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Review paper

Plant growth regulators in bryophytes

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ABSTRACT: Although classified as higher plants, and the second biggest group of terrestrial plants, bryophytes remain less studied and even unknown in many biological processes. Here, an overview on developmental processes in bryophytes known until now is presented. Special emphasis on growth regulators and their influence in bryophytes is given.

Key words: bryophytes, mosses, liverworts, plant growth regulators, development

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INTRODUCTION

The group of terrestrial plants jointly named bryophytes is paraphyletic by origin. Bryophytes (subkingdom of Plantae Bryobiotina) include mosses (Bryophyta), hornworts (Antocerotophyta) and liverworts (Marchantiophyta). Bryophytes represent a very diverse group which have in common a life cycle that comprises two alternating heterophasic and heteromorphic generations, ie. gametophyte and sporophyte. The gametophyte is the dominant generation in bryophytes represented by green plants. In contrast to seed plants, where sporophytes are dominant, these remain attached and completely or partly dependent on the gametophyte for nutritional supply. The sporophyte generation begins with zygote (2n) production which proliferates in seta (pedicel) attached or stalked within the gametophytic plant body (Fig. 1). There, within the capsules, haploid spores are produced by meiosis, which by germination will produce branched filamentous (most of the mosses) or thallous protonema (in *Sphagnum*). In filamentous protonema, two types of cells can be recognized: chloronema cells rich in chloroplasts with perpendicular walls and caulonema cells containing few chloroplasts and with oblique cell walls. Small rounded cells within the protonemal filaments can sometimes be found. They are termed tmema cells (abscission cells) and have a function in separating protonemal filaments for vegetative reproduction. Tmema cells are formed in other bryophyte organs and are responsible for abscission of gemmae, various diaspores for vegetative reproduction (e.g. tubers, clusters, brachycytes). Brachycytes are thick-walled, drought-tolerant brood cells or parts of brood bodies formed on primary or secondary protonema (usually on chloronema). In some species, protonema can be short-lived while in others, they can be a long-living stage to persistent. In protonema, formation of meristematic buds with tree-faced apical cells represents the transition to the gametophore. A fully-developed gametophore can be regarded as an adult bryophyte plant. In mosses, gametophores developed from buds are shoot-like stems bearing phylloids and rhizoids at their base. Phylloids are leaf-shaped structures with similar function to but different anatomy from angiosperm leaves. Rhizoids are filaments, which play a role in attaching to substrate and no or less role in water or nutrient uptake of gametophores. Sex organs, female (archegonia) and male (antheridia) are usually produced at the tips of gametophores. If both sexes are produced in one gametophore, the plant is defined as a monoecious species, while if these are in different gametophores the species is dioecious. Within the antheridia, motile biflagellate spermathozoids are formed, that are capable of moving in the presence of a thin water film in the direction of archegonia (single egg cell). Fertilization occurs within the archegonium where the diploid zygote is embedded. Antheridia are often

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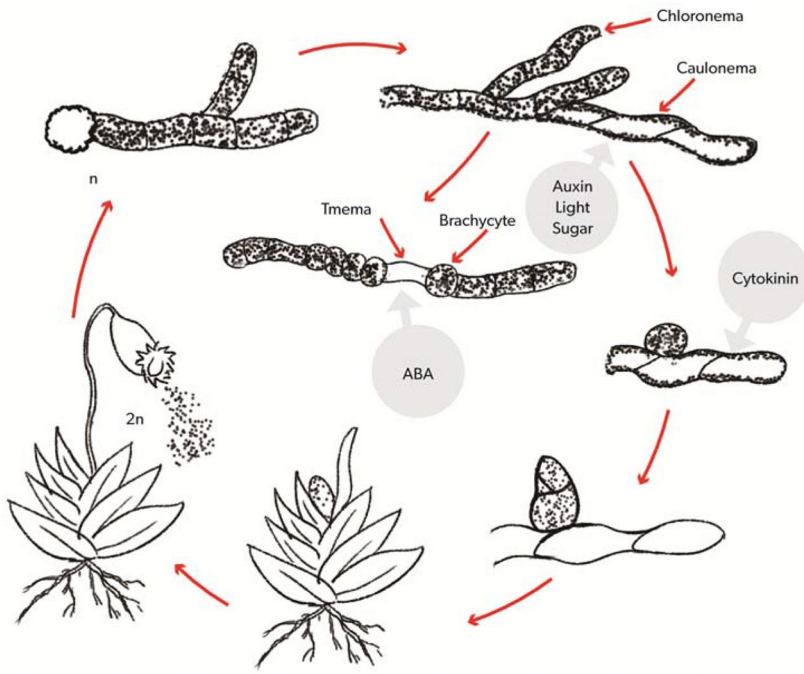

Fig. 1. Scheme of developmental processes in the life-cycle of a model bryophyte.

protected by differentiated phyloids in mosses or a cup-like sheath in liverworts (perichaetium) and archegonia (perigonium). In an apical spore capsule produced from the zygote, hundreds of haploid spores are produced, which can be differentially spread from mother plants upon capsule ripening, and with propagation the life cycle starts again.

Spore capsules often have a protective layer called the calyptra, which breaks after ripening and can be specific in shape. The capsule can open by decaying of the outer layer, rupture or simply by losing the operculum, a lid-like structure at the top of the capsule which falls off when the capsule ripens, leaving the capsule mouth, stoma, for releasing the spores. Some mosses have a tooth-like structure named the peristom, which has function in spore dispersal.

Plant growth regulators. Plant growth regulators (PGRs) are a varied group of molecules produced in plants in extremely low concentration that act in plant developmental process as signal molecules. PGRs include five groups of compounds commonly known as phytohormones - auxins, cytokinins, gibbellins, ABA and ethylene, as well as some other signal molecules. Without PGRs, plant cells would remain an undifferentiated mass. PGRs affect gene expression, transcription levels, cellular division and growth. Although they are naturally produced within plants, very similar compounds can be produced by bacteria and fungi. These can affect plant growth as well as some synthetically-produced compounds.

Considering that recent investigations on phytohormone effects on bryophyte morphogenesis have focused on the model moss *Physcomitrella patens* (Hedw.) Bruch & Schimp., and *Funaria hygrometrica* Hedw. there are only a few reports bringing new information on other bryophyte species: *Aloina aloides* (Schultz) Kindb., *Atrichum undullatum* (Hedw.) P. Beauv., *Bruchia vogesiaca* Schwaegr., *Bryum argenteum* Hedw., *Dicranum scoparium* Hedw., *Molendoa hornschuchiana* (Hook.) Lindb. ex Limpr., *Pogonatum urnigerum* (Hedw.) P. Beauv. or *Thamnobryum alopecurum* Nieuwland ex Gangulee (Sabovljević *et al.* 2002, 2003; Bijelović & Sabovljević 2003; Bijelović *et al.* 2004; Vukojević *et al.* 2004; Cvetić *et al.* 2005; Sabovljević *et al.* 2005; Rowntree 2006).

A few moss species have been used to investigate the influence of phytohormones on their development *in vitro*. Bopp and co-workers (Bopp 1953, 1955, 2000; Bopp & Bohrs 1965; Bopp & Jacob 1986; Bopp *et al.* 1978, 1991) concentrated on the physiology of *F. hygrometrica*, and Reski and coworkers (Reski 1998, 1999; Reski & Abel 1985; Reski *et al.* 1991, 1994; Decker *et al.* 2006) have carried out substantial research using *P. patens*. Several other species have also been used for such investigations, but reports are scattered and not detailed (Briere *et al.* 1977; Rahbar & Chopra 1982; Alcalde *et al.* 1996; Sastad *et al.* 1998). The present knowledge of

plant growth regulator interactions in mosses is mainly based on auxins and cytokinins. There is very little work on the influence of other groups of growth regulators in bryophytes to be found.

Auxins and Cytokinins. From the five main groups of phytohormones, only auxins and cytokinins have been rather extensively studied in mosses as compared to other PGRs (Cove & Ashton 1984; Bhatla & Bopp 1985). Not only do both of these hormone groups exist in mosses, but they also have basic functions in the regulation of normal development. Previous investigations indicate that the hormonal system of mosses includes the sequential interaction of auxin and cytokinin as a main component.

The known effects to date of auxins on moss development include inhibition of protonema growth, stimulation of rhizoid formation, transformation of buds into filaments, torsion of young stems, complete supression of leaves on gametophores, and callus induction (Bopp 1953; Sokal *et al*. 1997).

Bud formation, the number of buds and their position along the caulonema, and cell division in protonema are determined by cytokinins (Szweykowska *et al*. 1971).

Chemical control of protonemal differentiation and growth has been demonstrated in recent years. There are data concerning the correlation between protonemal growth and bud formation in mosses. In some moss systems the protonema must reach a "critical size" before bud formation starts, and in others, protonemal age rather than its size appears to be important (Chopra & Kumra 1988). There is a report that only low levels of auxin are necessary for the differentiation of caulonema and higher levels are required to induce the formation of gametophores (Cove & Ashton 1984). The effect of auxins on bud formation depends on their concentration. At lower levels, auxins stimulate bud induction, whereas at higher concentrations they cause complete inhibition of bud formation as well as de-differentiation of bud primordia.

Studies on the morphogenetic effects of applied cytokinins have played an important role in better understanding of plant development. Cytokinin activity is restricted to a specific morphogenetic change during protonema development, the formation of buds on certain caulonemal cells. However, cytokinin does not act as a "trigger" (Ashton *et al*. 1979). It needs to be present for a critical period of time during which caulonema differentiation is "stabilized" (Brandes 1973). According to the literature, in almost all cases with a short exposure to cytokinins, the induced buds have been abnormal and often-described as "callus-like" (Brandes 1973). In most moss species investigated, normal gametophore development occurs only when very low concentrations of cytokinins are used (Ashton *et al*. 1979). Gametophytes are defective or abortive at extreme cytokinin concentrations (very low or very high) (Chopra & Kumra 1988).

The specific growth regulator bryokinin has been isolated from bryophytes. Bryokinin (a type of cytokinin) can replace kinetin as a growth factor in tissue culture of vascular plants. In mosses, bryokinin is physiologically active at several stages of development. At the caulonema stage it promotes bud formation. In the phase immediately before sexual maturation, it supports apogamous sporogonium formation. Bryokinin is a type of cytokinin found in moss callus cells and chemically corresponds to the free base N^6-γ,γ dimethylallyladenine.

To understand the hormonal effect in more detail, it is important to know more about such components as synthesis, metabolism, and transport. For this purpose, mutants have been introduced into moss research. As mutants having a low degree of auxin production are relatively insensitive to exogenously supplied cytokinins, it can be concluded that sensitivity to cytokinins for bud formation must be dependent on the presence of auxin, which must be present in sufficiently high concentrations (Cove & Ashton 1984; Schumaker & Dietrich 1998).

Gibberellins. Gibberellins (GAs) are a large family of phytohormones involved in an array of various responses throughout the life cycle of plants. The general role of GAs in vascular plants can be summarized in germination stimulation, flowering time regulation and cell expansion. They were isolated from the fungus *Giberella* but found afterwards in various bacteria (MacMillan 2001) and many plant species including unicellular and multicellular algae (Radley 1961; Kato *et al*. 1962; Mowat 1965; Tarakhovskaya *et al*. 2007). However, the role of gibberellins in bryophyte species is still unknown.

Hardly any effects of GAs have been reported for mosses, in contrast to ABA, cytokinins or auxins which are known to have an effect on the developmental stages of bryophytes (Decker *et al*. 2006; Yasumura *et al*. 2007). Chopra & Mehta (1992) and Chopra & Dhingra-Babbar (1984) reported the effect of GAs on moss growth. Chaban *et al*. (1998, 1999) reported on interference with gravitropism when GA was applied to *Ceratodon purpureus* (Hedw.) Brid. and *Pottia intermedia* (Turn.) Fürn.. Sabovljević *et al*. (2010) investigated the influence of GA on morphogenesis of the moss *Bryum argenteum* Hedw.. It was shown that both gibberellins (GA_3 and GA_7) aplied *in vitro* had a positive effect on *B. argenteum* morphogenesis. In experiments where gibberellin biosynthesis inhibitors were applied, it was

shown that these retardants had inhibitory effects on shoot multiplication *in vitro*. However, these substances have almost no negative effects on protonema morphogenesis, though in vascular plants these substances have extremely negative effects on morphogenesis (Sabovljević *et al.* 2010). The above-mentioned results on GAs and GA inhibitors raise several questions, e.g. does protonemal growth increase due to cellular expansion or division; what can be expected when GAs and inhibitors are applied synergistically; or do GA inhibitors block the biosynthesis or the action of GAs. Further studies in bryophytes should provide answers to these questions.

Although Decker *et al.* (2006) reviewed phytohormones in the development of *Physcomitrella patens*, they did not mention any known role of gibberellins in developmental processes of *P. patens*. GAs in bryophytes have never been chemically identified (Anterola & Shanie, 2008). However, Ergun *et al.* (2002) reported that gibberellin-like substances have been also detected in mosses, but the presence of GAs in an organism does not necessarily mean that it is responsive to these compounds. As GAs have not yet been clearly identified in mosses, Yasumura *et al.* (2007) stated that this hormonal signaling pathway developed later in land plant evolution, but was not completely *de novo*. Hence, it could be suggested that GA biosynthetic precursors, like entkaurene should be present in mosses (Vandenbussche *et al.* 2007). Anterola & Shanie (2008) reported that according to a survey of the *Physcomitrella patens* genome, at least this moss species may have a shorter version of the gibberellin biosynthetic pathway relative to that of vascular plants.

According to Anterola & Shanie (2008), with the identification of putative gibberellin biosynthetic genes in *P. patens*, it is now possible to knock them out and make a functional characterization of these genes to establish whether or not GAs are necessary for moss growth and development. Although the *P. patens* (a model bryophyte plant) genome has been published (Rensing *et al.* 2008), the researches presented up to now indicate the classical physiological effects of gibberellins in bryophyte development (bryophyte species other than *P. patens*) and the importance and usefullnes of further investigations in bryophytes to achieve more data on the role of gibberellins in the developmental processes of this group of land plants.

While it is still not known whether or not bryophytes produce GAs, there are reports that some of them contain GA-related diterpenoids as secondary metabolites. Von Schwarzenberg *et al.* (2004) reported that in the moss *P. patens* the tetracyclic diterpene 16-alpha-hydroxykaurane is produced in huge amounts as a secondary volatile compound, and Hayashi *et al.* (2006) found the bifunctional ent-kauren synthase in the same species.

ABA. Abscisic acid (ABA) is a unique molecule found in organisms across kingdoms from bacteria to animals, suggesting its ubiquitous and versatile role in physiological functions of various organisms. ABA is widely known to be one of the growth regulators of tracheophytes, and is also known universally for its hormonal involvement in stress processes. In this case, ABA shows stress-dependent biosynthesis, and is transported to target cells, enabling the plant to cope better with the stressful conditions. Its widespread occurrence across the entire tree of life suggests an ancient origin of ABA. Although it is difficult to determine common roles in various organisms, the predicted function of ABA implies that ABA plays a role in modulating cellular responses to environmental signals, e.g. water deficit stress. As for the regulation of cellular water content, a tonoplast localized aquaporin has been shown to be inducible by ABA (Cuming *et al.* 2007). In aquatic organisms that occasionally colonize terrestrial habitats (e.g. aquatic liverworts, aquatic mosses), it has been shown that this terrestrial colonization is followed by an increase in endogenous ABA, even under mild drought stress. Subsequently, the desiccation protecting mechanisms are stimulated and the formation of terrestrial organs is induced (Hartung 2010). In vascular plants, ABA plays a general role as a growth inhibitor, sex determination and desiccation stress tolerance. Also, ABA is known to improve tolerance against drought and osmotic stress in the moss *Physcomitrella patens* (Cuming *et al.* 2007; Khandelwal *et al.* 2010). In addition, Yasumura *et al.* (2012) suggested enhanced drought tolerance by increasing ABA sensitivity in vascular plants. Thus, plants differ in their ABA sensitivities.

Although it was widely accepted that lunularic acid is a functional substitute for ABA in liverworts, and that ABA is not generally produced by this lineage of bryophytes (Goffinet & Shaw 2009), some studies have also reported the presence of ABA in thallose liverworts (Hartung & Gimmler 1994). Other studies also reported the presence of ABA in mosses (Werner *et al.* 1991; Ergün *et al.* 2002) and in hornworts (Hartung *et al.* 1987). Further indirect evidence of the presence of ABA in liverworts was reported by Hellwege & Hartung (1997). They detected phaseic acid, dihydrophaseic acid and the glucose ester of ABA in the thallose liverwort *Riccia fluitans* L., suggesting that degradation of ABA may occur through biochemical pathways similar to those known for tracheophytes.

The occurrence of 9'-*cis*-neoxanthin in bryophytes further indicates that an important precursor of the indirect biosynthetic pathway of ABA also exists in bryophytes (Takaichi & Mimuro 1998). Knowledge of the direct and indirect functional involvement of ABA in bryophytes is limited in comparison with our understanding of its functional roles in vascular plants

(Takezawa *et al.* 2011). For instance, the ABA-mediated biochemical processes in vascular plants include stomatal closure and protein synthesis (Gomez *et al.* 1988; Mundy & Chua 1988; Bartels *et al.* 1990). Generally, in non-tracheophytes where ABA and ABA-like substances have been detected in bioassays, no clear physiological functions of ABA could be demonstrated, suggesting alternative functions to those in vascular plants (Hartung 2010).

Ethylene and ethylene generators. Ethylene, unlike the rest of the other plant hormone compounds is a gaseous hormone. Of all the recognised plant growth substances, ethylene has the simplest structure. It is produced in all higher plants and is usually associated with fruit ripening and the triple response (slowing of stem elongation, stem thickening and curvature of stem) (Salisbury & Ross 1992). Ethylene production in bryophytes has been demonstrated for the liverwort *Pellia epiphylla* (Thomas *et al.* 1983) and the moss *F. hygrometrica* (Rowher & Bopp 1985). However, the physiological role of ethylene in bryophytes needs to be investigated as it is not clear at the moment (Von Schwarzenberg 2009). In the genome of *P. patens*, two putative genes encoding ACC-synthases (ethylene precursor, 1-aminocyclopropane-1-carboxylic acid) were detected (Rensing *et al.* 2008). It was also shown that six ETR-like ethylene receptors are encoded in *P. patens*, from which at least one is able to bind ethylene (Wang *et al.* 2006).

Other growth regulators

Salicylic acid (SA). Salicylic acid is involved in endogenous signaling in plant cells, mediating plant defense against pathogens. Christianson & Duffy (2003) have shown that salicylic acid and acetylsalicylate can inhibit the later stages of bud formation in *F. hygrometrica* in a dose-dependent manner. This indicates that mosses might use these substances as developmental signals. However, more data are necessary to understand their distribution and signal transduction mechanisms in the bryophytes.

Jasmonates (JA). JA are a group of plant hormones that have an important role in controlling defense responses to a wide range of biotic stresses (arthropod herbivores and necrotrophic pathogens, UV radiation and ozone, and depending on the plant species, male and female reproductive development) (Howe & Jander 2008; Glazebrook 2005; Browse 2005; Browse & Howe 2008). In general, JA promotes defense and reproduction while inhibiting growth-related processes such as cell division and photosynthesis. Jasmonic acid and its precursor (*cis*-(+)-OPDA) are derived from oxygenated polyunsaturated fatty acids called oxylipins (Andreou *et al.* 2009). A few studies have described the occurrence and function of cyclopentanones and cyclopentenones as an important group of oxylipins in flowering plants (Browse 2009a, b). However, our knowledge of oxylipins in non-flowering plants is still scarce (Andreou *et al.* 2009). One of the important enzymes in oxylipin metabolism is AOC (allene oxide cyclase). As *P. patens* serves as a model system for nonflowering plants, Stumpe *et al.* (2010) investigated the formation of cyclopentanones and cyclopentenones by analyzing recombinant AOCs and putative functions of these AOC products via target-knockout mutants of *P. patens*. An EST library from *P. patens* harboured two sequences with similarity to AOCs. The recombinant PpAOC1 and PpAOC2 formed the corresponding cyclopentenone, but this cyclopentenone cannot be a precursor of JA because it has an octenyl instead of pentenyl side-chain. As *P. patens* is JA-deficient but able to accumulate *cis*-(+)-OPDA, Stumpe *et al.* (2010) investigated the possible function of cyclopentanones via targeted knockout mutants of PpAOC1 and PpAOC2. Targeted disruption of single members of the two PpAOC genes resulted in reduced fertility and in defective sporogenesis. Both mutants developed capsules (sporophytes) that did not release mature meiospores. It seems that both genes are required for fertilization, spore maturation and for subsequent dehiscing of the capsules. Described phenotypes suggest that a role of oxylipins in reproductive development of plants is evolutionarily conserved, but is specified differentially in different branches of the plant kingdom, as was described for auxin (Ludwig-Mueller *et al.* 2009) and gibberellin signaling (Vandenbussche *et al.* 2007).

Brassinosteroids (BRs). BRs are growth-promoting steroid hormones that regulate diverse physiological processes in plants. There is no report on brassinosteroid function in bryophytes. Kim *et al.* (2002) have demonstrated the occurrence of a BR, castasterone in a liverwort, *Marchantia polymorpha* L.. In addition, the presence of a brassinolide which is biosynthesized from castasterone, was suggested. Although physiological roles of BRs in bryophytes have not yet been established, the result implies that BRs are probably involved in regulation of some events in growth and differentiation of these plants.

Strigolactones (SLs). SLs are implicated in inhibition of shoot branching. Both strigolactones and karrikins can regulate *A. thaliana* seed germination and seedling photomorphogenesis in a *MAX2*-dependent manner, but only strigolactones inhibit shoot branching. The moss *Physcomitrella patens* utilizes strigolactones and MAX2 orthologs are present across the land plants, suggesting that this signaling system could have an ancient origin (Waters *et al.* 2011).

As the liverwort *Marchantia polymorpha* lacks the CCD8 gene (Carotenoid Cleavage Dioxygenase), it has been suggested that an alternative (more ancient) CCD8-independent SL-biosynthesis pathway would operate in this basal embryophyte and in Charales (Delaux *et al.* 2012). Moreover, the MAX1 gene, encoding a cytochrome P450 (Booker *et al.* 2005) is present in all embryophytes except the moss *P. patens* and the liverwort *M. polymorpha*, and absent from algae genomes (Proust *et al.* 2011; Nelson & Werck-Reichhart 2011; de Saint Germain *et al.* 2013). As *P. patens* produces complex SLs another, P450 may ensure MAX1 function, or the final steps in SL synthesis are different in moss, again highlighting flexibility in the SL synthesis pathways. Genome sequencing and strigolactone quantification in other land plants (e.g. hornworts) and algae groups are needed for a better understanding of evolution of the SL pathway.

Karrikins (KA). This group of plant growth regulators is found in the smoke of burning plant material. They stimulate seed germination. However, there are no data so far on whether karrikins can influence moss spore germination or development, as do strigolactones (Waters *et al.* 2011).

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Botanica SERBICA

REZIME

Regulatori rastenja kod briofita

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Briofite, iako spadaju u više biljke, i predstavljaju drugu grupu po brojnosti terestričnih biljaka posle cvetnica, neuporedivo su slabije istražene po pitanju brojnih bioloških procesa i fenomena. U ovom radu dat je pregled fenomena tokom procesa razvića kod briofita. Posebna pažnja je data regulatorima rastenja i njihovom uticaju na razviće briofita.

Ključne reči: briofite, mahovine, jetrenjače, regulatori rastenja, razviće