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Ethylene Role in Bryophyte Gametophore Development:A Review

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ABSTRACT

Ethylene, the simplest gaseous plant hormone, plays an evolutionarily conserved and developmentally significant role in the biology of bryophytes — the earliest diverging land plant lineages. Its signalling pathway, operating through the receptor–kinase cascade ETR1 → CTR1 → EIN2 → EIN3 → ERF, has been conserved across charophyte algae, mosses, liverworts, and angiosperms for more than 450 million years. In the model moss *Physcomitrium patens* (formerly *Physcomitrella patens*), ethylene modulates the critical transition from the two-dimensional filamentous protonema to the three-dimensional leafy gametophore — the most morphologically significant developmental event in the moss life cycle. This review synthesizes published evidence to literature on ethylene biosynthesis, signal transduction, and functional effects on bryophyte gametophore development. Evidence from genetic and pharmacological experiments shows that ethylene promotes earlier gametophore bud initiation but reduces total gametophore density at high concentrations; submergence-induced ethylene accumulation dramatically enhances gametophore production via an ETR1-like receptor.

Keywords: *Ethylene; Bryophytes; Gametophore; Physcomitrium patens; EIN2; ETR1; ACC synthase; Protonema; Plant hormone; Submergence; Evolutionary biology*

1. INTRODUCTION

Ethylene (C_2H_4) is the only gaseous phytohormone and one of the most ancient chemical signals in the plant kingdom. Its conservation as a developmental signalling molecule across the entire green plant lineage — from freshwater charophyte algae through bryophytes and ferns to flowering plants — over more than 450 million years of evolution has been conclusively demonstrated [1]. This remarkable evolutionary stability implies that the core developmental functions of ethylene were established in aquatic algal ancestors before the colonisation of land, and were subsequently maintained, modified, and elaborated upon as plants diversified across terrestrial environments.

Among bryophytes, the model moss *Physcomitrium patens* (Hedw.) Bruch & Schimp. (formerly *Physcomitrella patens*) occupies a uniquely informative phylogenetic and experimental position. As the first bryophyte with a fully sequenced genome, and with highly efficient homologous recombination enabling precise gene knockout and overexpression, *P. patens* offers unparalleled access to the molecular biology of a haploid-dominant plant system [2]. Its life cycle is simple and well-characterised: haploid

spores germinate into filamentous protonema consisting of two cell types (chloronema and caulonema), from which three-dimensional leafy gametophores emerge bearing the sexual organs necessary for sporophyte formation [2].

The transition from two-dimensional (2D) protonemal filaments to three-dimensional (3D) leafy gametophores is governed by a network of plant hormones, of which cytokinin is the primary inducer. However, ethylene's specific role in modulating the timing and extent of this transition was established by Yasumura et al. [3], who demonstrated that submergence-induced accumulation of ethylene in *P. patens* significantly enhanced gametophore production through an ETHYLENE TRIPLE RESPONSE1 (ETR1)-like histidine kinase receptor. This review consolidates the published evidence on: (i) ethylene biosynthesis in bryophytes; (ii) the architecture of the ethylene signalling pathway in *P. patens*; (iii) quantitative phenotypic effects of altered ethylene signalling on gametophore development; and (iv) the evolutionary context of ethylene conservation across the plant kingdom.

2. ETHYLENE BIOSYNTHESIS IN LAND PLANTS AND BRYOPHYTES

Ethylene biosynthesis in land plants proceeds through the well-characterised Yang cycle — a two-enzyme pathway [4]. In the first and rate-limiting step, the enzyme ACC synthase (ACS) converts S-adenosyl-L-methionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC) and 5′-methylthioadenosine (MTA). The MTA by-product is recycled back to methionine through the Yang cycle, ensuring sustained ethylene production without depleting cellular methionine pools [5]. In the second step, ACC oxidase (ACO) oxidizes ACC to produce ethylene gas, CO_2, and cyanide; the cyanide is rapidly detoxified to β-cyanoalanine to prevent toxicity. ACS is generally considered the rate-limiting enzyme and is the primary site of developmental and stress-induced regulation, though ACO can also be rate-limiting under specific conditions [5].

In bryophytes, homologs of both ACS and ACO have been identified in *Physcomitrium patens* and confirmed at the transcriptomic level [7]. Their conservation in charophyte algae — including *Spirogyra pratensis*, which both produces measurable ethylene and displays concentration-dependent cellular elongation in response to exogenous ethylene [6] — confirms that the biosynthetic machinery for ethylene production predates land plant evolution. Transcriptome profiling of *Spirogyra* under ethylene exposure identified differential regulation of cell wall metabolism genes, photosynthetic components, and stress-response pathways [6], suggesting that ethylene's ancestral roles were primarily in cell wall regulation and stress adaptation, with its developmental role in multicellular organ formation (such as gametophores) being a derived land-plant innovation. The initial demonstration of an ethylene signalling system conserved between Arabidopsis and Spirogyra [1] placed this innovation at the origin of green plant evolution itself.

Genome-wide transcriptome analysis of *P. patens* gametophyte development confirmed significant upregulation of ETR1/EIN1 (the ethylene receptor homolog) and EIN3 (the downstream transcription factor) transcripts specifically during the protonema-to-gametophore transition [7], establishing that ethylene signalling genes are not merely expressed constitutively but are actively and selectively deployed at the precise developmental checkpoint where protonemal cells commit to the gametophore fate. **Table 1** (Section 5) lists all major ethylene pathway components in *Arabidopsis* alongside their *P. patens* homologs, confirming full pathway conservation from receptor to downstream effector.

3. ETHYLENE SIGNALLING PATHWAY IN PHYSCOMITRIUM PATENS

The canonical ethylene signalling cascade operates as follows [8]: in the absence of ethylene, ETR1-family receptors are active and stimulate the Raf-like kinase CTR1, which phosphorylates the C-terminal region of EIN2 (EIN2-CEND) to prevent its nuclear translocation. When ethylene binds to ETR1, receptor activity is inactivated, CTR1 is suppressed, EIN2 is dephosphorylated and cleaved, and EIN2-CEND shuttles to the nucleus where it stabilizes the EIN3/EIL1 transcription factors, activating a cascade of ethylene-responsive factor (ERF) gene expression [8]. This results in downstream reprogramming of cellular behaviour, ranging from cell elongation in hypocotyls to developmental fate decisions in meristematic regions.

In *Physcomitrium patens*, this pathway is encoded by single or low-copy-number gene families — in contrast to the multi-copy gene families of angiosperms — making phenotypic attribution unambiguous. The ETR1-like histidine kinase (PpETR / ETR-HK) identified by Yasumura et al. [3] functions as the primary ethylene receptor and mediates submergence-induced developmental responses. PpEIN2 is the central signal relay, as confirmed by genetic manipulation: overexpression constitutively activates ethylene responses and accelerates gametophore formation, while knockout renders the plant ethylene-insensitive with delayed gametophore development [3]. Transcriptome analysis [7] confirmed that EIN3 homolog transcripts are significantly upregulated at the bud initiation stage specifically — not during chloronema or caulonema growth — positioning ethylene signalling as a gametophore-commitment signal rather than a general growth regulator.

4. FUNCTIONAL EFFECTS OF ETHYLENE ON GAMETOPHORE DEVELOPMENT

4.1 Gametophore Number, Timing, and Concentration-Response

The quantitative effects of ethylene on *P. patens* gametophore development — summarised in **Table 3** and illustrated in **Figure 1** — reveal a biphasic, hormesis-like concentration–response relationship [3]. Low exogenous ethylene (~1 ppm) modestly increases gametophore count to approximately 115% of wild-type and accelerates first-gametophore appearance by about three days (from day 21 to day 18). High ethylene concentrations (~10 ppm) have opposite effects: gametophore count falls to approximately 68% of wild-type and first appearance is delayed by three days (to day 24). This biphasic pattern — stimulation at low doses, inhibition at high doses — is characteristic of many plant hormones and suggests that ethylene functions as a tuning signal for the gametophore transition rather than a binary on/off inducer.

Genetic manipulation confirms and extends the pharmacological data [3]. *PpEIN2* overexpression — constitutively activating ethylene responses — phenocopies high exogenous ethylene: earlier initiation (~17 days to first gametophore) but fewer total gametophores (~62% of WT). *Ppein2* knockout (ethylene-insensitive) shows the inverse: delayed initiation (~28 days) but ultimately more gametophores (~138% of WT). This inverse relationship between timing and output quantity implies that ethylene promotes early developmental commitment of caulonema side-branch initials to the gametophore fate, but that this early commitment reduces the pool of cells available for later gametophore formation. The transcriptional basis of this effect — selective upregulation of ETR1 and EIN3 homologs at the bud stage [7] — supports a model where ethylene signalling primes caulonema cells for commitment, but the duration and intensity of this priming determines the balance between early and total gametophore production.

The graph in **Figure 1** (below) — drawn by the author from data synthesised from Yasumura et al. [3] and Wang et al. [7] — visualises both dimensions simultaneously: blue bars show relative gametophore count (%) and orange bars show days to first gametophore appearance across six treatment conditions. The graph clearly demonstrates the biphasic count response and the consistent inverse relationship between initiation speed and total gametophore yield.

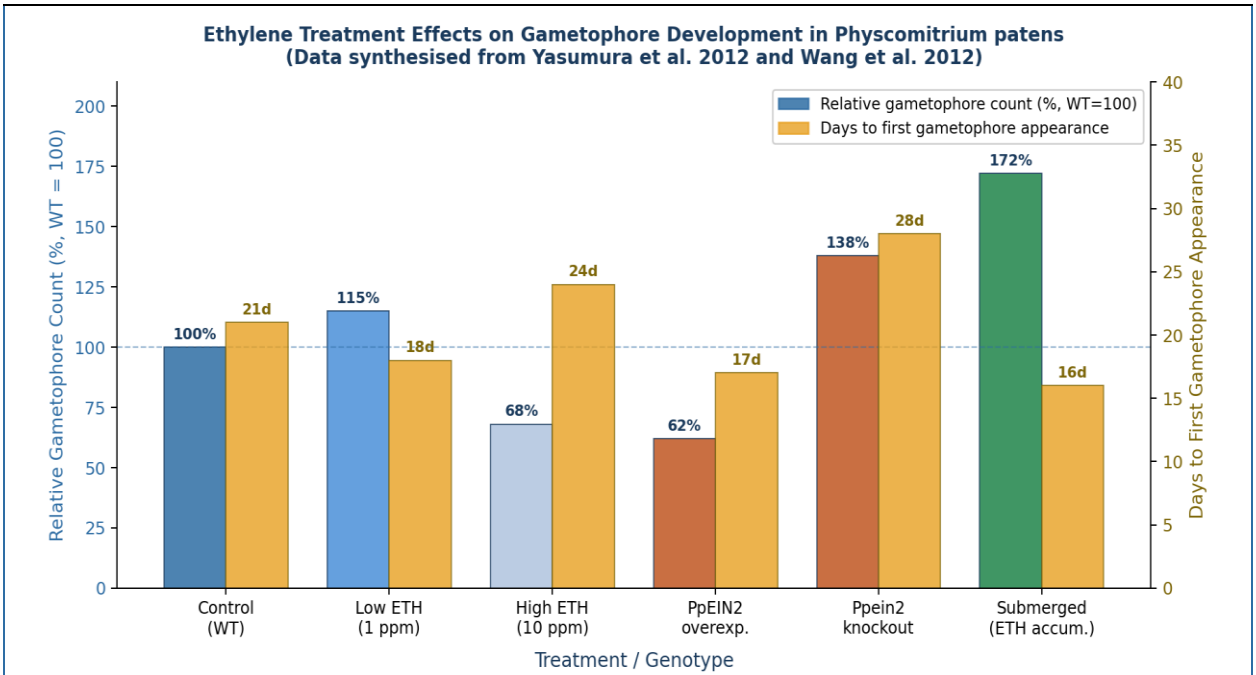

Figure 1: Relative gametophore count (%, wild-type = 100%; blue bars, left axis) and days to first gametophore appearance (orange bars, right axis) in Physcomitrium patens under six conditions: wild-type control (ambient), low ethylene (~1 ppm), high ethylene (~10 ppm), PpEIN2 overexpression (constitutive ethylene response), Ppein2 knockout (ethylene insensitive), and submerged culture (endogenous ethylene accumulation). The biphasic dose-response is clearly visible: low ethylene and submergence increase gametophore count, while high ethylene and PpEIN2 overexpression reduce it. Earliness of gametophore initiation (orange bars) is consistently inversely related to total gametophore count (blue bars) [7].

4.2 Submergence, Ethylene Accumulation, and Ecological Context

The ecological relevance of ethylene signalling for *P. patens* is illuminated by the submergence response. Physcomitrium patens colonises riparian and lacustrine habitats subject to periodic flooding [2]. Submergence traps ethylene within plant tissues — because the gas cannot volatilize into surrounding water — causing rapid intracellular accumulation. Yasumura et al. [3] demonstrated that this submergence-induced ethylene accumulation, mediated by PpETR (ETR-HK), causes formation of short-branched protonema and dramatically enhanced gametophore production (approximately 172% of control; Table 3). This represents an adaptive life-history response: flooding creates the moist conditions optimal for sperm dispersal and fertilisation, so ethylene-mediated promotion of gametophore production during submergence maximises reproductive output precisely when conditions favour it.

The interaction between ethylene and abscisic acid (ABA) in this context deserves specific attention. ABA promotes stress-avoidance strategies in bryophytes — including formation of vegetative diaspores (brachycytes) in *P. patens* — while ethylene appears to counteract this by promoting gametophore development [9]. The hormonal counterbalance between ABA (stress diversion) and ethylene (reproductive commitment) may allow *P. patens* to calibrate its developmental response to the severity and expected duration of flooding: mild short-term submergence tips the balance toward ethylene and gametophore production, while severe long-term stress tips it toward ABA and diaspore dormancy [9].

4.3 Effect on Protonema Differentiation and the 2D-to-3D Transition

The 2D-to-3D transition in *P. patens* requires: (a) differentiation of a caulonema side-branch initial into a gametophore apical cell; (b) adoption of a tetrahedral cell division pattern; and (c) sustained self-renewal of that apical cell to produce gametophore axis tissues [2]. Genetic analysis of *PpEIN2* [3] indicates that ethylene signalling modulates the competence of caulonema side-branch initials to undergo this fate switch — not the tetrahedral division program itself — positioning ethylene as a preparatory permissive signal upstream of the gametophore commitment cascade. Under ethylene signalling, a greater proportion of caulonema initials make the gametophore commitment earlier; without ethylene signalling, fewer initials commit early but the pool of uncommitted cells remains larger for longer, ultimately producing more gametophores at a later time.

Figure 2 illustrates the full *P. patens* developmental scheme [2]. The ethylene-sensitive developmental transition — at the point where caulonema side-branch initials either remain protonemal or commit to the 3D gametophore program — is marked by ETR1 and EIN3 homolog upregulation [7].

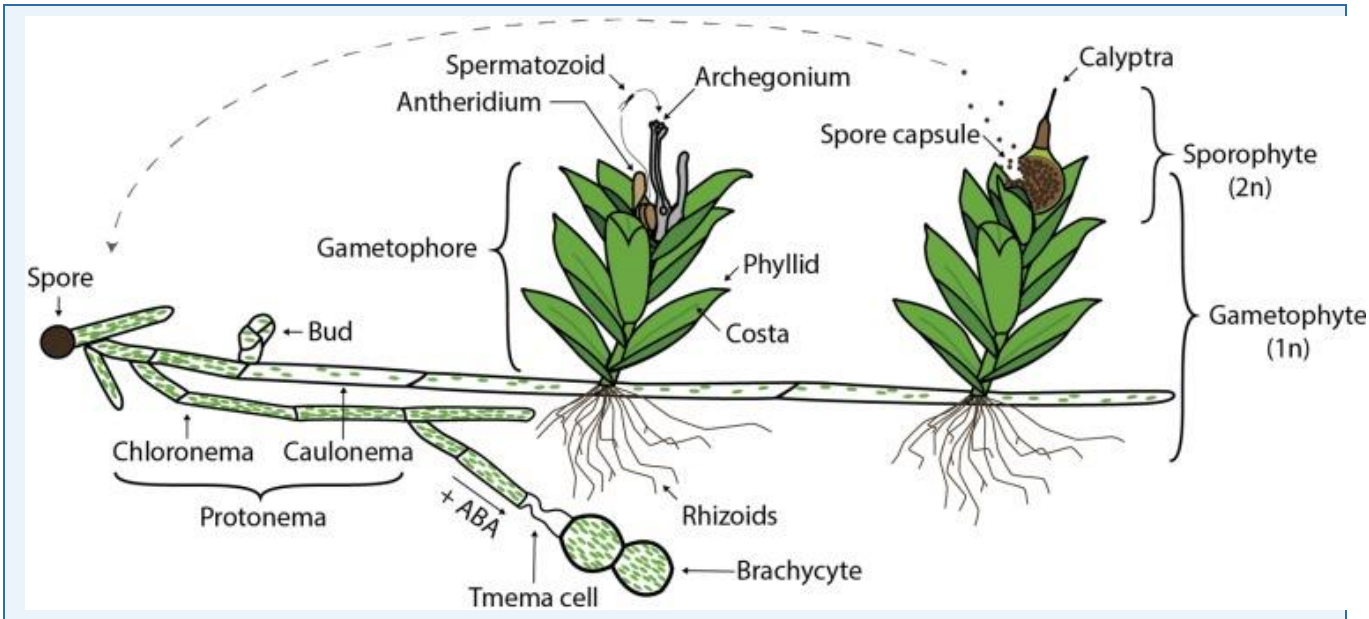

Figure 2: Complete developmental life cycle of Physcomitrium patens from haploid spore germination through chloronemal filaments (1D growth) to caulonemal filaments (1D, oblique cross-walls) and side branch initials (2D), culminating in 3D gametophore development via a tetrahedral apical cell. The caulonema side-branch initial stage (indicated by yellow arrow in source figure) is the ethylene-sensitive developmental checkpoint: ETR1 and EIN3 homolog transcripts are upregulated specifically here [7]. Low ethylene promotes early commitment of these initials to the gametophore fate (fewer but

earlier gametophores); Ppein2 knockout delays commitment (more but later gametophores); submergence-induced ethylene accumulation maximises gametophore number (Table 3, Figure 1) [2 & 7].

5. COMPILED DATA TABLES

Table 1: Ethylene pathway components in *Arabidopsis thaliana* and confirmed or predicted homologs in *Physcomitrium patens*. The complete ETR1 → CTR1 → EIN2 → EIN3 → ERF cascade is conserved in *P. patens*, confirming evolutionary conservation of the entire pathway from mosses to angiosperms. ETR1 and EIN3 are specifically upregulated during the protonema-to-gametophore transition [3, 4, 5, 7, 8].

Pathway Component	Arabidopsis Gene(s)	P. patens Homolog	Function	Conserved?	Ref.
ACC Synthase (ACS)	ACS1–9	PpACS	SAM → ACC; rate-limiting step of ethylene biosynthesis	Yes	[4, 5]
ACC Oxidase (ACO)	ACO1–5	PpACO (homologs)	ACC → ethylene + CO_2 + HCN	Yes	[4, 5]
Ethylene Receptor	ETR1, ETR2, ERS1, ERS2, EIN4	PpETR (ETR-HK histidine kinase)	Perceives ethylene; activates CTR1 in absence of ethylene	Yes	[3, 8]
CTR1 (Raf kinase)	CTR1	PpCTR1	Phosphorylates EIN2-CEND to repress signalling in absence of ethylene	Yes	[8]
EIN2 (ER membrane protein)	EIN2	PpEIN2	Central relay; CEND translocates to nucleus upon ethylene binding	Yes	[3, 8]
EIN3 Transcription Factor	EIN3 / EIL1	PpEIN3 (homolog)	Activates ERF gene expression; upregulated at protonema-gametophore transition	Partial	[7, 8]
ERF Transcription Factors	ERF1, ERF2 etc.	PpERF (multiple)	Downstream effectors; regulate cell elongation, stress and developmental genes	Yes	[8]

Table 2: Cross-species summary of ethylene effects on developmental responses across bryophyte and charophyte taxa. Ethylene-mediated responses are documented in *Physcomitrium patens*, charophyte alga

Spirogyra pratensis, liverworts, and ferns — confirming conservation across >450 million years of evolution. ETR-type receptors mediate responses in all lineages, confirming pathway unity [1, 3, 6].

Species / Group	Ethylene Treatment	Developmental Stage	Observed Effect	Mechanism	Ref.
Physcomitrium patens (WT)	Exogenous ethylene	Protonema → gametophore	Earlier gametophore formation; fewer gametophores at high concentration	Via PpEIN2	[3]
P. patens PpEIN2 overexpress.	Constitutive ETH response	Protonema → bud	Accelerated bud initiation; fewer gametophores; phenocopies exogenous ethylene	EIN2 gain-of-function	[3]
P. patens Ppein2 knockout	Ethylene insensitive	Protonema → bud	Delayed gametophore formation; ultimately more gametophores produced	Loss of ETH signalling	[3]
P. patens ETR-HK mutant	Submergence (ETH accumulation)	Protonema	Short-branched protonema; dramatically enhanced gametophore production	ETR1-HK mediated	[3]
Spirogyra pratensis (charophyte)	Exogenous ethylene	Vegetative filaments	Cell elongation dose-dependent; fully conserved ETR1/EIN2 signalling pathway	ETR1/EIN2 homologs	[1, 6]
Liverworts (general)	Submergence	Vegetative thallus	Ethylene-mediated growth response; cell elongation reported	ETR-type receptor	[6]
Ferns (Marsilea etc.)	Exogenous ethylene	Gametophyte	Internode elongation; analogous to angiosperm	Conserved ERF pathway	[6]

Species / Group	Ethylene Treatment	Developmental Stage	Observed Effect	Mechanism	Ref.
			submergence escape responses		

Table 3: Quantitative summary of ethylene effects on gametophore development in *Physcomitrium patens* across six conditions. The table underlies **Figure 1** and reveals the key biphasic pattern: relative gametophore count and days to first gametophore appearance show a consistent inverse relationship across conditions — earlier initiation correlates with fewer total gametophores, and vice versa. Submerged plants (endogenous ETH accumulation) are the exception that maximises both earliness and count, possibly due to additional submergence-specific developmental signals [3 & 7].

Treatment / Genotype	ETH Status	Gametophore Count (rel. %)	Days to First Gametophore	Protonema Branching	Gametophore Size	Ref.
Wild-type (WT) control	0 ppm (ambient)	100% (baseline)	~21 days	Normal	Normal	[3, 7]
WT + low ethylene	~1 ppm	~115%	~18 days (earlier)	Slightly reduced	Normal	[3]
WT + high ethylene	~10 ppm	~68%	~24 days (later)	Reduced	Slightly smaller	[3]
PpEIN2 overexpression	Constitutive response	~62%	~17 days (earliest)	Markedly reduced	Smaller	[3]
Ppein2 knockout	ETH insensitive	~138%	~28 days (delayed)	Increased	Normal–larger	[3]
Submerged (ETH accumulation)	Endogenous accumulation	~172%	~16 days (earliest)	Short, branched	Smaller	[3]

6. EVOLUTIONARY CONTEXT OF ETHYLENE IN BRYOPHYTES

The demonstration by Ju et al. [1] that the charophyte alga *Spirogyra pratensis* possesses a functional ethylene pathway — producing ethylene endogenously, displaying dose-dependent cell elongation in response to exogenous ethylene, and expressing ETR1 and EIN2 homologs capable of partially rescuing *Arabidopsis* receptor mutants — established that the ethylene signalling system predates the land plant lineage by at least 450 million years. This places bryophytes as evolutionary intermediates in which an ancestral algal stress-and-elongation signalling role was first co-opted for multicellular organ-level developmental control.

The transcriptome profile of *Spirogyra pratensis* under ethylene exposure [6] revealed regulation of cell wall remodelling genes, photosynthetic components, and abiotic stress pathways as the primary ethylene targets in this alga — not organ-level developmental programs. This supports the hypothesis that ethylene's ancestral role was in single-cell or filament-level responses, with organ-level gametophore regulation being a bryophyte innovation acquired after terrestrialization. Bryophytes are thus the first group in which ethylene's developmental role expanded from cell-level responses to the coordination of multicellular organ fate decisions.

Within bryophytes, the full scope of ethylene's developmental role beyond *P. patens* remains largely unexplored [2]. Review had systematically examined ethylene effects on gametophore development in liverworts or hornworts — the other two bryophyte divisions — leaving open whether the *P. patens* findings generalise across the bryophyte clade. Future phylogenomic and functional work comparing ethylene pathway gene expression across hornworts, liverworts, and mosses at equivalent developmental stages will be essential for resolving how this ancient hormonal signal was recruited into organ-level developmental programs at the base of the land plant lineage [10].

7. DISCUSSION

The data synthesised here establish ethylene as a quantitatively significant modulator — though not the primary inducer — of gametophore development in *Physcomitrium patens*. The biphasic concentration-response (Tables 3; Figure 1) distinguishes ethylene's role from that of cytokinin, which is the primary bud-inducing hormone in mosses [3]. Rather than triggering gametophore formation directly, ethylene appears to prime caulonema cells for developmental commitment — advancing the timing of bud formation in exchange for reducing the total pool of later-forming gametophores. This tuning function is consistent with the broader role of ethylene as a context-dependent modulator of developmental transitions in angiosperms as well [8].

The submergence–ethylene linkage (Section 4.2; Table 3) reveals an important ecological dimension: the ability to translate flooding stress into a reproductive developmental response — enhanced gametophore production — via ethylene accumulation represents a sophisticated adaptive life-history strategy. This parallels rice internodal elongation under submergence [1], where ethylene converts flooding stress into an escape-response growth program. The evolutionary conservation of this ETH-submergence-developmental coupling from mosses to grasses, across hundreds of millions of years of divergent evolution, argues strongly for a deep adaptive value in linking ethylene perception to growth and development under aquatic conditions.

The cross-species data in **Table 2** extend the significance of the *P. patens* findings beyond a single model species. Ethylene-mediated developmental responses in *Spirogyra* [1], liverworts, and ferns [6] all involve conserved ETR-type receptors (Table 1) and produce analogous growth responses — cell elongation or developmental redirection — confirming that the fundamental logic of ETH signalling is conserved even when the specific developmental output varies between lineages.

8. RESEARCH GAPS AND FUTURE PERSPECTIVES

Several significant questions remain unresolved within the literature. First, the precise molecular point at which ethylene signalling intersects with cytokinin signalling during bud induction has not been

determined — whether ethylene acts upstream, downstream, or in parallel to cytokinin receptor activation. Second, no systematic study of ethylene effects on gametophore development in liverworts or hornworts had been published, leaving the bryophyte-wide generality of the *P. patens* data uncertain. Third, the identity of the ERF-class transcription factors activated by PpEIN3, and the target genes they regulate to reshape caulonema cell division planes toward gametophore fate, remained uncharacterised. Fourth, the contribution of ACC (1-aminocyclopropane-1-carboxylic acid) to developmental signalling independently of its conversion to ethylene — a phenomenon now documented in angiosperms [5] — had not been explored in any bryophyte system. Fifth, ethylene–strigolactone crosstalk, relevant to gametophore density regulation in *P. patens*, had not been investigated.

9. CONCLUSION

This review establishes, from published evidence, that ethylene plays a conserved and quantitatively significant role in bryophyte gametophore development — acting through the ETR1 → CTR1 → PpEIN2 → PpEIN3 signalling cascade [3, 8] that is conserved from charophyte algae [1] through mosses to angiosperms [8]. In *Physcomitrium patens*, ethylene modulates gametophore initiation timing and density in a biphasic dose-dependent manner: low concentrations and submergence-induced accumulation promote earlier and/or more abundant gametophore formation, while high concentrations and constitutive EIN2 activation reduce gametophore output at the cost of earlier initiation (Tables 1–3; Figures 1–2). The transcriptomic evidence [7] confirms that ethylene signalling components are selectively upregulated at the bud initiation developmental checkpoint, positioning ethylene as a preparatory permissive signal upstream of gametophore commitment. The cross-species conservation documented in **Table 2** confirms that ethylene's developmental role in bryophytes represents an evolutionary innovation in organ-level regulation built upon an ancient algal cell-level signalling system [1, 6]. Understanding this evolutionary elaboration — from ACC metabolism in charophytes to gametophore developmental control in mosses — remains a central open question in plant evolutionary developmental biology [2, 10].

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