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Morphological Characteristics of Turion Formation and Development in *Spirodela polyrhiza*

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ABSTRACT

This study explored the formation and germination of turions—specialized asexual storage organs—in the greater duckweed *Spirodela polyrhiza*, under conditions of phosphate limitation. These turions accumulate significant amounts of starch to serve as energy reserves for overwintering and future metabolic activity. Using visual inspection and light microscopy, researchers observed that immature turions develop from pockets in the mother fronds, showing violet spots on their surfaces due to the presence of anthocyanins. Germination was marked by the emergence of new fronds and roots from the turion's prophyllum. The findings highlight the distribution of anthocyanins in both the fronds and turions, providing insights into the developmental processes involved in turion formation and sprouting in *S. polyrhiza.*

INTRODUCTION

Aquatic plants have the ability to survive under overwintering conditions. The formation of a specialized survival organ, known as a turion, is typically observed at the beginning of autumn and progresses through several stages, including formation, dormancy, germination, and sprouting **(Adamec, 2018)**. Turion formation has been documented in 14 genera of aquatic plants, including *Ceratophyllum* (Ceratophyllaceae), *Brasenia* (Cabombaceae), *Aldrovanda* (Droseraceae), *Utricularia* (Lentibulariaceae), *Myriophyllum* (Haloragaceae), *Potamogeton* (Potamogetonaceae), *Caldesia* (Alismataceae), *Hydrocharis*, *Elodea*, *Hydrilla*, *Stratiotes* (Hydrocharitaceae), *Spirodela*, *Lemna*, and *Wolffia* (Araceae) **(Adamec, 2018)**.

Interestingly, species such as *Spirodela*, *Lemna*, and *Wolffia* belong to the monocot order Alismatales, commonly known as the duckweed family **(Acosta *et al.*, 2021)**. Duckweeds are small aquatic plants known for their rapid growth and vegetative propagation. They are widely recognized for their applications in food production, wastewater treatment, and bioremediation **(Acosta *et al.*, 2021)**. To date, 36 species of duckweeds have been identified, classified into five genera: *Landoltia*, *Lemna*, *Spirodela*, *Wolffia*, and *Wolffiella* **(Ziegler *et al.*, 2023)**.

Duckweeds have evolved diverse mechanisms to cope with adverse environmental conditions, one of which is the development of turions—structures that ensure their long-term survival **(Kuehdorf *et al.*, 2014; Oláh *et al.*, 2016)**. Turions have been observed in nearly all *Wolffia* species and in *Lemna turionifera*, *L. perpusilla*, and *L. aequinoctialis* **(Acosta *et al.*, 2021)**. Among these, *Spirodela polyrhiza* turions have been extensively studied. Their formation is triggered by factors such as nutrient limitation (phosphate, nitrate, sulfate) and low temperatures, both in laboratory and natural settings **(Appenroth *et al.*, 2014; Xu *et al.*, 2019; Adamec *et al.*, 2020)**.

The rate of turion formation in different strains has been genetically linked to local climatic conditions, including temperature and precipitation patterns throughout the year **(Kuehdorf *et al.*, 2014)**. Abscisic acid (ABA) has also been identified as a strong inducer of turion formation and may function as an intracellular mediator for other inducing factors **(Appenroth *et al.*, 2014)**. In *Spirodela* species observed in West Java, Indonesia, a notable change in frond coloration was recorded **(Andriani *et al.*, 2019)**. However, detailed studies focusing specifically on turion development remain scarce.

In *Spirodela polyrhiza*, the developmental process shifts from forming frond primordia to producing dormant structures that eventually detach and sink to the bottom of the water body **(Adamec *et al.*, 2020)**. These turions are generally round, dark green or brownish-green, and 1–3 mm in diameter **(Adamec *et al.*, 2020)**. Compared to normal fronds, turions are smaller, lack aerenchyma, and possess thicker cell walls **(Xu *et al.*, 2019; Jewell & Bell, 2023)**.

In natural environments, turions form during autumn and sink. Their dormancy is broken by exposure to low winter temperatures. When spring arrives, the turions generate gas bubbles that allow them to float to the surface, where they receive light cues—mediated by phytochrome—for germination and renewed growth **(Ziegler *et al.*, 2023)**.

Over the past decade, turions in duckweeds have been widely studied with respect to their formation and germination in response to environmental stress, gene expression related to starch accumulation, and morphology **(Appenroth *et al.*, 2014; Pasaribu *et al.*, 2023)**. Morphological stages of frond and turion development have been observed at the intracellular level, though observations have largely been limited to short-term, ABA-induced turion development **(Appenroth *et al.*, 2014)**. Intracellular studies show that turion cells exhibit dense cytoplasm, small vacuoles, large starch granules (several microns in diameter), plastids, and abundant plasmodesmata **(Kim, 2013)**.

Spirodela polyrhiza has been shown to form turions under low phosphate conditions. These mature turions detach from the parent fronds and sink to the bottom. However, detailed characterization of the morphological stages during turion induction, maturation, and germination is still lacking. This represents a key area of research, especially considering the ecological and biotechnological importance of turions in survival, biomass production, and nutrient cycling in aquatic ecosystems.

Understanding the morphological and developmental dynamics of turion formation under phosphate-deficient conditions is crucial to elucidating the adaptive mechanisms used by *Spirodela* species. Such knowledge is essential not only for advancing botanical and physiological understanding but also for optimizing the application of duckweed in wastewater treatment, carbon sequestration, and renewable bioresource development.

Therefore, this study aimed to clarify the mechanisms underlying turion formation and germination in *Spirodela polyrhiza* under phosphate-deficient conditions. Morphological analysis reveals that turions are formed from pockets in the parent fronds. Upon maturation, they detach and sink. To comprehensively understand the structural transitions involved in turion induction, maturation, and germination, detailed developmental observations are needed.

MATERIALS AND METHODS

1. Duckweed material

Spirodela polyrhiza was obtained from the Rutgers Duckweed Stock Collection (RDSC) at Rutgers University, New Brunswick, NJ, USA. The clone was maintained on 0.5× SH medium supplemented with 0.8% (w/v) agar, 0.5% (w/v) sucrose, and 100mg/ L cefotaxime at the Culture Room of Expedca, Department of Marine Science, Universitas Padjadjaran.

For experimental use, 5–10 fronds from the stock plates were transferred to three working plates, each containing 0.5× SH medium with 0.5% sucrose and 100mg/ L cefotaxime. Contamination-free working plates were incubated at 25°C under continuous illumination of 150µmol m^{-2} s^{-1} (16h light / 8h dark) until use.

2. Turion induction

Two- to three-frond colonies of *S. polyrhiza* were pre-cultured in liquid 0.5× SH medium containing 0.1% sucrose for two weeks. Then, 200mg of fresh fronds were transferred into 177mL glass jars containing 50mL of mineral salt medium with the following composition:

- 60 µM KH_2PO_4
- 1 mM $Ca(NO_3)_2 \cdot 4H_2O$
- 8 mM KNO_3
- 5 mM H_3BO_3
- 13 µM $MnCl_2 \cdot 4H_2O$
- 0.4 µM Na_2MoO_4
- 1 mM $MgSO_4 \cdot 7H_2O$
- 25 µM Fe (III)-EDTA

After one week of growth, turion induction was initiated by transferring 50mg of fresh fronds into identical jars containing 50mL of the same mineral salt medium, except with a reduced phosphate concentration of 2µM KH_2PO_4. Mature turions were considered ready for harvest when they had visibly formed and naturally sank to the bottom of the jars.

3. Turion germination

Surface sterilization of harvested turions was performed using a 10% sodium hypochlorite solution, followed by three rinses with sterile distilled water. Then, 3–4 turions were placed on 0.5× SH medium solidified with agar and incubated at 25°C under 150µmol m^{-2} s^{-1} light intensity with a 16h light / 8h dark photoperiod. Germination was monitored over 14 days, and successful germination was confirmed by the emergence of new fronds from the turions (Fig. 1).

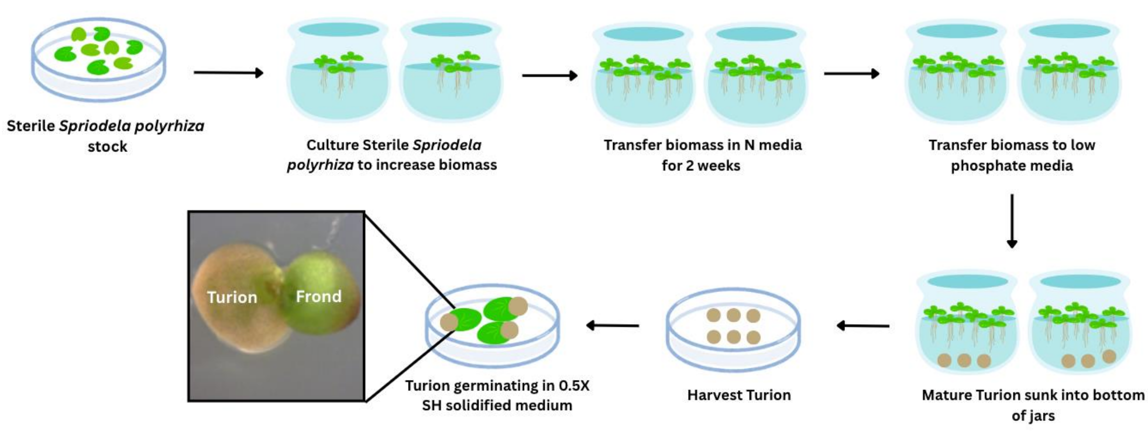

Fig. 1. Schematic representation of the experimental procedure for *Spirodela polyrhiza* preparation and turion induction.

Spirodela polyrhiza biomass was initially cultivated in 0.1% (w/v) sucrose-supplemented liquid N-medium under aseptic conditions. The biomass was subsequently transferred to N-medium for two weeks, followed by cultivation in low-phosphate medium. Mature turions were harvested and subsequently germinated on 0.5× SH solid medium.

RESULTS

1. Morphology of frond and turion of *Spirodela polyrhiza*

Spirodela polyrhiza, commonly known as the Greater Duckweed, is the simplest and fastest-growing aquatic flowering plant belonging to the *Spirodela* genus of the Lemnaceae family **(Pasaribu *et al.*, 2023)**. *S. polyrhiza* is notable for its ability to form a specialized survival structure known as a turion **(Kim, 2013)**. Intracellular observations have revealed that turion cells contain chloroplasts with multiple thylakoids, large starch granules, and cytoplasm with small vacuoles **(Kim, 2013)**.

These turions are typically produced in response to cold environmental conditions during autumn. Once mature, they detach from the parent frond and sink to the bottom of water bodies, where they remain dormant through winter. Under favorable conditions—such as adequate light, temperature, and nutrient availability—these turions germinate and develop into new fronds **(Appenroth *et al.*, 2021)** (Fig. 2).

Morphologically, the vegetative structure of *S. polyrhiza* consists of fronds and roots (Fig 3). This species can be clearly distinguished from other members of the Lemnaceae family by the presence of a greater number of root buds **(Bog *et al.*, 2019)**.

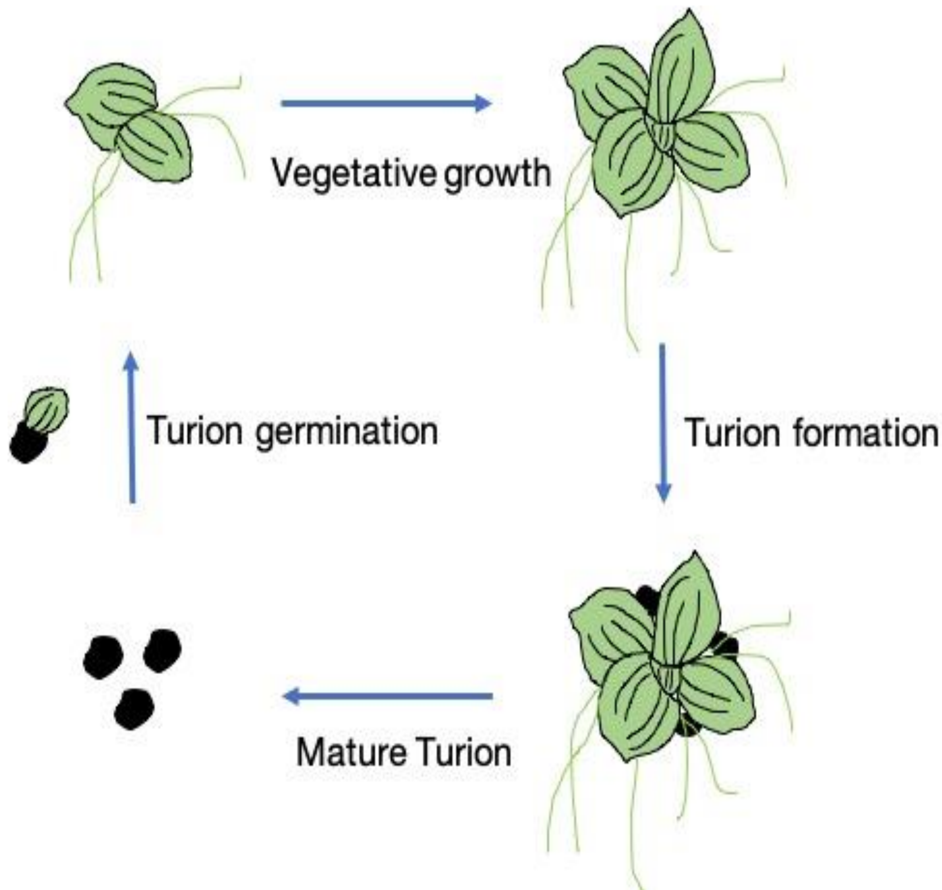

Fig. 2. Life cycle of *Spirodela polyrhiza* turion. (Picture modified from Appenroth, 2022)

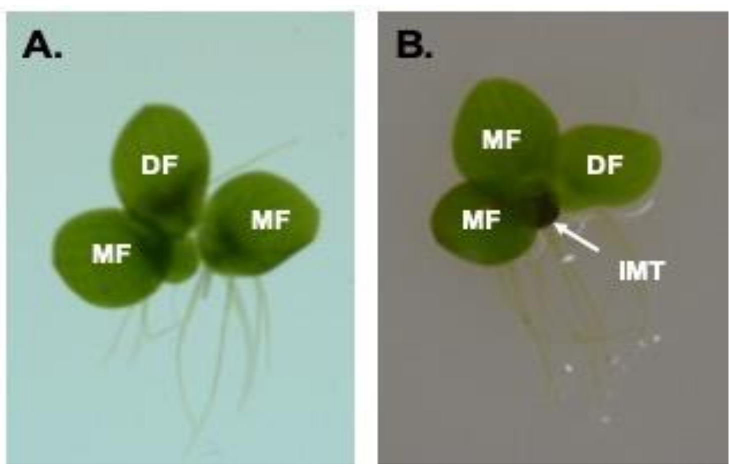

Fig. 3. Morphology of *Spirodela polyrhiza*. A) Vegetatif *Spirodela polyrhiza*, B) *Spriodela polyrhiza* with turion attached in mother frond. MF: Mother Frond, DF: Daughter frond, IMT: Immature Turion.

2. Induction of turion formation in *Spirodela polyrhiza*

To obtain both immature and mature turions, it is essential to determine an efficient method for turion induction. Several artificial treatments have been established to induce turion formation in duckweed, including the application of exogenous abscisic acid (ABA), exposure to low temperatures, nutrient deficiency (particularly phosphate and nitrate), and blue light **(Oláh *et al.*, 2016; Strzałek *et al.*, 2019)**.

Notably, the majority of turion-related studies have been conducted on *Spirodela polyrhiza*, which exhibits a strong survival response under abiotic stress conditions. Its capacity to form turions in response to unfavorable environmental conditions makes this species an ideal model for studying turion formation.

In this study, we examined phosphate deficiency as a turion-inducing factor in *S. polyrhiza*, based on previous findings showing that phosphate limitation can induce turion formation at 25°C **(Ziegler *et al.*, 2015)**. We further analyzed the cellular characteristics of mature turions through microscopic observation.

Our results demonstrated that turions formed within the frond pockets of *S. polyrhiza*, with anthocyanin pigmentation visible on the surface of the mature turions (Fig. 4).

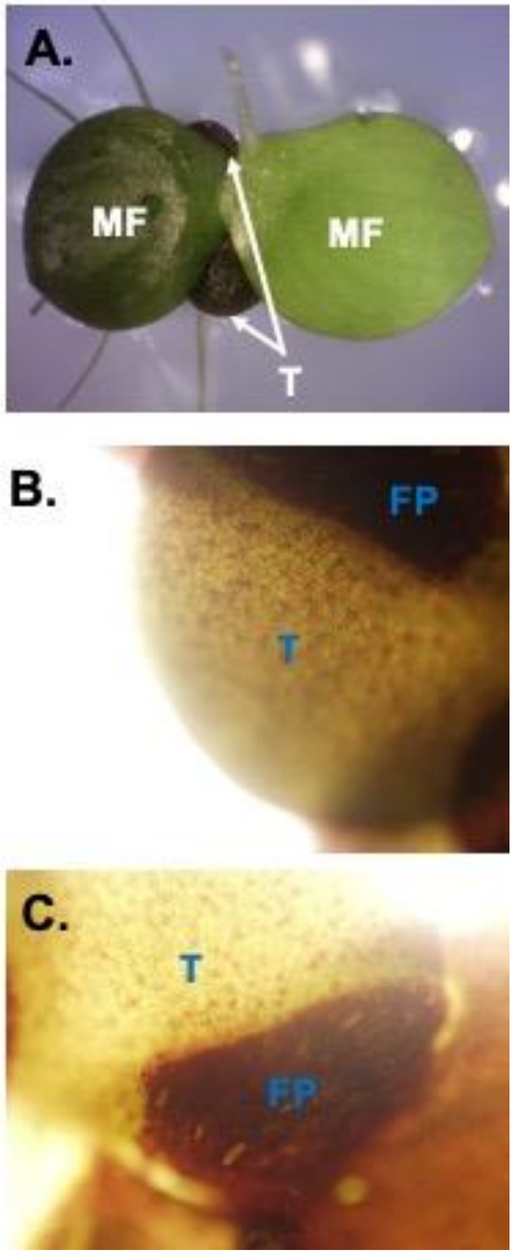

Fig. 4. Immature Turion of *Spirodela polyrhiza*. A) Immature turion attached to mother fronds of *Spirodela polyrhiza*, B and C) Immature turion buds from Frond pocket. MF: Mother Frond, T: Turion, FP: Frond Pocket

3. Germination of turion dormant organ

We observed that turions formed from clusters within the mother frond and, upon maturation, detached and sank to the bottom of the water bodies (Fig. 4). The diameter of *Spirodela polyrhiza* turions ranged from approximately 0.9 to 1.5mm (Fig. 4B). Previous studies have reported that turions contain a high starch content—up to 79%—but show significantly lower chlorophyll levels compared to vegetative fronds **(Pasaribu *et al.*, 2023)**. This is likely due to the lower density of chloroplasts and other organelles in turion cells, which is a consequence of cellular distortion caused by the accumulation of large starch granules. The abundance of starch suggests that *S. polyrhiza* stores energy in the form of carbohydrates as a survival strategy **(Huang *et al.*, 2014)**.

We also investigated the germination of mature turions under controlled conditions. To prepare them for germination, turions were surface sterilized using a 1% sodium hypochlorite solution and rinsed three times with distilled water (ddH_2O). After sterilization, 3–4 turions were placed on 0.5× SH agar medium and incubated for 14 days. Successful germination was indicated by the emergence of new fronds and roots. The turions germinated effectively on gel-based 0.5× SH medium supplemented with 0.1% sucrose. Notably, the new fronds developed from the turion prophyllum **(Pasaribu *et al.*, 2021** (Fig. 5).

To our knowledge, this is the first successful demonstration of turion germination in gel-based medium, showing the emergence of new fronds under these conditions. It has been previously reported that the germination rate of *S. polyrhiza* turions—based on frond and root emergence—ranges from approximately 55 to 100% after six months of storage at 15°C under light conditions **(Pasaribu *et al.*, 2021)**.

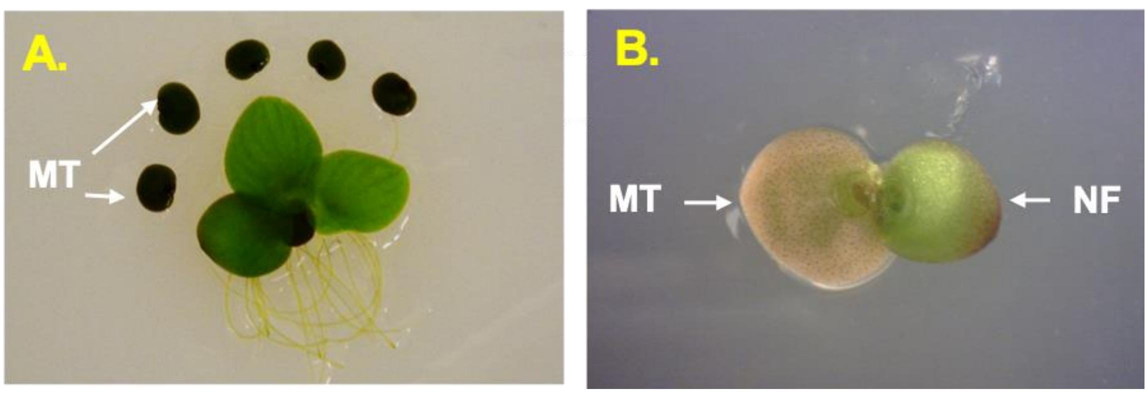

Fig. 5. Mature turion of *Spirodela polyrhiza*. A) Mature turion collected from the bottom of baby jars compare to the immature turion attached to mother frond, B) Newly frond germinated from mature turion. MT: Mature Turion, NF: New Frond

DISCUSSION

Duckweed responds to seasonal changes by forming dormant tissues that enable survival through winter conditions. In *Spirodela polyrhiza*, the development of fronds begins with the formation of offspring within reproductive pockets, which are initially protected by a foliage sheath until the daughter fronds separate. During this separation, metabolic activity is high, and the daughter fronds are composed of four layers of mesophyll and contain few intercellular air spaces **(Kim, 2013)**.

Under normal environmental conditions, fronds grow vegetatively, with the mother frond producing daughter fronds from the meristematic pocket **(Ziegler *et al.*, 2023)**. These vegetative fronds are thin, green, elliptical structures made of meristematic tissue and have an area of approximately 30mm² (Fig. 3). However, *S. polyrhiza* can also respond to cold, overwintering conditions by forming dormant tissues known as turions **(Acosta *et al.*, 2021)**. These turions originate from the meristematic pocket of the vegetative frond (Fig. 3).

The turions of *S. polyrhiza* are smaller, round in shape, thicker, and dark green in color, often rich in anthocyanin pigments. They measure approximately 2mm in length and 3mm in width **(Pasaribu *et al.*, 2023)**. The presence of anthocyanin has been confirmed in previous studies, which reported its abundance in *S. polyrhiza* turions **(Jewell & Bell, 2023)**. Anthocyanins are water-soluble pigments that belong to the class of secondary metabolites known as flavonoids **(Mattioli *et al.*, 2020)**. These compounds play a protective role in plants, helping to defend against extreme temperatures, photo-oxidative stress, and radiation damage **(Sharma & Kaur, 2020)**.

Furthermore, studies have shown that the only flavonoid derivatives present in *S. polyrhiza* are apigenin and luteolin **(Borisjuk *et al.*, 2018; Baek *et al.*, 2021; Golob *et al.*, 2021)**. However, it remains to be determined whether *S. polyrhiza* flavonoids could have nutritional or health-promoting benefits as food supplements.

Variation in turion germination rates may be influenced by environmental factors experienced during parental frond induction, similar to how seed germination is affected by provenance and seed age **(Baek *et al.*, 2021)**. When environmental conditions are favorable, turions undergo morphological development, including internal cell changes that lead to the emergence of roots and fronds **(Kim, 2013; Adamec, 2018; Golob *et al.*, 2021)**. The young frond sprouts from the prophyllum of the mature turion, followed by the elongation of a single root. As the frond grows, the turion gradually changes color from green to brownish.

Germination is also influenced by the culture medium, as it affects chlorophyll retention and overall turion viability **(Wang *et al.*, 2014; Liu *et al.*, 2022)**. It has been demonstrated that turion formation can be induced in *S. polyrhiza* and that the turions can be maintained in a dormant state **(Pasaribu *et al.*, 2021)**. However, whether mature turions can be stored for a long-term and still retain the ability to regenerate viable *S. polyrhiza* germplasm remains to be further investigated.

CONCLUSION

Spirodela polyrhiza turions were successfully induced under phosphate-limited conditions, with sizes ranging from 0.9 to 1.5mm in diameter. Turions developed within the frond pockets and, upon maturation, detached from the mother fronds. Under favorable environmental conditions, these mature turions germinated successfully, producing new fronds emerging from the prophyllum.

The ability of *S. polyrhiza* to form turions in response to environmental stress represents a key adaptive survival strategy, allowing the species to withstand unfavorable conditions and persist in dynamic aquatic ecosystems.

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