light-regulated protein kinase. *Plant Mol. Biol.*, 20**:**1003-1017.

Tietz, A., Köhler, R., Ruttkowski, U. and Kasprik, W. (1987). Further investigations on the occurrence and the effects of abscisic acid in algae. Proc. XIV Intl. Bot. Congr., Berlin. Abst. 2-113b-7.

Urao, T., Yamaguchi-Shinozaki, K. and Shinozaki, K. (2000). Two-component systems in plant signal transduction. *Trends Plant Sci.*, 5:67-75.

Valdon, L. R. G. and Mummery, R. S. (1971). Quantitative relationship between various growth substances and bud production in *Funaria hygrometrica*. A bioassay for abscisic acid; *Physiol Plant.*, 24**:**232-234.

von Schwartzenberg, K., Núñez, M. F., Blaschke, H., Dobrev, P.I., Novák, O, Motyka, V. And Strnad, M. (2007). Cytokinins in the bryophyte Physcomitrella patens: analyses of activity, distribution, and cytokinin oxidase/dehydrogenase overexpression reveal the role of extracellular cytokinin. *Pl. Physiol.*, 145:786-800.

Waaland, S. D. (1986). Hormonal coordination of the processes leading to cell fusion in algae: a glycoprotein hormone from red algae. In *Plant Growth Substances 1985*, (Ed. Bopp, M.), Springer-Verlag, Berlin,. pp. 257-262.

Walters, J. and Osborne, D. J. (1979). Ethylene and auxin-induced growth in relation to auxin transport and metabolism and ethylene production in the semi-aquatic plant, *Regnellidium diphyllum*. Planta, 146:309-317.

Waters, E. R. and Vierling, E. (1999). The diversification of plant cytosolic small heat shock proteins preceded the divergence of mosses. *Mol. Biol. Evol.*, 16:127-139.

Webster, T. R. (1969). An investigation of angle meristem development in excised stem segments of *Selaginella martensii. Can. J. Bot.*, 47:255-263.

Werner, O. and Bopp, M. (1993). The influence of ABA and IAA on in vitro phosphorylation of proteins of *Funaria hygrometrica*. *J. Plant Physiol.*, 141:93-97.

Werner, O., Ros-Espin, R. M. and Bopp, M. and Atzorn, R. (1991). Abscisic acid-induced drought tolerance in *Funaria hygrometrica* Hedw. *Planta,* 186:99-103.

Wochok, Z. S. and Sussex, I. M. (1974). Morphogenesis in *Selaginella*. II. Auxin transport in the root (rhizophore). *Plant Physiol.*, 53**:**738-741.

Wochok, Z. S. and Sussex, I. M. (1975). Morphogenesis in *Selaginella*. III. Meristem determination and cell differentiation. *Dev. Biol.,* 47:376-383.

Wood, A. J., Duff, R. J. and Oliver, M. J. (1999). Expressed sequence tags (ESTs) from desiccated *Tortula ruralis* identify a large number of novel plant genes. *Plant Cell Physiol.*, 40**:**361-368.

Wright, A. D., Sampson, M. B., Neuffer, M. G. , Michalczuk, L., Slovin, J. S. and Cohen, J.D. (1991). Indole-3-Acetic Acid biosynthesis in the mutant maize orange pericarp, a tryptophan auxotroph. Science, 254: 998 – 1000.

Yamane, H., Takahashi, N., Takeno, K. and Furuya, M. (1979). Identification of gibberellin A_9 methyl ester as a natural substance regulating formation of reproductive organs in *Lygodium japonicum. Planta,* 147:251-256.

Yamane, H., Watanabe, M., Satoh, Y., Takahashi, N. and Iwatsuki, K. (1983). Identification of cytokinins in two species of pteridophyte sporophytes. *Plant Cell Physiol.*, 24:1027-1032.

Young, J.P. and Horton, R.F. (1985). Heterophylly in *Rananculus flabellaris:* the effect of abscisic acid. *Ann. Bot.* 55:899-902.

Zahradnicková, H., Marðálek, B. and Poliðenská, M. (1991). High-performance thin-layer chromatographic and high-performance liquid chromatographic determination of abscisic acid produced by cyanobacteria. *J. of Chromatograph,* A 555:239-245.

Zhang, B., Pan, X., Cannon, C. H., Cobb, G. P. and Anderson, T. A. (2006). Conservation and divergence of plant microRNA genes. *Plant J.*, 46:243-59.

Zhao, T., Li, G., Mi, S., Li.S., Hannon, G. J., Wang, X. J., and Qi, Y. (2007). A complex system of small RNAs in the unicellular green alga *Chlamydomonas reinhardtii*. *Genes Dev.,* 21:1190-1203.