



RESEARCH ARTICLE

Pseudo-vivipary in graminoids of Kerala: A reproductive adaptation

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Abstract

Pseudo-vivipary is a vegetative reproductive strategy wherein the development of adventitious buds occurs from the latent meristematic tissue in the vegetative part of the inflorescence. This unusual phenomenon is ecologically significant in graminoids, where species inhabit habitats that are stressed, such as marshy environments and grasslands. During field observations in different ecological regions of Kerala, instances of pseudo-vivipary in 11 monocotyledon species were recorded, providing new insights into this phenomenon. The results show that the occurrence of pseudo-vivipary in *Cyperus surinamensis* Rottb., *Fuirena umbellata* Rottb., *Schoenoplectiella mucronata* (L.) J.Jung & H.K.Choi and *Carex filicina* Nees. reported here for the first time, constituting the first record of this proliferation phenomenon in this area to the best of our knowledge. In addition, this reproductive plasticity was observed for the first time in the genera *Fuirena* and *Carex*. The changing climatic conditions create an adverse habitat for the sedge population. The proposed reasons are the rising water levels in the lower part of the culm, resulting in decay and causing the inflorescence to bend towards the water level and activate plantlet growth. Other reasons include lower water levels, decreased oxygen and eventual stagnation stress. The observations are discussed and colour photographs are provided.

Keywords: *Carex*; *Cyperus*; *Fuirena*; *Juncus*; pseudo-vivipary; *Schoenoplectiella*

Introduction

Graminoids, comprising the families Poaceae (grasses), Cyperaceae (sedges) and Juncaceae (rushes), are among the most ecologically dominant groups of monocotyledonous plants. These herbaceous plants contribute significantly to the biodiversity and ecosystem services, including primary productivity, nutrient cycling, soil stabilisation, hydrological regulation and habitat formation, across diverse ecosystems (1). Members of these families exhibit remarkable morphological and ecological diversity, enabling them to colonise environments ranging from grasslands and riverbanks to periodically inundated wetlands and high-altitude regions (2, 3). The ecological success of graminoids is largely associated with their diverse reproductive strategies and adaptive survival mechanisms. In addition to conventional sexual reproduction through seeds, many graminoids possess efficient vegetative reproductive systems involving rhizomes, stolons, tillers, bulbils and proliferating spikelets (4). Such reproductive flexibility enhances dispersal, persistence, regeneration and establishment under fluctuating environmental conditions where seed germination and seedling survival may be limited (1, 5). Vegetative propagation is particularly advantageous in marshy and unstable habitats subjected to flooding, mechanical disturbance, sediment deposition or seasonal climatic stress (6).

Among the various forms of vegetative reproduction, pseudo-vivipary represents a specialised reproductive adaptation observed in several graminoid taxa. Pseudo-vivipary is characterised by the replacement of floral structures with vegetative propagules or plantlets within the inflorescence axis or spikelets (7). These adventitious buds were developed from the latent meristematic tissue in the axils of inflorescence branches, bracts and glumes of spikelets (8). In graminoids, pseudo-vivipary is generally associated with the species inhabiting marshy environments with periodic water fluctuations, as well as areas where seed germination is hindered by biotic and abiotic stress. Unlike true vivipary, in which seeds germinate while still attached to the parent plant, pseudo-vivipary involves the reactivation or persistence of meristematic tissues that subsequently develop into leafy shoots or plantlets (9). Environmental factors such as excessive moisture, flooding, low temperature, nutrient imbalance, reproductive failure, or mechanical injury to inflorescences often trigger pseudo-vivipary and within a brief favourable period, enabling them to complete their life cycle (7, 10). This adaptive strategy allows rapid colonisation and survival in habitats where sexual reproduction becomes unreliable or physiologically constrained (1).

Pseudo-vivipary has been reported in several grasses and sedges worldwide; however, comprehensive accounts from peninsular India, particularly Kerala, are still scarce. Hence, the present study aims to document pseudo-viviparous graminoids in Kerala, characterise their proliferative patterns and evaluate their adaptive significance across diverse ecological conditions.

Materials and Methods

Study area and field surveys

Field investigations were conducted in different ecological regions of Kerala, including wetlands, marshes, paddy fields, grasslands, river margins and hilly tracts during the monsoon and post-monsoon seasons from 2022–25. Species were selected for the present study based on the occurrence of pseudo-vivipary, which was identified by the replacement of floral structures with vegetative propagules exhibiting leaf primordia or root initiation. Repeated surveys were undertaken in such localities in different climatic conditions. Representative populations showing pseudo-vivipary were photographed in the field and sampled for detailed examination.

Collection and identification of specimens

Specimens exhibiting pseudo-vivipary were collected and voucher specimens were processed following standard herbarium techniques. Collected specimens were identified using regional floras, monographs and relevant taxonomic revisions of Poaceae, Cyperaceae and Juncaceae (11–14). Herbarium comparisons and available literature records were consulted to evaluate the novelty and distribution of pseudo-vivipary in the recorded taxa (Jawaharlal Nehru Tropical Botanic Garden and Research Institute Herbarium (TBGT), Calicut University Herbarium (CALI), Madras Herbarium (MH)) (7, 15–17). Voucher specimens were deposited at the Herbarium of the Department of Botany, Christian College, Kattakada, Thiruvananthapuram.

Morphological observation

Fresh specimens were examined under a stereo-zoom microscope to study the morphology and developmental stages of proliferative structures. Observations focused on occurrence of vegetative propagules within the inflorescence, position of plantlet initiation, type of proliferative structure and development of roots and leaves. The approximate number of proliferative structures per inflorescence and the developmental stage at which proliferation occurred were also recorded from multiple individuals within each population. At least 10–15 individuals from each population were examined whenever available.

Anatomical investigation

To determine the origin of proliferative structures, anatomical studies were carried out on selected species showing active plantlet development. Fresh proliferative spikelets and inflorescence branches were taken; free-hand transverse and longitudinal sections were prepared. Sections were stained with safranin and mounted in glycerin for microscopic observation. Anatomical characters such as meristematic regions, vascular continuity, leaf primordia, root primordia and the origin of adventitious buds were examined and photographed.

Environmental parameters

Habitat conditions associated with pseudo-vivipary were recorded during field observations. Ecological parameters, including habitat type, water availability, degree of inundation, stagnation condition, exposure to sunlight and seasonal moisture stress, were qualitatively assessed for each population. In selected localities, soil moisture, ambient temperature and soil pH were measured using a portable 3-in-1 field instrument during specimen collection. Take 3–5 readings around the plant population and calculated the mean. Soil moisture was assessed using a 0–10 ordinal scale (0 = extreme dry; 10 = waterlogged).

Data analysis

The occurrence of pseudo-vivipary among different taxa was compared based on habitat condition, type of proliferation and position of plantlet origin. Descriptive comparisons were used to evaluate similarities and differences in proliferative morphology among the studied graminoid species.

Results

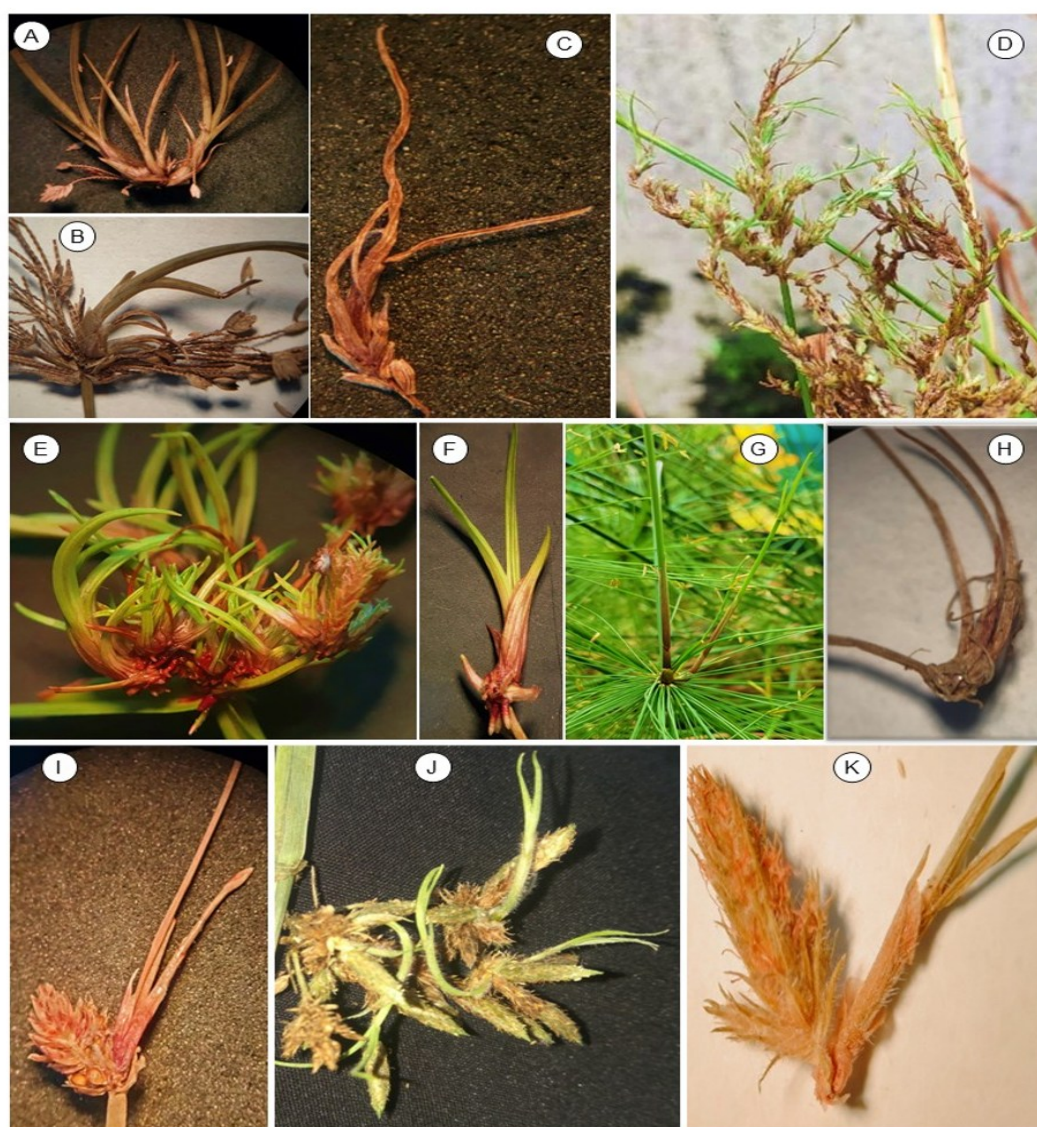
The present study led to the identification of 11 pseudo-viviparous species across 5 genera of sedges, one rush and one grass species across 19 habitat regions of Kerala (Table 1). Among these, pseudo-vivipary in *Cyperus surinamensis* Rottb., *Fuirena umbellata* Rottb., *Schoenoplectiella mucronata* (L.) J.Jung & H.K.Choi and *Carex filicina* Nees. is reported here for the first time. Most pseudo-viviparous taxa were associated with waterlogged habitats (9 species). The proliferation predominantly occurred through inflorescence branch meristem (5 species) or through spikelet modification (6 species). Among these, the proliferation of branch meristem occurs in two ways: either they develop from the base of rays or from spikelets. The frequency of plantlet production ranges from solitary propagules per spikelets to numerous per inflorescence, which is often associated with the proliferation of inflorescence branches (Table 1). The adventitious buds that develop are products of asexual reproduction, arising from the vegetative parts of the parent plant and are therefore referred to as clones. A leaf-like structure, resembling a cap, is observed to form at the base of new plantlets, which are the expanding glumes. Environmental conditions associated with pseudo-vivipary generally include high ambient temperature and high soil moisture.

Pseudo-vivipary in sedges

In species of the genus *Cyperus*, plant proliferation was observed primarily from the meristematic tissues between the axillary branches and the involucre bracts of the inflorescence (Fig. 1). In *C. surinamensis*, plantlet production was also noted from the meristems of higher-order branching within the globose heads; the axillary meristems between the rudimentary branches promote the production of new plantlets (Fig. 2A, B). The development of plantlets in *Cyperus haspan* L. was as numerous corresponded to the number of rays (Fig. 2C, D). However, in the pseudo-viviparous population of *Cyperus iria* L., plantlets were generated from the uppermost glume through the modification of the rachilla of the spikelets (Fig. 2E, F). Since the arrangement of flowers in the spikelets is acropetal, the development is not truly viviparous, as all the succeeding flowers are still in the early stage.

Table 1. Occurrence of pseudo-vivipary in graminoids

Sl. No.	Name of species	Habitat	Site of plantlet initiation	Type of proliferative structure	Number of plantlets produced	Ambient Temperature	Soil moisture status	Soil pH
1.	<i>Carex filicina</i> Nees.	Hilly tracts	Spikelet proliferation	plantlet	1 per spikelet	30 °C	Dry (0–1)	8
2.	<i>Cyperus haspan</i> L.	Paddy fields and marshes	Inflorescence branch base	plantlet	numerous	31 °C	Waterlogged (10)	6.5
3.	<i>Cyperus iria</i> L.	marshes	Spikelet proliferation	plantlet	1 per spikelet	33 °C	Waterlogged (10)	7.5
4.	<i>Cyperus prolifer</i>	wetlands	Inflorescence	plantlet	1–5 per	--	Waterlogged (10)	6.5
5.	<i>Cyperus surinamensis</i> Rottb.	Waterlogged roadsides	Inflorescence branch base	plantlet	numerous	31 °C	Waterlogged (10)	7.5
6.	<i>Eleocharis congesta</i> D. Don	Marshes	Spikelet proliferation	Plantlet/ bearing spikelet	1–2 per inflorescence	28 °C	Waterlogged (10)	7.5
7.	<i>Eleocharis retroflexa</i> (Poir.) Urb.	Marshes, paddy fields	Spikelet proliferation	Plantlet/ bearing spikelets	1–3 per spikelet	30 °C	Waterlogged (10)	7.5
8.	<i>Fuirena umbellata</i> Rottb.	Marshes, waterlogged areas	Spikelet proliferation	plantlet	1 per spikelet	31 °C	Waterlogged (10)	6.5
9.	<i>Juncus prismatocarpus</i> R. Br.	Grasslands	Between spikelets	plantlet	1–3 per spike	28 °C	Waterlogged (10)	8
10.	<i>Setaria parviflora</i> (Poir.) Kerguelen	Roadsides	Spikelet proliferation	plantlet	1–3 per spikelet	32 °C	Dry (0–1)	8
11.	<i>Schoenoplectiella mucronata</i> (L.) J. Jung. & H. K. Choi	River margins and marshes	Between spikelets	Plantlet/ bearing spikelets	1–4 per inflorescence	31 °C	Waterlogged (10)	6.5

**Fig. 1.** Pseudo-vivipary in different species. A & B: *Cyperus surinamensis*; C & D: *Cyperus iria*; E & F: *Cyperus haspan*; G: *Cyperus prolifer*; H: *Eleocharis retroflexa*; I: *Eleocharis congesta*; J & K: *Fuirena umbellata*.

Cyperus prolifer Lam. is a potential ornamental exotic species known for its proliferous nature. The inflorescence is an umbel with numerous subequal rays arranged on a receptacle and it undergoes frequent vegetative proliferation when it comes into contact with either water or soil. The plantlets and adventitious roots originate from the axils of the involucre bracts, which are modifications of the inflorescence rays (Fig. 2G). This proliferative nature facilitates easy propagation for cultivators, as even a cut piece of the inflorescence, when immersed in water for 1–2 weeks, can promote vegetative growth.

In *Eleocharis*, clones were found to develop only from the axils of the basal glumes, which are distichous, while other glumes are spirally arranged. Species in the *Eleocharis retroflexa* (Poir.) Urb. complexes appear dimorphic, but in the true sense, branching results from the proliferous nature of the culm (Fig. 2H). The spikelets from which clones develop seem to differ in size from the normal spikelets, even though the development of the ovary is complete. The proliferous spikelet of *Eleocharis congesta* D. Don is observed to have 1–3 rays arising from the basal glumes of the parent spikelet, which further terminate in a smaller spikelet still attached to the parent culm (Fig. 2I). The new spikelet has not been observed to develop into a new plantlet, as such development requires caudex formation and the cap-like structure arising from the base of the glumes, which are absent in this case.

Fuirena umbellata Rottb. is the foremost pseudo-viviparous species in the genus. The plantlet develops solely from the meristematic tissues in the axils of the lower glumes of the spikelet (Fig. 2J, K). However, this proliferative nature does not inhibit the development of spikelets; the florets are perfect and contain mature ovaries, which are surrounded by hypogynous scales.

The inflorescence of *Carex* is considered the most derivative type, formed by the reduction of spikelets. In *C. filicina*, the spike is androgynous; the female flowers are grouped along the basal portion of the spikelets, while the male flowers are positioned along the apical portion. The production of plantlets is observed from the apical portion of the spikelets, originating from the male flowers (Fig. 2A).

The inflorescence of *S. mucronata* is pseudo-lateral, with spikes developing just below the tip of the culm. The plantlets originated from the meristems between the spikelets and some of these plantlets bear spikelets at their tips. The proliferative spikelets exhibit a retarded growth pattern, in which the number and size of spikelets are smaller compared to the normal ones (Fig. 2B, C).

Pseudo-vivipary in rushes

In rushes, reproduction through asexual clones was more frequent among the genus *Juncus prismatocarpus* R. Br. collected from the Gavi regions of Kerala shows pseudo-vivipary (Fig. 2D, E). The inflorescences were proliferative and leafy and the plantlets were developed between the spikelets. Apart from the floral regions, new plants were also developed from the nodal portions of the culms. Root primordia were also developed in the plantlets.

Pseudo-vivipary in grasses

The study also recorded the occurrence of proliferative spikelets in *Setaria parviflora* (Poir.) Kerguelen from some specimens collected from Kerala (Fig. 2F–H). Mature and immature spikelets are modified and bear small plantlets. The plantlets consist of a leaf with a sheath and blade, without any root formation. The tips of some spikes also seemed to develop leaves.

Anatomical observations

Anatomical sections of the pseudo-viviparous inflorescence of *C. haspan* and the spikelet of *S. parviflora* were examined to investigate the localised meristematic activity and vegetative reorganisation within the inflorescence tissues (Fig. 3). Transverse sections of proliferating inflorescence revealed clusters of meristematic cells near the proliferating floral regions. Also, certain regions exhibited foliar appendage-like structures resembling developing leaves, along with organised cellular regions suggestive of root initiation near the propagules.

Longitudinal sections further demonstrated chlorophyllous reactivation along the floral axis, particularly during advanced stages of proliferation. Green-pigmented tissues and persistent meristematic organisation within the spikelets indicate partial vegetative conversion of floral structures. The observed anatomical features indicate a progressive vegetative differentiation within the spikelet and are consistent with early stages of pseudo-viviparous development.

Discussion

Pseudo-vivipary is a result of irregular habitat conditions and fluctuations in water levels that influence the balance between sexual and asexual reproduction, which leading to vegetative proliferation. It results in rapid colonisation of the species and helps in seedling survival. The phenomenon is known from over 19 genera and 100 species of grasses worldwide (16) and about 40 sedges (8). Induced vivipary also occurs due to the infection of *Balansia cyperi* Edg., in *Cyperus virens* Michx., which leads to the production of new plantlets within the inflorescence and retards the growth of the inflorescence (17). Vegetative reproduction is more common among perennial species with long stolons, which extensively spread in their habitats. Even in sexual reproduction, sedges show unusual behaviour in the development of androspores; three androspores will degenerate after meiosis (18). However, pseudo-vivipary and amphicarp are the less obvious methods adopted by this group, other than sexuality.

Genetic factors, injury, or unfavourable environmental conditions can cause spikelet proliferation through pseudo-vivipary (8). Still, non-viviparous races are not hereditary and occur in the temperate zone when the day length is decreasing. The promising reasons proposed were the rising of water levels in the lower part of the culm, resulting in decaying, causing the inflorescence to bend the water level and activate plantlet growth. This proliferative phenomenon was observed among species such as *C. haspan* and *E. retroflexa*.

Other reasons include lowered water levels, decreasing oxygen and eventual stagnation stress. These also trigger pseudo-vivipary, as in the case of *C. iria*, *C. surinamensis*, *S. mucronata* and *F. umbellata*. In *C. surinamensis* and *C. iria* water is plentiful in their habitat, even though the temperature is high and this stress leads to the phenomenon. This feature will be advantageous for their rapid distribution and survival. However, the stress response does not seem to affect its normal reproduction, as the development of the ovary and the embryo is perfect. Normally, *C. iria* reproduces from seeds that are dormant but can germinate about 75 days after shedding and this compound inflorescence produces numerous nuts. Even though the number of nuts is enough for their successful establishment as a weed, the actual reason for the proliferation is unclear.

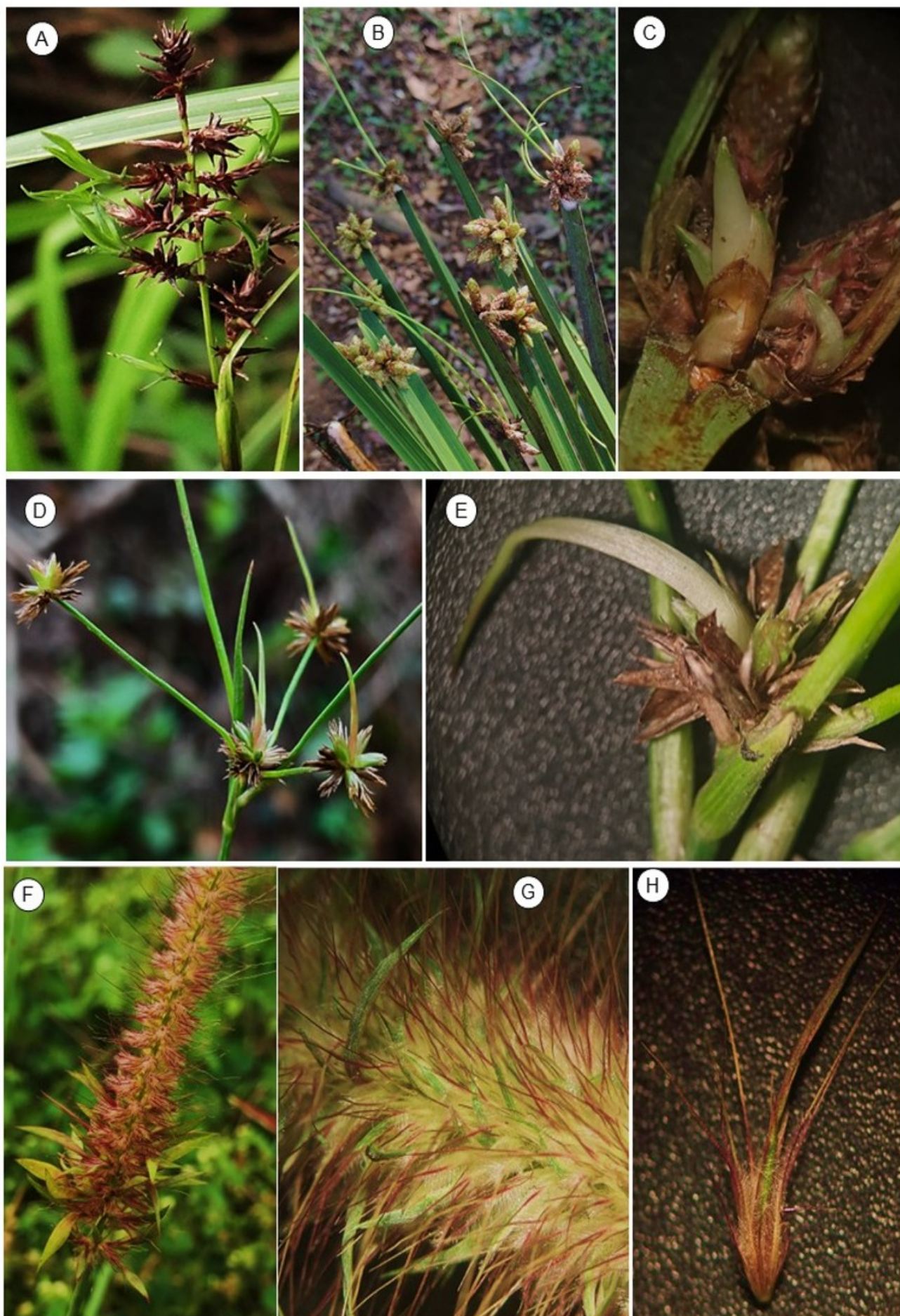


Fig. 2. Pseudo-vivipary in different species. A: *Carex filicina*; B & C: *Schoenoplectus juncooides*; D & E: *Juncus prismatocarpus*; F–H: *Setaria parviflora*.

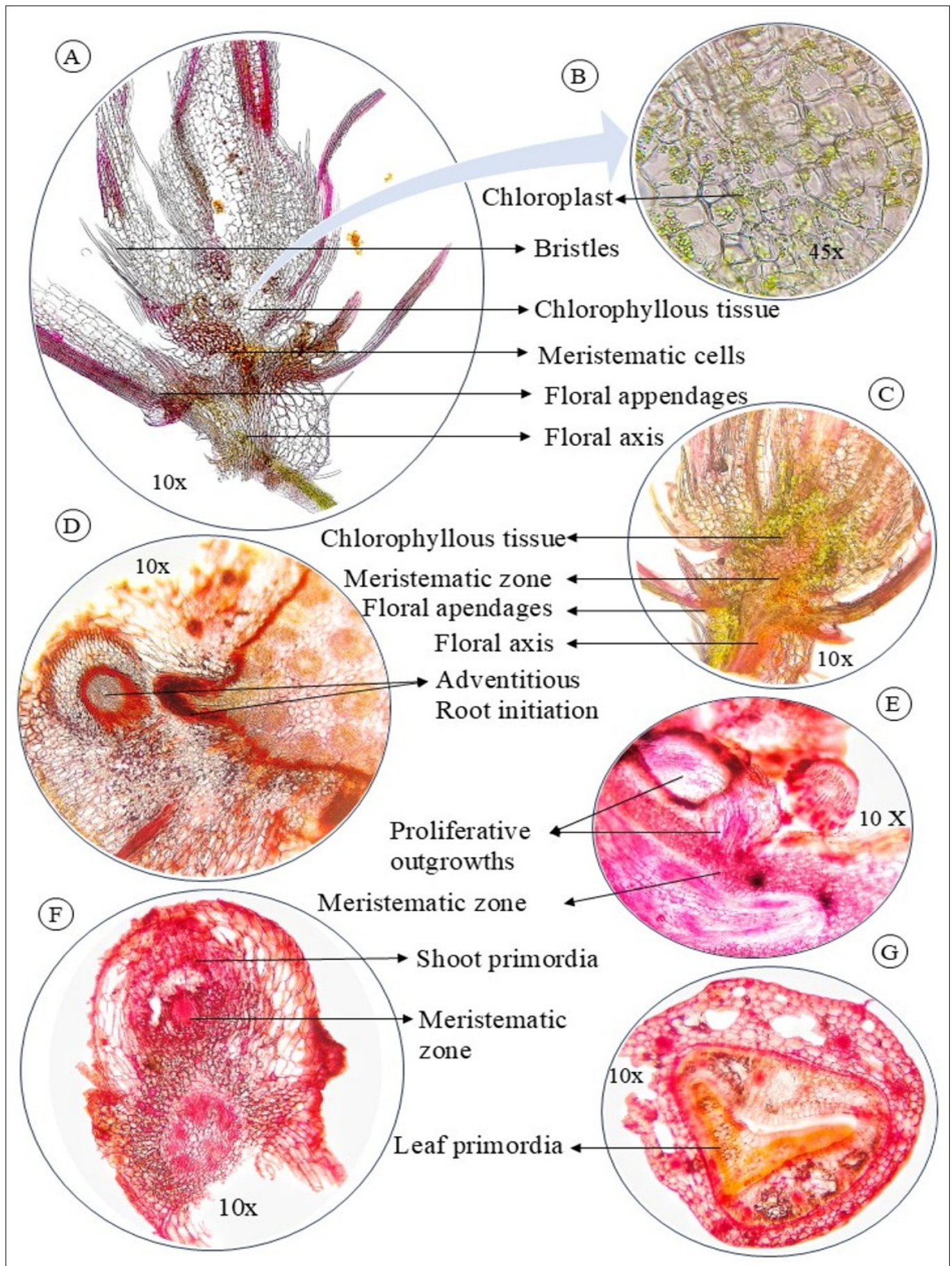


Fig. 3. Anatomical evidence of Pseudo-vivipary. A–C: Spikelet of *Setaria parviflora*; D–G: Inflorescence branches of *Cyperus haspan*; A: Longitudinal section of the spikelet showing floral appendages, floral axis, meristematic tissue and development of chlorophyllous tissue associated with proliferative activity; B: Enlarged view showing chloroplast-rich cells within the proliferating spikelet; C: Longitudinal section illustrating chlorophyllous cells associated with vegetative transition; D: Initiation of an adventitious root primordium; E: Proliferative outgrowths exhibiting localised meristematic reactivation; F: Developing shoot primordia with actively dividing meristematic tissue; G: Transverse section showing differentiation of leaf primordia.

The study observed that, except for *C. filicina* and *J. prismatocarpus*, all other pseudo-viviparous species were collected from waterlogged areas, while these populations were in a hilly tract, the aforementioned reasons did not apply to these species. The specimen was collected during May when the local temperature was high and humid. So, humidity has a certain effect on the induction of vivipary. Also, the increasing daily temperature and drought stress were promising reasons for the proliferative phenomenon in *S. parviflora*. First reports on the occurrence of pseudo-vivipary from this species were from Tripura (15).

Reports on *Cyperus involucratus* Rottb. showing pseudo-vivipary has been published from South Africa (8); however, this feature is not observed among this species from the study region. Studies on grasses revealed that elevated pCO₂ and nutrient availability have the potential to limit pseudo-viviparous reproduction. From the present study, it was clear that the C₃ and C₄ characterisation of sedges cannot be a supporting factor for this process because both plant groups exhibit vegetative proliferation. For example, *C. iria* comes under the C₄ category. However, all other species come under the C₃ category and both of them produce plantlets through pseudo-vivipary.

In grasses and sedges, pseudo-vivipary is associated with chlorophyll regeneration in floral parts and continued meristematic activity within inflorescence tissues (9). The proliferating spikelets exhibited localised meristematic activity associated with early floral reversion and vegetative reorganisation. Similar meristematic transition associated with pseudo-vivipary and reproductive to vegetative switching has been reported in grasses and rice mutants exhibiting spikelet-derived plantlet formation (19–21). The proliferated spikelets of *S. parviflora* exhibited chlorophyll regeneration in the floral parts, suggesting floral reversion towards a vegetative developmental pathway. Similar chlorophyllous activity in pseudo-viviparous grass propagules has been reported in *Poa alpina* var. *vivipara* L. (22).

Conclusion

In monocots, pseudo-vivipary occurs by the development of a small sprout adjacent to an inflorescence or floret within a spikelet. The present study reported 11 species under 6 genera exhibiting pseudo-vivipary, of which four are new records. In addition, pseudo-vivipary was newly observed in the genera *Fuirena* and *Carex*. Unfavourable environmental conditions, such as water stress, mechanical injury to the inflorescence and high daytime temperatures, are the primary contributing factors inducing pseudo-vivipary. Because the specimens were collected from places with high daytime temperatures and high humidity, which followed the monsoon season. Under such conditions, latent or residual meristematic tissues within the inflorescence regain vegetative activity, leading to the formation of vegetative shoots capable of direct establishment after detachment from the parent plant. This adaptive mechanism allows rapid colonisation and survival in habitats where sexual reproduction becomes unreliable or physiologically constrained. This stress mechanism might be a recent evolutionary trend among the species. However, further anatomical, developmental and ecological studies are needed for the identification of the main factors responsible for this rare behaviour.

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Authors' contributions

ABS carried out the field work and microscopic evaluation of the specimens. KKN also carried out the field work and microscopic examination of the specimens. ARV helped in the identification and final drafting of the manuscript. All authors have 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

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Grammarly. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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