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PHYTOHORMONES IN THE REGULATION OF GROWTH AND DEVELOPMENT OF WATER FERNS OF SALVINIACEAE FAMILY: A REVIEW

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Water ferns of the Salviniaceae family are successfully used for bioremediation and bioindication of contaminated waters. Due to intensive propagation they are able to produce a great volume of biomass enriched with natural plant growth regulators. Simultaneously, water ferns have become an impediment to the use of water resources through the fast spread. Their growth and development is under control of phytohormones, which are main chemical messengers regulating the responses to environmental changes. Today hormonal system of water ferns of the Salviniaceae family remains understudied. In this review, we analyzed and summarized the literature data and the results of our own research about the role of auxins, cytokinins, gibberellic, abscisic, salicylic and jasmonic acids in regulation of growth and development of water ferns from *Salvinia* and *Azolla* genera emphasizing the specific hallmarks of these phytohormones in ferns. We have submitted brief information about methodological approaches for endogenous phytohormones determination in water ferns of the Salviniaceae family. The effects of exogenous regulators on growth, development and tolerance of water macrophytes from *Salvinia* and *Azolla* genera were discussed, as well as the possibility of using water ferns to create ecological biofertilizers.

Keywords: *Salvinia* and *Azolla* genus, phytohormones, growth regulation, resistance

INTRODUCTION

Phytohormones are considered the most important endogenous substances in the modulation of physiological and molecular responses that ensure the survival of plants under adverse conditions. Auxins (IAA), gibberellins (GAs), cytokinins (CKs), abscisic (ABA) and salicylic (SA) acids, and jasmonates (JA) coordinate all stages of plant ontogenesis. Phytohormones interact with each other, forming a super-complex network of closely intertwined pathways of biosynthesis, metabolism, transport and signaling, forming responses to external influences (Kosakivska *et al*., 2022a; Liu *et al*., 2017; Munné-Bosch & Müller, 2013). The presence of phytohormones in representatives of different taxa, the uniformity of their main structural elements indicate that these compounds arose at the earliest stages of evolution. Vascular spore plants are among the most ancient higher plants, having originated more than 300 million years ago. The most widespread among them are representatives of the phylum Polypodiophyta. They grow in all climatic zones, are distinguished by a significant diversity of life forms, and have a wide range of adaptive features, which allows them to exist in any environmental conditions (Kosakivska *et al*., 2019). In recent decades, hydrophyte ferns, in particular representatives of the Salviniaceae family, have attracted special attention from biologists and ecologists, as they are promising plants for phytoremediation and bioindication (Kosakivska *et al*., 2022b). The hydrophyte fern family Salviniaceae unites two genera: Salvinia and Azolla (Smith *et al*., 2006). The genus Salvinia, characterized by high growth rates, adaptability and resistance to adverse environmental factors, includes twelve species. Within the temperate-meridional range, the species occurs sporadically, is widespread in mesoeutrophic and eutrophic freshwater closed or low-flow reservoirs, with a muddy-sandy bottom and irrigation canals. Only one wild relict species *Salvinia natans* L. is found in Ukraine (Dubyna *et al*., 2003). Significant populations of *S. natans* have been reported in the north of Europe, in particular, in the delta of the Vistula River (Gałka & Szmeja, 2013). The genus Azolla unites eight species of ferns, which are characterized by small size and bright color. Due to the considerable water repellency of the scaly fronds, the fern floats on the surface of stagnant water in tropical, subtropical, and temperate regions around the world (Kumar *et al*., 2021; Raja, 2014). A unique feature of ferns of this genus is the formation of symbiosis with nitrogen-fixing cyanobacteria *Nostoc azollae* (Eily *et al*., 2019).

To understand the mechanisms of plant growth and development, studying the hormonal regulation system is crucial. The hormonal system of hydrophytic ferns of the Salviniaceae family remains one of the most poorly understood (Kosakivska *et al*., 2016). Therefore, the purpose of our review is to analyze and summarize the literature information and the results of our own research devoted to the study of endogenous phytohormones and the effects of exogenous phytohormones on the growth, development and tolerance of the Salviniaceae family ferns.

Methodological approaches for endogenous phytohormones determination in the Salviniaceae family. The quantification of endogenous phytohormones in plant tissues is a challenging analytical process due to their extremely low content (nanograms or picograms per gram of fresh weight). Currently, high-performance liquid chromatography (HPLC) and ultra-high-performance liquid chromatography (UHPLC) methods coupled with a mass spectrometric detector equipped with triple quadrupole MS/MS are used for analytical determination of phytohormones. Solid-state extraction cartridges are employed for the extraction of phytohormones from complex plant matrices (SPE) (Dobrev *et al*., 2012; Kosakivska *et al*., 2020). Despite their distinctive morphology, significant adaptation potential, wide distribution and effective use in phytoremediation, the phytohormonal complex of species in the Salviniaceae family remains inadequately researched. The first successful attempt to analyze endogenous cytokinins in *Azolla* sp. was reported by T. Hashizume *et al*. (1986). They employed preparative liquid chromatography to obtain separate fractions of the primary extract, after which substances with cytokinin activity were quantified using a gas chromatograph in tandem with a mass spectrometer. To quantify IAA in symbiotic *Arthrobacter* species isolated from *Azolla pinnata* R. Br. and *Azolla filiculoides* Lam., researchers used a reaction with Salkovsky's reagent in the presence of tryptophan in the culture medium (Forni *et al*., 1992). They emphasized the need for considering the presence of symbionts that also actively produce phytohormones when determining phytohormones in Azolla species (Forni *et al*., 1992; De Vries *et al*., 2018). W. A. Stirk and J. Van Staden (2003) detected cytokinin activity in different fractions from *A. filiculoides* and *Salvinia molesta* D. Mitch. (*Salvinia adnata* Desv. according to the modern nomenclature of ferns, http://www.theplantllst.org) extracts using a soybean callus bioassay. They employed cation exchange resin, paper chromatography, and preparative HPLC for the purification of plant extracts and culture media and their fractionation. J. Hur and A. R. Wellburn (1994) determined the levels of ABA in *A. pinnata* using the radioimmunoassay method. A. Chiappetta and A. M. Innocenti (2006) studied zeatin translocation in *A. filiculoides* stem cells using immunocytochemical methods, revealing differences in zeatin translocation compared to angiosperm plants. G. D. Arthur *et al.* (2007) investigated sixteen forms of cytokinins during the growth and composting of *S. molesta* by HPLC, using a diode-matrix analyzer and a Micromass ZMD 2000 single-quadrupole mass spectrometer equipped with an electrospray ionization interface as detectors. IAA analysis was conducted using a specific competitive ELISA method with IAA-antibodies and IAA-alkaline phosphatase indicator, as well as a fluorescent detector attached to HPLC. The study also analyzed the changes in the levels of endogenous IAA, GA_3, and ABA after the addition of tryptophan to the growing medium of *A. pinnata*, while hormone methylation was employed for identification and quantitative analysis. The prepared samples were separated in a glass column of a gas chromatograph equipped with a flame ionization detector (El-Araby *et al*., 2010). The levels and distribution of endogenous IAA and ABA (Voytenko *et al*., 2016), GA_3 (Vasyuk *et al*., 2016), active and store cytokinins (Vedenicheva *et al*., 2016) in *S. natans* sporophytes at different ontogeny stages were determined using HPLC-MS with diode-matrix detector and a single-quadrupole mass spectrometer.

Auxins in ferns of the Salviniaceae family. All natural auxins are weak organic acids with an aromatic skeleton and a carboxylic acid residue. Auxins play a central role in the plant growth and development control under various conditions of existence. Auxins activate the division and elongation of cells, stimulate the formation and support the growth of lateral roots, control the development of vascular tissues, vegetative and reproductive organs, accelerate seed germination, fruit ripening, are involved in tropism and apical dominance, the formation of stress resistance (Gallavotti, 2013; Gomes & Scortecci, 2021; Velasquez *et al*., 2016). Auxins exist in plants in a free and conjugated state (Korasick *et al*., 2013). The most widespread among auxins is indole-3-acetic acid (IAA) found in bacteria, fungi, spore and seed plants, insects and humans (Ross & Reid, 2010). IAA is synthesized from tryptophan amino acid in two steps. This conservative path of biosynthesis is present in all representatives of the plant kingdom (Zhao, 2014). The site of auxin synthesis is located in the apical meristem of shoots and roots, as well as in the young parts of shoots and leaves (Olatunji *et al*., 2017; Wang *et al*., 2015). The effects of auxins are determined by the concentration of active forms of the hormone in plant tissues. Auxin homeostasis depends on the intensity of biosynthesis and degradation of the hormone and the direction and rate of transport flows (Korasick *et al*., 2013). Auxin transport occurs in an active and passive way. Passive transport does not have its own regulation and depends on the rate of the phloem flow. By contrast, active polar transport is energy-dependent and is provided by transporter proteins encoded by *AUX1*, *PIN* and *PGP* genes (Mohanta *et al*., 2018; Simon *et al*., 2016). Physiological effects of auxin are manifested in crosstalk with other phytohormones which regulate synthesis, degradation, transport, signaling and location of each other (Mazzoni-Putman *et al*., 2021).

The available information on auxins in the Salviniceae family is limited and sometimes contradictory (**Table 1**), primarily based on the results obtained from the application of exogenous growth regulators (**Table 2**). Under constant conditions of lighting, temperature and nutrition, exogenous IAA, 1-naphthalene-acetic acid (NAA) or 2,4-dichlorophen-oxyacetic acid (2,4-D) added to the culture medium of the water fern *Salvinia rotundifolia* Willd. (*Salvinia auriculata* Aubl. according to the modern nomenclature of ferns, http://www.theplantllst.org) stimulated the elongation of internodes and growth of submerged fronds, while the edges of floating fronds were curled and narrowed. However, after four weeks, the effects of auxin treatment diminished. Low concentrations of auxins (0.1 to 1 mg·L^{-1}) induced an increase in fresh (FW) and dry (DW) weight of ferns, while high concentrations (>1 mg·L^{-1}) inhibited their growth (Gaudet & Koh, 1968). Exogenous IAA has been shown to slow down the senescence of *S. molesta* fronds. However, treatment with IAA led to a decrease in the content of chlorophyll, proteins and carbohydrates, as well as catalase activity in the separated fronds during the period from 48 to 144 hours. These changes occurred more slowly compared to samples not treated with the hormone (Pati & Bhattacharjee, 2013).

Addition of tryptophan, a precursor of IAA synthesis, to the culture medium of *A. pinnata* resulted in an increase in endogenous IAA content, stimulated fern growth and enhanced biomass accumulation. The levels of IAA in fronds increased depending on the concentration of tryptophan and the duration of the incubation period. The maximum accumulation of the hormone was observed at a tryptophan concentration of 15 ppm on the 40th day of incubation. However, when the concentration of tryptophan was elevated to 30 ppm, the content of IAA declined, but was still higher than in the absence of tryptophan. The use of tryptophan also shortened the time for the formation of new shoots (El-Araby *et al*., 2010). Similar results were reported by E. S. E. D. Radwan *et al.* (2002), where the addition of tryptophan to the culture medium of *A. pinnata* induced the accumulation of endogenous IAA and intensified fern growth. Spraying *Azolla microphylla* Kaulf. (two strains), *Azolla caroliniana* Willd. and *A. pinnata* with IAA solution induced an increase in the frequency of sporulation and the amount of microsporocarps. An increase in the number of megasporocarps was observed in *A. microphylla* at a hormone concentration of 4 μg·mL^{-1}, in *A. caroliniana* at 6 μg·mL^{-1} and in *A. pinnata* under the action of all concentrations of IAA. The optimal concentration of IAA for sporulation induction in these species was 6 μg·mL^{-1}. In two strains of *A. microphylla*, exogenous naphthaleneacetic acid (NAA) and indolebutyric acid (IBA) at concentrations of 2–10 μg·mL^{-1} significantly enhanced sporulation and the number of sporocarps. The combined use of IAA and GA_3 led to the formation of an even greater number of megasporocarps (Kar *et al*., 2002). Application of exogenous GA and IAA had a positive effect on the formation of sporocarps in *A. microphylla*. Exogenous addition of these phytohormones significantly increased the rate of fern biomass accumulation, even in the presence of inhibitors dinitrophenol, sodium azide, and thiourea (Kar & Singh, 2002). After spraying *A. filiculoides* with a solution of IAA at a concentration of 5 μg·mL^{-1}, the rate of sporulation and the number of spores increased, and the female/male and C/N ratio elevated (Xu *et al*., 2021).

Table 1. **Current state of studies on endogenous phytohormone in water ferns of the Salviniaceae family**

Hormone	Plant species	Source of material analyzed	Reference
Indole-3-acetic acid	*Salvinia molesta*	In culture medium, and compost	Arthur *et al*., 2007
Indole-3-acetic acid	*Azolla pinnata*	In floating fronds	El-Araby *et al*., 2010; Radwan *et al*., 2002
Indole-3-acetic acid	*Salvinia natans* L.	In floating and submerged fronds, and sporocarps at different phases of ontogenesis	Voytenko *et al*., 2016
16 isoprenoid cytokinins	*Salvinia molesta*	In the whole plant	Arthur *et al*., 2007
Zeatin, zeatin riboside, dihydrozeatin, isopentenyladenine isopentenyladenosine	*Azolla filiculoides*	In the whole plant	Stirk, Van Staden, 2003
Zeatin, zeatin riboside, dihydrozeatin	*Salvinia molesta*	In the whole plant	Stirk, Van Staden, 2003
Trans-zeatin, *cis*-zeatin, zeatin riboside, zeatin-*O*-glucoside, isopentenyladenine, isopentenyladenosine	*Salvinia natans*	In floating and submerged fronds, and sporocarps at different phases of ontogenesis	Vedenicheva *et al*., 2016
Giberellic acid	*Azolla pinnata*	In floating fronds	El-Araby *et al*., 2010
Giberellic acid gibberellin-like substances (GLS)	*Salvinia natans*	In floating and submerged fronds, and in sporocarps at different phases of ontogenesis	Vasyuk *et al*., 2016
Abscisic acid	*Azolla pinnata*	In culture	Hur, Wellburn, 1994
Abscisic acid	*Azolla pinnata*	In culture	El-Araby *et al*., 2010
Abscisic acid	*Salvinia natans*	In floating and submerged fronds, and in sporocarps at different phases of ontogenesis	Voytenko, Kosakivska, 2017
Salicylic acid	*Azolla filiculoides*	In floating and root-like structure	De Vries *et al*., 2019

Water fern *S. molesta*, characterized by fast growth rates, is considered a promising organic fertilizer. It has been reported that the concentration of IAA in the organs of *S. molesta* reached 393.6 pmol·g^{-1} DW, significantly higher than in the culture medium (30.8 pmol·g^{-1} DW). The concentration of IAA in compost reached 148.1 pmol·g^{-1} DW, 62% lower compared to plant material. The filtrate collected on the 7th and 14th days had biological activity indicating that auxin-like compounds were released from *S. molesta* during decomposition (Arthur *et al*., 2007). The relationship between growth processes and the distribution and content of IAA in the organs of the *S. natans* sporophyte was analyzed. It was shown that the accumulation of IAA in the submerged fronds occurred during the growth of their pubescence (Voytenko *et al*., 2016), which allows us to assume that the physiological function of IAA in the submerged fronds of *S. natans* is similar to that in the roots of higher vascular plants (Benkova & Hejatko, 2009). A high content of free IAA was recorded in clusters of mature sporocarps during the dying off of vegetative organs and spore maturation, indicating a possible involvement of the hormone in the regulation of the spore maturation process (Voytenko *et al*., 2016).

Arthrobacter isolated from the cavities of *A. pinnata* and *A. filiculoides* floating fronds and microsporocarps produced IAA when tryptophan was added to the medium at concentrations of 100, 200, 400, and 600 µg·mL^{-1}. The maximum production of the hormone by bacteria located in the frond cavities was observed during the first two days of incubation and amounted to 7.3 and 10.1 µg·mL^{-1} at a concentration of 600 µg·mL^{-1} tryptophan, while bacteria localized on the microsporocarps of *A. filiculoides* produced 4.4 µg·mL^{-1} in a medium containing 400 µg·mL^{-1} tryptophan. In the absence of tryptophan, IAA was not produced, and part of tryptophan was transformed into *N*-acetyl-L-tryptophan (Forni *et al*., 1992). 2,4-dichlorophenoxyacetic acid (2,4-D) reduced the negative effects of toxic sodium (Na) and arsenic (As) in *S. natans*. The hormone moderated the effects of oxidative stress caused by heavy metals (Dolui *et al*., 2022). Dried *Azolla*, together with IAA-producing bacteria, is used as a biofertilizer to improve the growth of agricultural crops (Raut *et al*., 2017). The use of organic extracts is a relevant direction for improving the productivity and yield of plants in agriculture. They are used to intensify growth processes, modify the chemical composition, stimulate photosynthetic activity, increase antioxidant protection, and optimize the development of the root system. Treatment with organic extracts improves the assimilation of nutrients from the soil by plants and contributes to the progresses in agriculture (Atteya *et al*., 2022).

In conclusion, auxins have been identified in a number of species of the Salviniaceae family. They are involved in the regulation of sporophyte growth and development, affect morphometric traits and sporulation, and induce the formation of spores. Due to the high content of auxins, species of the Salviniaceae family are proposed to be used as organic fertilizers.

Cytokinins in ferns of the Salviniaceae family. Cytokinins (CKs) are the family of pleiotropic phytohormones that regulate the vital functions of plant organism. Isoprenoid CKs are widespread in wild, while aromatic CKs have only been synthesized chemically for a long period are adenine derivatives with an aromatic ring or an isoprenoid chain at the N^6 position. CKs occur as free bases, such as isopentenyladenine, dihydrozeatin, *cis*-zeatin, and *trans*-zeatin, which are considered active hormone forms, as well as their nucleosides and nucleotides. While nucleotides are usually inactive, the question about activity of nucleosides remains still open (Nguyen *et al*., 2021). CK molecules can also be conjugated to a glucose moiety, with *N*-glucosides likely forming for irreversible hormone deactivation, while *O*-glucosides are thought to be a reversible storage metabolite (Kieber & Schaller, 2018). Although assumptions have previously been made about the functions of individual CK metabolites (Mok & Mok, 2001), they have not been decisively established to date. Manipulating the genes that encode key enzymes of CK biosynthesis (isopentenyl transferase and LONELY GUY) and degradation (cytokinin dehydrogenase) allows for the production of mutants with elevated or reduced CK levels, suggesting a functional difference between CK metabolites (Frébort *et al*., 2011). CKs act as signaling molecules at very low concentrations and participate in transduction of both local and long-distance signals. The perception of CK signals by histidine kinase receptors localized on the endoplasmic reticulum membranes is followed by transmission of the phosphate through histidine phosphotransfer proteins into the nucleus to response regulators of A- and B-type (Zürcher & Müller, 2016). CKs, in crosstalk with other phytohormones, regulate cell cycle progression (Schaller *et al*., 2014), meristem formation (Kurepa *et al*., 2019), photosynthesis and senescence (Hönig *et al.*, 2018), absorption of macro- and micronutrients (Pavlů *et al*., 2018), reproductive development (Terceros *et al*., 2020), response to biotic and abiotic stressors etc. (Cortleven *et al*., 2019; Mandal *et al*., 2022). CKs are ancient and highly conserved molecules that have been identified in almost all known organisms (Spíchal, 2012). Nevertheless, it is apparent that CKs progressively acquired functions of growth-regulating hormones in plants throughout evolution. Components of CK signaling pathways likely appeared evolutionarily in plants of various taxa they developed. The crucial moment in this process was the emergence of land photosynthetic plants (Pils & Heyl, 2009). To understand the origin and evolutionary pattern of CKs, comparative analysis of the distribution and functioning of these hormones in cryptogamous and spermatophyte plants is necessary. Water ferns of Salviniaceae family are the least studied in this regard.

The earliest investigations into the role of cytokinins in development of ferns from the Salviniaceae family were associated with exogenous treatment (**Table 2**). G.Blackman, (1961) noted that low concentration of kinetin stimulated an increase in the area of the youngest fronds of *S. natans*, while inhibiting internode elongation. Later, J. J. Gaudet and D. V. Koh (1968) discovered that kinetin at concentrations ranging from 0.01 mg·L^{-1} to 10 mg·L^{-1} FW had an inhibitory effect on *S. rotundifolia* plants after four weeks of exposure, resulting in a decrease in weight of up to one-third at the lowest concentration. After four weeks of exposure, submerged fronds exhibited a ball-like structure. However, during the first week of exposure to kinetin concentration of 0.01–5 mg·L^{-1}, an initial stimulatory effect on floating frond growth was reported.

Plants exposed to kinetin at 0.01 mg·L^{-1} began to produce new floating fronds in 20 days. The authors also revealed the inhibitory effect of kinetin on the respiration of plant fragments. Other cytokinins, such as adenine and BAP, had a similar influence on *S. rotundifolia* growth (Gaudet & Koh, 1968). Additionally, it was shown that *Salvinia* plants have the ability to uptake kinetin-8^{14}C from the culture medium, which was correlated with the inhibition of stem elongation and floating frond growth (Gaudet & Huang, 1967).

In a more recent study, J. de Vries *et al*. (2016) characterized the influence of cytokinin and auxin on removed roots of *A. filiculoides*. They found that *trans*-zeatin promotes root meristem development whereas indole-3-acetic acid restricts it. This effect was opposite to that observed in Arabidopsis and other seed plants, where cytokinins are known to act as a negative regulator of root development (Chapman & Estelle, 2009). The authors suggest that their data support the idea of the evolution of ferns' root meristems from shoot meristems (de Vries *et al.*, 2016). This opinion seems dubious in view

Table 2. **Current state of studies on exogenous phytohormone treatment on water ferns of the Salviniaceae family**

Hormone	Plant species	Effect	Reference
Indole-3-acetic acid (IAA)	*Salvinia molesta*	Slowed down the aging process of fronds	Pati, Bhattacharjee, 2013
IAA, 1-naphthalene acetic acid (NAA) 2,4-dichlorophen-oxyacetic acid (2,4-D)	*Salvinia rotundifolia*	Promoted submerged fronds' growth and elongation of internodes	Gaudet, Koh, 1968
IAA	*Azolla filiculoides*	Increased sporulation and the number of spores produced, raised female/male and C/N ratios	Xu et al., 2021
IAA, NAA, indole butyric acid (IBA)	*Azolla caroliniana* *Azolla microphylla* *Azolla pinnata*	Significantly increased sporulation and the number of sporocarps, and enhanced fern growth	Kar *et al.*, 2002
Kinetin	*Salvinia natans*	Increased the area of the youngest fronds, and inhibited internode elongation	Blackman, 1961
Kinetin	*Salvinia* sp.	Inhibited stem elongation and floating frond growth	Gaudet, Huang, 1967
Kinetin	*Salvinia rotundifolia*	Decreased the accumulation of fresh weight and induced the appearance of ball-like structure of submerged fronds, along with inhibiting respiration	Gaudet, Koh, 1968
Trans-zeatin	*Azolla filiculoides*	Promoted meristem development and cell wall changes in submerged fronds and triggered *CYTOKININ RESPONSE 1* gene expression	de Vries *et al.*, 2016
Kinetin	*Azoll caroliniana*	Increased sporocarp germination	Singh *et al.*, 1990
Benzyl amino purine (BAP)	*Azolla rubra*	Induced sporocarp development	Sini *et al.*, 2015
Gibberellic acid	*Salvinia rotundifolia*	Increased the accumulation of fresh and dry weight	Gaudet, Koh, 1968
Gibberellic acid	*Azolla microphylla* *Azolla caroliniana* *Azolla pinnata*	Induced the frequency of sporulation while decreased the number of megasporocarps and increased the number of microsporocarps	Kar *et al.*, 1999; 2002

of the fact that the ferns of the Salviniaceae family are rootless and the so called “roots” are in fact the submerged fronds (Gałka & Szmeja, 2013). In our view, this explains the stimulating effect of cytokinin on meristem development in *A. filiculoides*. It is worth noting that exogenous cytokinin treatment resulted in pronounced cell wall changes modifying expansin expression, and triggered specific components of cytokinin signaling pathways (*CYTOKININ RESPONSE 1*) in *A. filiculoides* (de Vries *et al*., 2016).

Cytokinins play a crucial role in the reproductive processes of *Azolla* ferns. Treatment with 100 ppm of kinetin increased sporocarp germination of *A. caroliniana* in sterile culture by 67% compared to 40% in the control group. A mixture of kinetin and gibberellic acid (100 ppm each) resulted in 84% sporocarp germination (Singh *et al*., 1990). Similarly, the addition of BAP to the culture medium for *in vitro* growth of *Azolla rubra* R. Br., induced the development of sporocarps in dose-response manner, even though it is a non-sporocarp producing fern under natural conditions that propagates by vegetative fragmentation (Sini *et al*., 2015).

Endogenous cytokinins were studied in *A. filiculoides* and *S. molesta* using soybean callus bioassay. After 31 days of fern cultivation in laboratory conditions, cytokinin-like activity co-eluted with isopentenyladenine, isopentenyladenosine, zeatin, zeatin riboside and dihyrdozeatin for the *A. filiculoides* plant extracts and with zeatin, zeatin riboside and dihyrdozeatin for the *S. molesta* plant extracts was detected. The same results were obtained when the culture medium in which the ferns had been growing was analyzed (Stirk & Van Staden, 2003). A more detailed investigation of *S. molesta* by HPLC demonstrated the presence of sixteen isoprenoid cytokinins, including *trans*- and *cis*-zeatin, dihyrdozeatin, isopentenyladenine and their metabolites, resulting in a total cytokinin content of 81.62 pmol·g^{-1} DW. However, when the plant material was composted for 14 days in the air, only twelve cytokinins were detected, and the total cytokinin content decreased by 17%, mainly due to a decline in the concentrations of all the *t*-Z type cytokinins (Arthur *et al*., 2007). These findings suggest that *A. filiculoides* and *S. molesta* can be used as source of plan growth regulators for agriculture. Moreover, they indicate that water ferns can influence the water in which they are grow and thus manipulate the growth of other water plants.

Gas chromatography-mass spectrometry analysis revealed the presence of five cytokinins (isopentenyladenine, isopentenyladenosine, zeatin, *trans*- and *cis*-zeatin riboside) in *A. pinnata* plants growing in culture. The dominant cytokinin was isopentenyladenosine, which comprised approximately 66% of the total cytokinin level. The concentration of zeatin was about an order of magnitude lower and amounted to 0.25 ng·g^{-1} FW (Hashizume *et al*., 1986).

The localization of cytokinins in tissues of *A. filiculoides* has been studied using immunocytochemical method, and some specific traits have been established (Chiappetta & Innocenti, 2006). It was shown that zeatin was located in a sheet of numerous contiguous cells of the endoderm and parenchyma, which encircle vascular tissues, whereas in seed plants, cytokinins are usually translocated via vascular bundles. This cytokinin was also detected in a few shoot meristem target cells and in numerous contiguous cells of “root” meristem. Unfortunately, these authors did not distinguish between floating and submerged fronds and did not take into account the absence of roots in the discussion of their results. Another interesting finding concerns the abundance of zeatin in the teat cells delimiting the pore that connect the frond cavities with the environment. *A. filiculoides* is known to coexist in symbiosis with the diazotrophic cyanobacterium *Anabaena azollae*, living in frond cavities. Therefore, cytokinins could be involved in the regulation of movement and growth of this microorganism (Chiappetta & Innocenti, 2006).

The dynamics of endogenous cytokinins in *S. natans* during one vegetative season were studied using HPLC method (Vedenicheva & Kosakivska, 2016). The highest total active free cytokinin levels was detected in floating fronds in the period of intensive sporophyte growth, whereas in submerged fronds, cytokinin content was twice lower, indicating functional difference of these organs and a more significant role of floating fronds in hormone production. The decline of growth intensity was accompanied by a decrease in total cytokinin amount and the emergence of zeatin-*O*-glucoside. High cytokinin levels were determined in sporocarps where spore intensive formation and maturation occurred. These results confirmed the participation of cytokinins in the regulation of *S. natans* growth and reproduction (Vedenicheva & Kosakivska, 2016).

Thus, despite the scarcity of information about CKs in water ferns (**Table 1**), it is possible to consider the phytohormones of this class as growth regulators for these plants. Evidently, the functioning of CKs ferns of Salviniaceae family is similar to that in seed plants, although certain specificity was noted. Further investigations on the participation of CKs in the control of aquatic ferns' development and reproduction are of practical importance because these plants are agronomically valuable as biofertilizers and phytoremediants, but on the other hand, they have become an impediment to the use of water resources due to fast spread.

Gibberellins in ferns of the Salviniaceae family. Gibberellins are a group of diterpenoid hormones that play a critical role in seed germination, cell division and elongation, stem, shoot and root growth, leaf surface expansion, internode number, and flowering induction (Gantait *et al*., 2015; Gupta & Chakrabarty, 2013). In ferns, gibberellins regulate sexual determination, gametophyte formation and development, and spore germination (Vasyuk & Kosakivska, 2015). Each plant species has a unique qualitative and quantitative composition of gibberellins, with some being dominant (active or "working") gibberellins involved in the regulating physiological processes, and others being intermediate links in the synthesis of these hormones (Davière & Achard, 2013). Biologically active gibberellins, such as GA_1, GA_3, GA_4, and GA_7, regulate plant growth under stressful conditions, with the effects depending on stress strength and duration, ontogenetic phase, and plant resistance (Kosakivska & Vasyuk, 2021).

However, gibberellins from species of the Salviniaceae family have received little attention (**Table 1**). Studies have shown that *A. pinnata* stems accumulated 121.1 $ng \cdot mg^{-1}$ FW GA_3 under control cultivation conditions. After adding tryptophan to the nutrient medium at a concentration of 5, 15, and 30 ppm on the tenth day of cultivation, the content of GA_3 increased by 2.6, 4.5, and 3.9, respectively, but declined by the fortieth day. The DW and FW of ferns, which initially reached 4.8 and 90.9 $g\ (m^2)^{-1}$, respectively, increased with tryptophan concentration and reached their peak on the 30th day of incubation at a tryptophan concentration of 15 ppm (El-Araby *et al.*, 2010). In flowering plants, gibberellins act synergistically with auxins and antagonistically with cytokinins and abscisic acid to regulate most morphogenetic processes (Gupta & Chakrabarty, 2013; Tuan *et al*., 2018). It is believed that the addition of tryptophan to the nutrient medium can prevent GA_3 synthesis at various stages of cell elongation growth (Hopkins, 1998).

The distribution of gibberellin-like substances (GLS) in *S. natans* showed that submerged fronds are the main producer of GLS, acting as hormone donors for floating fronds, while GA_3 dominates in the latter. The maximum accumulation of GLS and GA_3

was recorded in clusters of sporocarps during the period of vegetative organs' death, which corresponded to the transition of spores to a state of dormancy and subsequent germination and development of the gametophyte. The high content of GLS and GA_3 during ontogenesis indirectly indicates the involvement of gibberellins in the regulation of growth and development of *S. natans* (Vasyuk *et al*., 2016). It is known that in spore plants, gibberellins control the processes of spore germination (Anterola *et al*., 2009, Zhang & Dai, 2010). Therefore, the use of exogenous gibberellins to optimize the germination of spores and the formation of the gametophyte of ferns in *in vitro* culture is considered promising (**Table 2**). Under constant lighting and temperature conditions, *S. rotundifolia* showed the greatest increase in biomass on the 28th day. At this age, old floating and submerged fronds were dark in color. Addition of exogenous GA_3 to a sterile culture of *S. rotundifolia* at a low concentration induced an increase in FW and DW of ferns by 6.0 and 6.7%, respectively, while high concentrations did not affect biomass accumulation. GA_3 had no effect on the overall morphology of *Salvinia*, except for a slight inhibition of floating fronds area (Gaudet & Koh, 1968). Exogenous GA_3 at a concentration of 2.5 $\mu g \cdot mL^{-1}$ induced an elevation in the frequency of sporulation by 66.0–88.1% and a decrease in the number of megasporocarps and an increase in the number of microsporocarps by 42.8–52.6% in *A. microphylla*, *A. caroliniana* and *A. pinnata*. The combined effect of exogenous IAA and GA_3 induced an increase in the amount of megasporocarps. These results may be useful for the stimulation of megasporocarp formation in *Azolla*, since megasporocarps give rise to new plants after fertilization and spore germination (Kar *et al*., 1999; 2002).

Therefore, gibberellins have been studied in individual species of the Salviniaceae family. They are involved in the regulation of sporophyte growth and development, affect morphometric indicators, induce the formation and germination of megasporocarps, and increase the frequency of sporulation. Species of the genus *Azolla* have been better studied due to their application as biofertilizers.

Abscisic acid in ferns of the Salviniaceae family. Abscisic acid regulates various phases of plant growth and development, including stem cell growth and primary root growth, moisture loss inhibition, wax synthesis and stomatal closure induction, bud dormancy, leaf senescence, starch breakdown, and carbon translocation. ABA protects plants from drought and regulates the accumulation of LEA proteins and proline (Chen *et al*., 2020). ABA is a sesquiterpene (C_{15}), and isomers *cis*- and *trans*-ABA are distinguished based on the spatial position of the carboxyl group near the second carbon atom. The active form of ABA in higher plants is the *cis*-isomer, while the *trans*-isomer is an inactive (Piotrowska & Bajguz, 2011). ABA is synthesized in leaves, roots, stems, and fruits, the main sites of hormone formation are chloroplasts, vascular system, and stomatal closing cells, with ABA accumulating mostly in vacuoles (Boursiac *et al*., 2013; Dejonghe *et al*., 2018; Sakata *et al*., 2014). ABA is transported through the xylem and phloem vessels in acropetal and basipetal directions to all plant organs with the participation of protein transporters (Sakata *et al*., 2014; Seo, 2014).

Studies of ABA in representatives of the Salviniaceae family are limited (**Tables 1** and **2**). The content of endogenous ABA in the culture of *A. pinnata* at different concentrations (30–50–80 $nl \cdot L^{-1}$) of atmospheric O_3 was analyzed. The highest rates of hormone accumulation were recorded at low ozone concentrations. It was shown that during one week of cultivation, fern growth and the intensity of nitrogen fixation (N_2) were inhibited. When the concentration of O_3 increased to 80 $nl \cdot L^{-1}$, the activity of glutamine synthetase (GS) and glutamate dehydrogenase (GDH), the total content of protein, polyamines putrescine and spermidine and xanthophyll-cycle precursor of ABA violaxanthin increased. As the concentration of ozone enhanced, the content of endogenous ABA decreased, which, according to the authors of the article, can be explained by the inhibition of the final stage of ABA biosynthesis by a high concentration of atmospheric O_3 (Hur & Wellburn, 1994). It was shown that the addition of tryptophan to the culture of *A. pinnata* at concentrations of 5, 15, and 30 ppm increased the level of endogenous ABA for ten days, after which it declined from 75.24, 76.2, and 73.7 $ng\cdot mg^{-1}$ to 58.2, 56.7 and 48.6 $ng\cdot mg^{-1}$, respectively, on the fortieth day of incubation (El-Araby *et al*., 2010). During active growth of the *S. natans* sporophyte, free ABA was concentrated in floating fronds (191.0 $ng\cdot g^{-1}$ FW), while during the stationary growth, it was concentrated in submerged fronds (154.4 $ng\cdot g^{-1}$ FW). A slight increase in the content of the conjugated form of the hormone in both floating and submerged fronds occurred during sporocarps formation, while during the initial phases of frond development, its content was at trace level (Voytenko & Kosakivska, 2017). Since ABA synthesis occurs in chloroplasts (Sakata *et al*., 2014), it is possible that the ABA accumulated during intense growth in floating photosynthetic fronds is transported to submerged modified fronds, which mainly serve an absorptive function. The highest amount of free ABA (266.0 $ng\cdot g^{-1}$ FW) was observed in the mature sporocarps of *S. natans* (Voytenko & Kosakivska, 2017). Comparing these findings with the information on the increase in endogenous ABA content in seeds during the nutrient accumulation phase the cessation of cell division (Taiz & Zeiger, 2002), it can be inferred that free ABA plays an active role in the regulation of fern spore maturation. In clusters of sporocarps formed after the death of *S. natans* vegetative organs, ABA was detected in a conjugated state, with an amount of 23.5 $ng\cdot g^{-1}$ FW (Voytenko *et al*., 2016).

Salicylic and Jasmonic acids in ferns of the Salviniaceae family. Salicylic acid (SA) is a phenolic phytohormone involved in the regulation of growth and development, photosynthesis, respiration, and transpiration, as well as responsible for a number of protective reactions and increasing the resistance of plants to a wide range of abiotic and biotic stressors (Janda *et al*., 2014; Roychoudhury *et al*., 2016; Wani *et al*., 2017). In angiosperms, SA is one of the main regulators of their interaction with microorganisms (Cheng *et al*., 2019).

Jasmonic acid (JA), a cyclopentanone derivative of the lipoxygenase pathway of oxidation of polyunsaturated fatty acids, accumulates in plant organs and tissues as a result of the expression of jasmonate-induced genes (Babenko *et al*., 2015; 2017). JA and its derivatives are involved in the regulation of the development of reproductive organs and the embryo, senescence, sex determination, seed germination, root growth, tuber formation, phototropism, adaptation (Chini *et al*., 2016; Wasternack & Strnad, 2016). In ferns, JA was first identified by radioimmunoassay using jasmonate-specific antibodies (Parthier, 1990). Lipoxygenase activity was recorded in *S. natans*, which proves the presence of JA in fern tissues (Babenko *et al*., 2016; Kosakivska *et al*., 2016). It has been reported that in ferns, JA stimulates the process of cell division, promotes the growth of rhizoids and the early development of gametophytes (Camloh *et al*., 1996). The role of JA and SA is clearly established in plant defense responses against pathogens (Pieterse *et al*., 2012; Robert-Seilaniantz *et al*., 2011). However, the function of these hormones in the interaction of representatives of the Salviniaceae family with symbionts is less known. The most studied is the symbiosis of *A. filiculoides* with nitrogen-fixing cyanobacteria (Carrapiço, 2010).

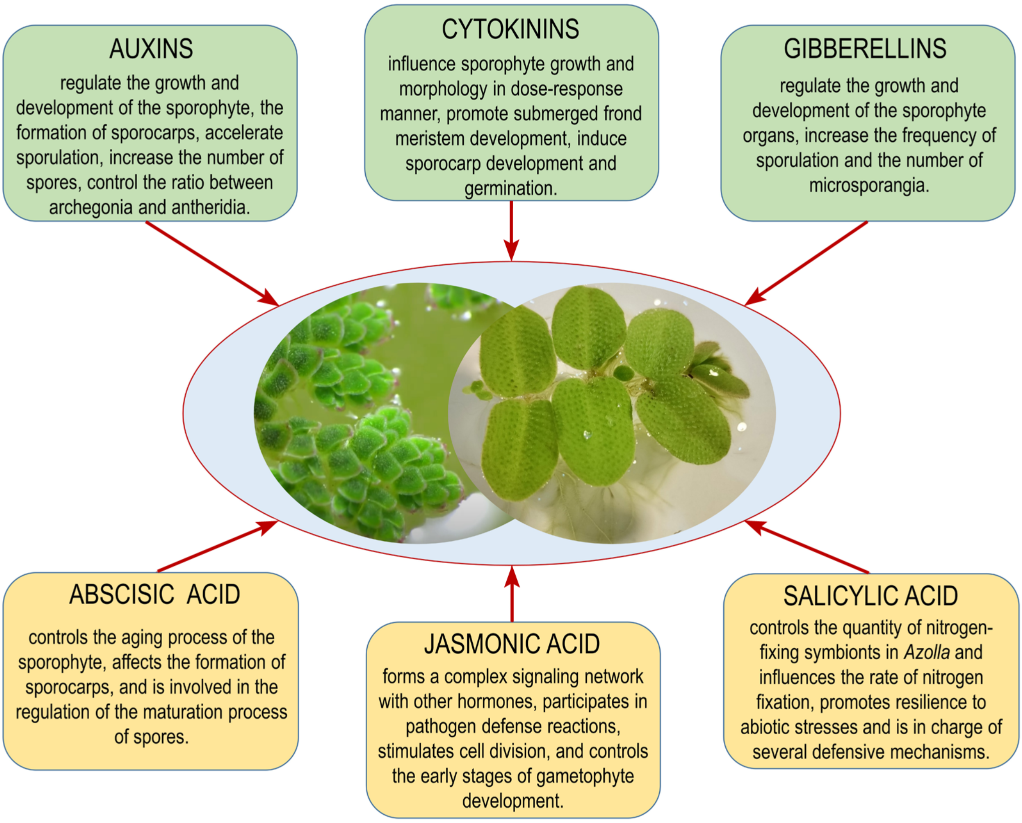
J. De Vries *et al*. (2018) sequestered the genome of *A. filiculoides* and found that the species possesses most of the genes required for the synthesis and reception of JA and SA. Treatment with exogenous methylated SA induced changes in the number of cyanobacteria, indicating the involvement of SA in the regulation of the interaction between *Azolla* and the nitrogen-fixing symbiont. The number of cyanobacteria not only significantly increased after long-term exposure to methylated SA, but SA treatment also negatively affected the expression of the *NaNifE* gene involved in the regulation of the biosynthesis of the nitrogenase iron-molybdenum cofactor, which inhibited the process of nitrogen fixation by the cyanobiont. In the case of *Azolla* infection by pathogenic organisms, this plays an important role because the pathogens use the hosts as a source of nitrogen (Mur *et al*., 2017).

SA levels of the *A. filiculoides* sporophyte were determined by the HPLC-MS/MS method (De Vries *et al*., 2019). In root-like structures, the hormone content was 0.18±0.03 nmol·g^{-1} FW, in photosynthetic organs, it was 0.09±0.02 nmol·g^{-1} FW. The detected levels of SA in *Azolla* are significantly lower than those in *Arabidopsis thaliana* (Rekhter *et al*., 2019). Identification and phylogenetic analysis of the SA biosynthesis genes of *A. filiculoides* showed that the most likely pathway of hormone biosynthesis is related to the derivatization of benzoic acid molecules, rather than the isochorismate pathway (De Vries *et al*., 2019).

CONCLUSION

The complex, multicomponent hormonal system of plants provides coordination and regulation of basic physiological and metabolic processes, including growth, development, photosynthesis, and respiration (**Figure**). Due to hormonal regulation and the influence of exogenous factors, the course of internal biological time changes. Certain stages of the implementation of the genetic program of a plant organism pass faster or slower depending on the available sum of influences (Bradford & Trewavas, 1994). Currently, the main classes of phytohormones have been identified in most species of the Salviniaceae family and the effects of treatment with exogenous hormones have been investigated.

Overall, these results suggest that exogenous phytohormones can be used as potential growth regulator for ferns due to their ability to enhance growth and reproduction, promote sporulation and increase the accumulation of fresh and dry weight. Auxins and cytokinins are the most well-studied phytohormones among the species of the Salvinia and Azolla genera. However, the features of phytohormonal balance, regulation of metabolic processes, and the involvement of phytohormones in ontogenesis control of the majority of species in the Salviniaceae family remain unknown. Further research on the phytohormonal system will contribute to understanding of the nature of ontogenesis regulation and the peculiarities of adaptation formation, as well as the creation of new ecological plant growth regulators. The sensitivity of macrophyte ferns in the Salviniaceae family to environmental pollutants allows for their use in biotesting contamination; their ability to absorb and neutralize harmful compounds opens up prospects for phytoremediation. Aquatic macrophytes are characterized by rapid growth, accumulation of significant biomass, the ability to absorb heavy metals and other adverse substances, and possess physiological and molecular mechanisms of adaptation to the toxic effects of contaminants. Species of the genera Salvinia and Azolla are successfully used to assess the ecological state of water bodies, study ecotoxicological effects of pollutants on them, and develop biotechnological approaches to biotesting.



AUXINS

regulate the growth and development of the sporophyte, the formation of sporocarps, accelerate sporulation, increase the number of spores, control the ratio between archegonia and antheridia.

CYTOKININS

influence sporophyte growth and morphology in dose-response manner, promote submerged frond meristem development, induce sporocarp development and germination.

GIBBERELLINS

regulate the growth and development of the sporophyte organs, increase the frequency of sporulation and the number of microsporangia.

ABSCISIC ACID

controls the aging process of the sporophyte, affects the formation of sporocarps, and is involved in the regulation of the maturation process of spores.

JASMONIC ACID

forms a complex signaling network with other hormones, participates in pathogen defense reactions, stimulates cell division, and controls the early stages of gametophyte development.

SALICYLIC ACID

controls the quantity of nitrogen-fixing symbionts in *Azolla* and influences the rate of nitrogen fixation, promotes resilience to abiotic stresses and is in charge of several defensive mechanisms.

The complex, multicomponent hormonal system in regulation of growth, development and basic physiological and metabolic processes in water ferns of the Salviniaceae family

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

Conceptualization, [I.K.]; methodology, [-]; validation, [-]; formal analysis, [N.V.].; investigation, [-]; resources, [-]; data curation, [-]; writing – original draft preparation, [I.K., N.V., L.V., V.V., M.S.]; writing – review and editing, [I.K., N.V.]; visualization, [M.S.] supervision, [I.K.]; project administration, [-]; funding acquisition, [-].

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ФІТОГОРМОНИ В РЕГУЛЯЦІЇ РОСТУ І РОЗВИТКУ ВОДЯНИХ ПАПОРОТЕЙ РОДИНИ SALVINIACEAE: ОГЛЯД

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Водяні папороті родини Salviniaceae успішно використовують для біоремедіації та біоіндикації забруднених водойм. Завдяки інтенсивному розмноженню вони здатні продукувати величезний об'єм біомаси, збагачений природними регуляторами росту рослин. Водночас водяні папороті через швидке розповсюдження створюють перешкоди для користування водними ресурсами. Їхній ріст і розвиток контролюється фітогормонами, які є головними хімічними месенджерами, що регулюють відповіді на зміни довкілля. На сьогодні гормональна система водяних папоротей родини Salviniaceae залишається малодослідженою. У цьому огляді ми проаналізували й узагальнили дані літератури і результати власних досліджень щодо ролі ауксинів, цитокінінів, гіберелінів, абсцизової, саліцилової та жасмонової кислот у регуляції росту й розвитку водяних папоротей родів *Salvinia* й *Azolla*, наголошуючи на специфічних особливостях цих фітогормонів у папоротей. Ми представили стислу інформацію про методичні підходи визначення ендогенних фітогормонів у водяних папоротей родини Salviniaceae. Обговорено впливи екзогенних регуляторів на ріст, розвиток і стійкість водяних макрофітів родів *Salvinia* й *Azolla*, а також можливість використовувати водяні папороті для створення екологічно чистих біодобрив.

Ключові слова: роди *Salvinia* й *Azolla*, фітогормони, регуляція росту, стійкість

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