



REVIEW ARTICLE

In vitro cultivation and propagation strategies in Bryaceae (Bryophyta): A review

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Abstract

Bryophytes, particularly mosses of the family Bryaceae, represent an evolutionarily significant group with considerable medicinal potential. Despite their ecological, evolutionary and pharmacological importance, *in vitro* studies on bryophytes remain limited when compared to those on vascular plants. To address this gap, the present review synthesizes existing protocols and methodologies for the *in vitro* propagation of Bryaceae, with a focus on species prevalent in India. It highlights key factors influencing successful culture, including sterilization techniques, temperature, photoperiod, culture vessels, media composition, sugar types and hormonal supplements. Sodium hypochlorite has emerged as the most effective sterilizing agent, while optimal growth temperature ranges from 22–27 °C. Standard photoperiods of 16/8 and 12/12 hr light/dark have been widely adopted. Petri plates are the preferred culture vessels due to ease of handling and observations. Among growth media, Knop and Murashige and Skoog media, sometimes in modified formulations, have shown the highest efficacy for protonema and gametophyte development across species like *Bryum argenteum*, *Rhodobryum giganteum* and *Anomobryum filiforme*. Hormonal responses are highly concentration-dependent and exhibit interspecific variability. Along with plant growth regulators, auxin and cytokinin are the two principal hormones that play a critical role in regulating bud initiation and gametophyte development. Additionally, sugars such as glucose and sucrose promote growth in certain Bryaceae species but may inhibit others. This review highlights critical research gaps in the understanding of light intensity and spectral quality (i.e., specific wavelength suitable for growth and development), temperature tolerance and nutrient formulations, underscoring the need for species-specific *in vitro* protocols. The findings will lay a foundation for advancing Bryaceae propagation for conservation and bio-industrial applications.

Keywords

Bryaceae; growth media; *in vitro* culture; moss propagation; phytohormones

Introduction

In vitro studies, particularly morphogenetic investigations, have predominantly focused on vascular plants, while non-vascular groups such as bryophytes and pteridophytes have received comparatively less attention. Bryophytes, representing the earliest lineage of land plants, are traditionally classified into 3 major classes, viz., Hepaticopsida (liverworts), Anthocerotopsida (hornworts) and Bryopsida (mosses). Among these classes, Bryopsida is the largest class, comprising approximately 13000 species distributed globally. Within the class Bryopsida, the Bryaceae family is recognized as one of the most taxonomically significant, being the second-largest moss family reported from India (1). Globally, this family includes about 500 species across 15 genera (2). In the Indian context, 102 species belonging to 9 genera have been recorded (1) and specifically in Gujarat, members of Bryaceae such as *Anomobryum auratum*, *Brachymenium turgidum*, *B. exile*, *B. sikkimense*, *Bryum coronatum*, *B. argenteum*, *B. paradoxum*, *B. capillare*,

B. recurvulum and *B. cellulare* have been reported (3). These mosses are typically acrocarpous in growth form and inhabit a range of substrates, including rock, soil, calcareous substratum and tree bark.

Bryophytes are known to synthesize a wide range of bioactive compounds with significant pharmacological properties, including antibacterial, antitumor, antiseptic, anticoagulant and cytotoxic effects (4, 5). Ecologically, they play vital roles in bioindication, moisture retention, nutrient biogeochemical cycling, plant colonization, seed germination, seedling growth and forest renovation (6). Their utility extends to landscape horticulture, vertical gardening and even the aquarium, especially in temperate zones (7). According to the doctrine of signatures, various bryophyte species are traditionally used in ethno-medicine, for instance, *Marchantia polymorpha* for liver ailments, *Plagiochasma appendiculatum* and *Targionia hypophylla* for dermatological issues and *Polytrichum commune* for hair disorders and anticancer applications. Certain taxa also exhibit insecticidal properties, such as *Conocephalum conicum* and *Dicranum scoparium* (7). Within the Bryaceae, species like *Rhodobryum roseum* and *R. giganteum* are employed in the treatment of neurological, cardiovascular, antipyretic and antihypertensive conditions, while *Bryum argenteum* is used for its antipyretic and antifungal activities (7).

The earliest documented *in vitro* culture of mosses was reported in an early study (8). Since then, techniques have been refined and customized based on species-specific requirements, incorporating variations in culture media, hormonal combinations, carbon sources and explant types. The primary motivations for cultivating bryophytes under controlled conditions include elucidating cellular and molecular processes such as gravitropism and hormone signaling (9), understanding reproductive biology and protonema development (10), resolving phylogenetic relationships (11), promoting *ex-situ* conservation of rare and endangered taxa, enabling largescale propagation and assessing their ecological functions in plant communities.

Given the existing research gaps, there is a critical need for extensive *in vitro* studies to explore and harness their potential. Despite the wide distribution of Bryaceae members in Gujarat's diverse habitats, research on their tissue culture and propagation remains minimal. This review aims to synthesize existing protocols and findings related to the *in vitro* culture of Bryaceae, thereby laying the groundwork for future research, conservation strategies and biotechnological applications.

Search strategy and selection criteria

This review paper on the culturing techniques of Bryaceae members involved a systematic and rigorous approach to ensure a comprehensive synthesis of existing knowledge. A thorough literature search was conducted using databases like Scopus, Web of Science, PubMed, JSTOR and Google Scholar, employing keywords such as 'Bryaceae culture techniques', 'Bryophyte cultivation' or 'Bryophyte *in vitro* culture'. Inclusion criteria prioritized studies detailing *in vitro* and *ex situ* methods, focusing on medium compositions, environmental major parameters (temperatures, pH and light), culture vessels, sugar, etc., while excluding irrelevant or insufficiently detailed articles. Gray and unpublished literature were also evaluated to supplement the findings. During the analysis, common patterns, effective methodologies and gaps in research were identified. A critical evaluation ensures the validity and reliability of the studies assessed, highlighting the area for future

research. This comprehensive approach contributes valuable insights into the propagation of members of Bryaceae and their ecological and industrial applications. Subsequently, in this review article, the word "mosses" or "bryophyte" refers to members of Bryaceae.

Sterilization

Sterilization is a critical step in the *in vitro* culture of mosses, as the success of the process depends on the effective removal of both exogenous and endogenous contaminants (12). Moss surface is naturally contaminated due to their attachment to humus-rich soil, which introduces challenges for culturing. This contamination is particularly problematic in mosses, as soil particles adhere to the rhizoids, often harbouring microorganisms such as bacteria and fungi. Mosses, being a delicate group of bryophytes, possess single-layered leaves in most species, making them highly sensitive to sterilizing agents. Therefore, the selection of sterilization methods ensures the removal of contaminants without causing damage to their internal and external tissues (13).

The sterilization process in plants typically depends on the species and the plant parts used. However, in mosses, the range of suitable chemicals is limited. Sodium hypochlorite (NaOCl) and mercuric chloride (HgCl₂) are the most used agents for all mosses, including members of Bryaceae. Study demonstrated that NaOCl is effective over a wide concentration range (0.5–15 %), indicating its flexibility for different moss tissues and contamination levels (6). Low concentrations, such as 0.5 % and 1 %, were reported to be sufficient for young or less contaminated explants, ensuring high survival rates (6, 14). Moderate concentrations around 1.5–2 % improved the sterilization of field-collected materials (15). Higher concentrations, including 5 % and 8 %, were recommended when contamination pressure was high, though exposure time was critical (6, 16). Very high concentrations (10–15 %) were tested for robust tissues, with studies emphasizing brief exposure to avoid tissue damage (17–20). Mercuric chloride is occasionally used at a concentration of 0.1 % (16, 21) but is generally avoided due to its toxicity to both plants and humans. Ethanol has been utilized in some cases (16), though it is less common compared to sodium hypochlorite. Given the delicate nature of mosses and the risks associated with certain chemicals, the choice of sterilizing agents remains a crucial consideration for successful *in vitro* culture (Table 1).

Temperature

Temperature plays a crucial role in plant growth and in bryophytes, evaporative cooling is particularly significant (22). As C₃ plants, bryophytes exhibit high net photosynthetic rates at low temperatures (23). Even tropical bryophytes grow at relatively lower temperatures compared to tracheophytes. This is attributed to their tendency to become dormant beyond the optimum temperature due to a reversible depression of photosynthesis (24). For bryophytes, temperature primarily refers to the microclimatic conditions in which they grow rather than the external climatic temperature (25). Most members of the Bryaceae family thrive within a similar temperature range, although slight variations in optimum temperature for growth have been observed. The initiation of growth typically occurs at a temperature between 22–27 °C (26). Limited studies have focused on the effect of temperature on the behaviour of species such as *Bryum klinggraffii*, *Bryum coronatum* and *Leptobryum pyriforme*, while it was observed that the growth of *Bryum argenteum* (silvery moss) across

Table 1. Chemical sterilization treatments applied to Bryaceae explants

Sr. No.	Name of the species	Chemical for sterilization with concentration	Reference
1.	<i>Bryum argenteum</i>	13 % solution of Sodium hypochlorite	(18)
2.	<i>Rhodobryum giganteum</i>	0.1 % HgCl ₂	(21)
3.	<i>Bryum argenteum</i>	Different concentrations (0.1 %, 0.5 % and 5 %) of NaClO, a combination of 70 % ethanol and different concentrations (0.1 %, 0.5 % and 5 %) of NaClO, 0.1 % HgCl ₂	(16)
4.	<i>Bryum coronatum</i>	Concentration of sodium hypochlorite (0.5, 1, 2, 4 and 8 %)	(6)
5.	<i>Anomobryum filiforme</i>	3 % Sodium hypochlorite solution	(14)

temperatures ranging from 8.4–35.7 °C, reporting optimum growth at 29.5 °C and gametophyte initiation at 10 °C, with maximum initiation at 22.5°C (17).

Photoperiod

Light is another critical factor for bryophyte growth, as it drives photosynthesis, with its absence significantly limiting growth (27). Photoperiod has been recognized as a critical factor influencing growth and morphogenesis in bryophytes. Early studies demonstrated that a 16 hr light/8 hr dark photoperiod significantly enhances protonema expansion and gametophytic development in members of the Bryaceae (6). Subsequently, studies reported improved chlorophyll synthesis and overall biomass accumulation under the same photoperiodic regime during *in vitro* culture (19). Similar observations were made in other studies, which found that a 16/8 hr light/dark cycle supported growth and physiological stability in cultured Bryaceae species (20). Further confirmation was provided by other researchers emphasizing the suitability of this photoperiod for maintaining healthy *in vitro* cultures (28). In contrast, studies also reported that 12 hr light/12 hr dark was also effective in promoting normal development, particularly early stages of gametophyte formation (29). However, specific studies on the light quality and quantity on the growth of Bryaceae remain scarce.

Culture vessels

Petri plates have been widely adopted for culturing mosses because they provide a uniform and spacious surface that supports extensive protonema development and allows precise assessment of colony expansion. Early studies demonstrated that Petri plate cultures are particularly effective for monitoring protonema initiation and subsequent growth stages (6, 14). Researchers highlighted their suitability for quantifying radial colony growth and comparing growth responses under controlled conditions (17, 21). Later investigations further emphasized the practicality of Petri plates for experimental intervention and repeatable measurements in bryophyte culture studies (30). Among the obtainable preferences, 90 mm glass Petri plates are particularly preferred for moss culture as they offer ample space for growth and their transparency allows for unobstructed monitoring of development without disturbing the culture. Additionally, these plates can be sealed with cellophane tape to minimize contamination, ensuring the integrity of the experiment.

While Petri plates remain the most employed apparatus, alternative vessels have also been explored. For instance, researchers utilized test tubes, which are suitable for smaller cultures and experiments requiring precise control overgrowth conditions (15). Similarly, flasks were also used, which are advantageous for experiments requiring larger volumes of medium or liquid culture conditions (29). Despite these alternatives, the simplicity, versatility and ease of handling associated with Petri plates make them the preferred choice for most researchers studying mosses, particularly

those in the Bryaceae family. Their compatibility with various growth media further underscores their utility in advancing bryophytes culture techniques.

Media

Since the early 1900s, the *in vitro* culturing of bryophytes has been carried out using defined media, with pioneering studies laying the groundwork (31–33). Knop medium has been widely employed in bryophyte culture due to its simple inorganic nutrient composition. Knop reported its effectiveness in supporting basic physiological processes and protonemal development (14). Subsequent studies by researchers demonstrated improved survival and steady growth of moss protonema on Knop medium (16). While later investigations confirmed its suitability for maintaining slow but stable vegetative growth under *in vitro* conditions. In contrast, Murashige and Skoog (MS) medium, originally formulated for rapid tissue proliferation, has been reported to promote enhanced cell division and biomass accumulation (6). Further studies highlighted the role of MS medium's higher nitrogen and micronutrient content in stimulating morphogenetic responses, whereas later experiments its effectiveness in accelerating regeneration and shoot induction (19,20). More recent findings reaffirmed the adaptability of MS medium across a wide range of plant taxa, including non-vascular plants.

Additionally, less conventional media such as White's medium (21), Parker's nutrient medium (34), BCD medium and Beneke medium (16) have also been employed. Research indicates that bryophytes generally exhibit normal growth across different media, although variations may arise with changes in media composition or the concentrations of specific elements (35). For example, full-strength media tend to favour the formation of protonemal gemmae, while their absence promotes tuber formation (36, 37). These variations are predominantly observed in mosses.

Solidified media are often preferred for moss culturing due to their ease of handling, with agar being the most used solidifying agent, particularly in India. Alternative gelling agents such as Gelrite or Phytagel, which form gels at lower temperatures and are free of organic impurities, have also been utilized (34). However, their tendency to liquefy over time due to pH changes or loss of essential salts limits their use, though they are particularly suitable for calcifuge bryophytes (38). While solid media are widely employed, liquid media are preferred for aquatic species, continuous cultures (39, 40) and protoplast culture (35). These approaches highlight the versatility of media selection based on the specific requirements of bryophyte growth and experimentation.

The results of various studies on *in vitro* culture media for species of the family Bryaceae reveal notable variations across different species and media types. Studies conducted *in vitro* culture of *Rhodobryum giganteum*, a medicinally significant bryophyte in China, using modified Knop medium, modified White medium and basic MS medium (21). Their findings indicated that modified Knop

medium was optimal for protonemal culture, modified White medium favoured gametophore formation and MS medium supported enhanced protonemal branching.

In vitro culture of *Anomobryum filiforme* var. *concinatum* using Knop medium (full and half strength), Nitsch trace elements with 10 ppm ferric citrate and Hoagland medium was carried out (14). Their results showed that half-strength Knop medium was superior, with bud formation observed in 22 days compared to 37 days in full-strength Knop and 46 days in Hoagland medium. Gametophore development was also faster in half-strength Knop medium (28 days) than in the other two media (50 and 60 days, respectively). Notably, no bud or gametophore formation was observed with Nitsch trace elements and ferric citrate. Additionally, use of the MS medium supplemented with Gambord vitamins to study the emergence of *Bryum argenteum* (silvery moss) from spores and bulbils. They found that the effectiveness of turf protection products in suppressing silvery moss growth varied between spores and bulbils (17). It was recorded that protonemal morphogenesis in various species of *Bryum* and allied genera, revealing that sexual reproduction via protonemal gemmae (32 species) was more prevalent than tubers (19 species) or bulbils (5 species) (34). Endangered species, viz. *Bryum schleicheri* and *B. radiculosum* exhibited distinct gemmae morphologies (34). Researchers investigated the *in vitro* propagation of *Bryum argenteum* using liquid and solid media, including Knop, BCD and Beneke media (16). Their study concluded that Knop liquid medium outperformed the others in protonemal multiplication and gametophore production (16). Similarly, studies on *Bryum coronatum*, found that 1/5 strength MS medium with 1.5 % sucrose yielded optimal protonema and rhizoidal growth among Bryaceae species, highlighting the need for species-specific approaches in bryophyte culture studies (6).

Phytohormones

In angiosperms and bryophytes, the role of hormones significantly differs from that in animals, as the site of hormone production and action can overlap. Both endogenous and externally supplemented hormones influence plant development (41). However, in *in vitro* cultures, externally supplemented hormones play a pivotal role in development due to the simple body organization and limited morphological adaptations of bryophytes, which restrict the variety of hormones that can be used (42). Studies have primarily focused on a few key hormones in Bryaceae, including auxins (18, 43), cytokinins (18, 43) and gibberellins (28, 43). Commonly used derivatives include Indole-3-butyric acid and α -Naphthalene acetic acid (NAA) for auxins, BAP-6 benzylaminopurine or kinetin for cytokinins and GA₃ for gibberellins. These hormones serve distinct functions, such as promoting gametophyte culture (auxins) and inducing bud formation (cytokinins) at specific concentrations (35, 36, 44). The effects of auxin (IAA), cytokinin (Kinetin), gibberellins (GA₃) and abscisic acid (ABA) on gametangia induction in *Bryum argenteum* were investigated (43). In this experiment, IAA and GA₃ showed positive influence on gametophore production in male clones, but negatively affected female clones, with GA₃ showing a stronger effect. Cytokinin (kinetin and 6-y, y- dimethylallylamino purine -DMAAP) positively impacted gametophore production in

female clones, exhibiting inhibitory effects on males, with both cytokinins showing similar efficacy. The interactive effects of these hormones revealed that certain concentrations, such as kinetin (107M) combined with IAA (107M), nullified the inhibitory effects in male and female clones. Cyclic AMP (cAMP) was also shown to modulate the response to kinetin, removing inhibition in male clones and enhancing the kinetin stimulatory effect in females. Conversely, ABA exhibited an inhibitory effect on vegetative and gametangia induction, more pronounced in female clones.

Morphogenesis of *Bryum argenteum* using MS medium supplemented with gibberellins (GA₃ and GA₇) and growth retardants (ancymidol, prohexadione and chlorocholine chloride) was studied. Both gibberellins positively influenced morphogenesis, whereas the growth retardants had a detrimental impact on protonema development (28). The effects of phytohormones (Indole -3-butyric acid, NAA and BAP) on the morphogenesis of *Bryum argenteum* and *Atrichum undulatum*. All three hormones had similar effects on concentrations between 0.03 and 0.1 μ M (18). These findings highlight the critical role of phytohormones in regulating growth and development in Bryaceae, with varying responses depending on the species, hormone type and concentration. The studies also underscore the importance of precise hormonal combinations and concentrations in overcoming inhibitory effects and optimizing *in vitro* propagation (Table 2).

Sugars

Sugars are fundamental to the metabolism of plants, including bryophytes, as they play a crucial role in physiological development and various metabolic processes (45–47). Variations in sugar solubility and type significantly influence development and signaling pathways. Studies on two Bryaceae members, *Bryum argenteum* and *Atrichum undulatum* examined the effects of three sugars: glucose and fructose (hexoses) and sucrose (a disaccharide). The results indicated that all three sugars positively impacted the growth and development of protonema in *Bryum argenteum*. However, in the case of *Atrichum undulatum*, these sugars exhibited a negative effect on growth and development (20).

Growth response of Bryaceae explants

The *in vitro* response of different members of Bryaceae varied with species, culture medium and phytohormone composition. Fig. 1 represents the different stages of growth of the explants of the Bryaceae family in different media. In *Bryum argenteum*, growing in MS medium with a 0.1 μ M NAA combination resulted in the formation of well-developed plants, signifying a positive role of low auxin concentration in promoting organized gametophytic growth (Fig. 1A). In *Rhodobryum giganteum*, distinct differences in protonemal development were observed in different media types. Protonemal colonies grown on Knop medium showed healthy and compact filamentous growth (Fig. 1B), while those cultured on modified White medium exhibited relatively slower and less dense protonemal expansion (Fig. 1C). In contrast, MS medium supported more vigorous and profuse protonemal proliferation, suggesting that nutrient-rich media help to enhance protonemal growth in this species (Fig. 1D).

Table 1. Phytohormonal treatments applied to Bryaceae explants

Sr. No.	Name of the species	Phytohormones with concentration	Reference
1.	<i>Bryum argenteum</i> .	0.03 μ M IBA 0.1 μ M NAA 0.03 μ M BAP-	(18)
2.	<i>Rhodobryum giganteum</i>	Combinations of 2,4-D and BA, 2,4-D and KT, NAA and BA, NAA and KT	(21)

Further growth and development were evident in other Bryaceae taxa under specific nutrient medium conditions. In *Bryum coronatum*, the formation of a protonemal bud on quarter-strength MS medium indicated that reduced nutrient concentration is conducive for bud initiation and early gametophore differentiation (Fig. 1E). Similarly, *Anomobryum filiforme* cultured on Knop medium showed the development of erect leafy gametophores, reflecting a

successful transition from protonemal to mature gametophytic stage (Fig. 1F).

Inclusive, these observations demonstrate that different *in vitro* conditions, such as media composition and hormonal balance, play a significant role in regulating protonemal growth, bud formation and gametophore development in the members of the Bryaceae family.

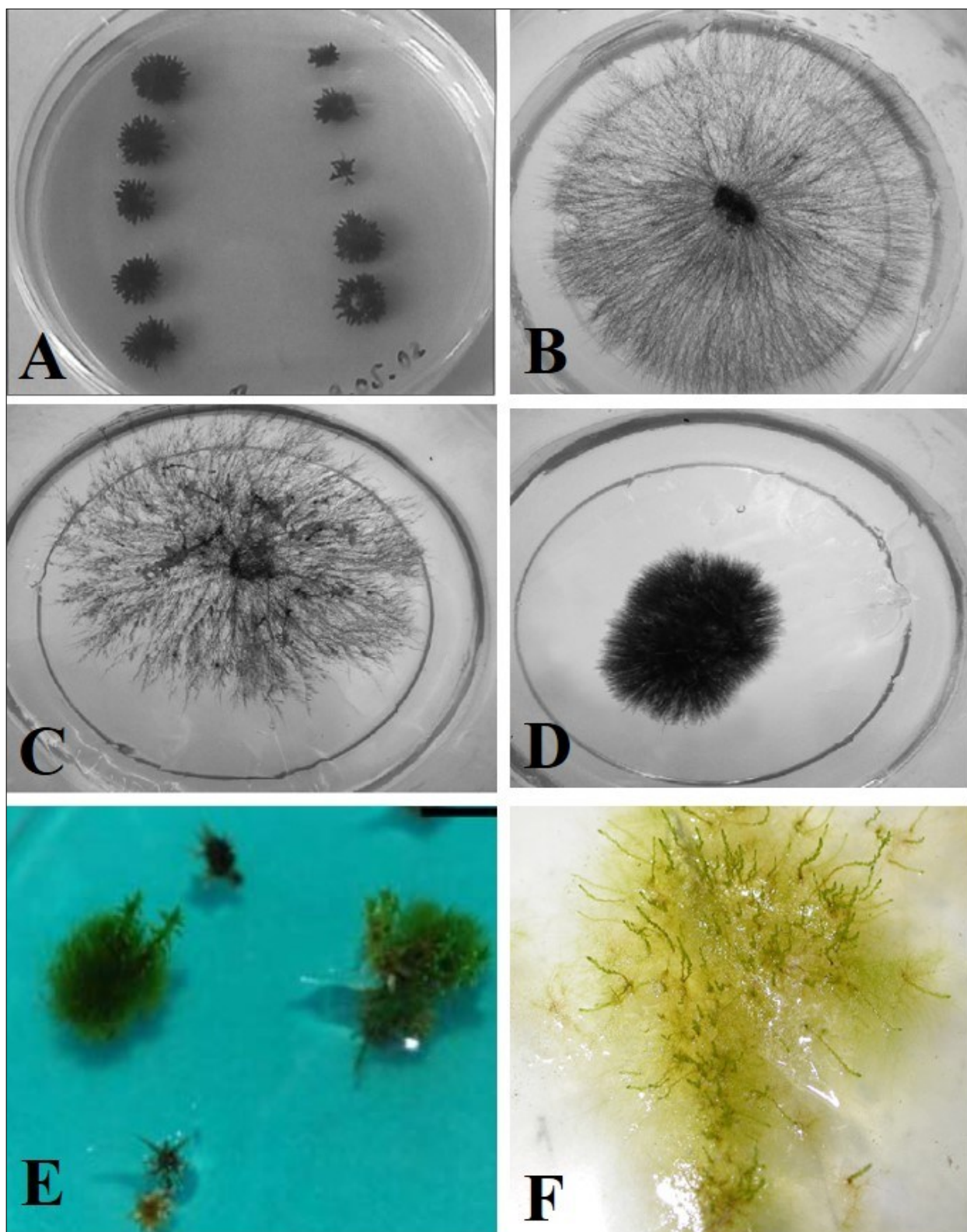


Fig. 1. Growth response of Bryaceae explants in various culture conditions and media (6,14,16,21).

(A) *Bryum argenteum*- 0.1 μ M NAA in MS medium-well developed plants; (B) Protonemal colonies of *Rhodobryum giganteum* on Knop medium; (C) Protonemal colonies of *Rhodobryum giganteum* on modified White medium; (D) Protonemal colonies of *Rhodobryum giganteum* on MS medium; (E) *Bryum coronatum*- development of protonemal bud in MS/4 nutrients medium; (F) *Anomobryum filiforme* development of erect leaf gametophores on Knop medium.

Conclusion

The comprehensive analysis of *in vitro* methodologies for Bryaceae has identified critical patterns, effective practices and research gaps, offering valuable insights into their propagation and applications. The review highlights the importance of sterilization, temperature, photoperiod, culture vessels and media solutions in optimizing the growth and development of members of Bryaceae. Each factor contributes uniquely to overcoming the inherent challenges of moss cultivation, such as contamination, sensitivity to environmental conditions and species-specific growth requirements. Sterilization methods using sodium hypochlorite and alternative agents highlight the delicate balance needed to eliminate contaminants while preserving tissue integrity. Temperature studies reveal that Bryaceae thrive in microclimatic conditions with optimal growth initiations at 22–27 °C, while photoperiod experiments emphasize the critical role of light duration in bryophyte development. The versatility of culture vessels, particularly Petri plates, demonstrates their efficacy in supporting protonema proliferation and gametophyte formation. Media selection emerges as a cornerstone of successful cultivation, with studies showcasing the adaptability of Bryaceae to various formulations. Knop and MS media, along with modifications customized to specific species, have proven effective in developing different growth stages. Research on species such as *Bryum argenteum* and *Rhodobryum giganteum* has further refined media formulations, enabling advances in protonemal and gametophore culture. Despite these advancements, gaps remain in understanding the effects of light quality and intensity, precise pH, temperature variations and alternative media compositions. Future research should address these areas to enhance the ecological and industrial applications of Bryaceae. This holistic approach not only strengthens the foundation of bryophyte culture techniques but also paves the way for their sustainable utilization in biodiversity conservation and bio-industrial innovations.

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Authors' contributions

MD and GRV contributed to the conceptualization, original draft preparation, the review and editing of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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