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Features of seeds of Podostemaceae and their survival strategy in freshwater ecosystems

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Abstract

Podostemaceae are strictly aquatic angiosperms that are found attached to rocks, boulders and even on wood pieces under waterfalls and in rapidly flowing streams or rivers. Seeds of Podostemaceae are very small and are produced abundantly in capsules. They germinate readily when provided with light and water and they remain viable for 18 months when stored dry at room temperature. It is believed that seed dispersal may occur through biotic or abiotic agents although no vectors are known for any member of Podostemaceae. In nature, seeds disperse in December and they remain on dry rocks and germinate in June during the onset of monsoon showers. The seeds stick to the substratum with the help of a gum present in the seed coat. There are no projections like papillae or hooks that could help the seeds in their dispersal. Pollutants in the river affect the podostemads that lead to the extirpation of some populations. Lack of vectors, seed structure and nature of substratum and water chemistry may be the reasons for the limitation of distribution of the family Podostemaceae.

Keywords: Adaptation, Aquatic Plants, Autogamy, Ovule:Seed Ratios, Rhizoidal Hairs, Seed Morphology, Seed-set

Introduction

Seed is a key life-history stage of angiosperms and gymnosperms. Typically, in a dicotyledonous flowering plant, seed is a fertilized ovule and contains a bipolar embryo, represented by a root, shoot axis and a pair of cotyledonary leaves. Flowering plants depend on seeds for perpetuation and establishment of new populations. Seeds play a significant role in recolonization of open habitats. It passes through the sequential events of dispersal through a variety of means, dormancy and germination before establishing into a new plant. During this crucial phase of establishment, the seeds and seedlings have to develop survival strategies under unfavourable ecological conditions. Seeds of the aquatic family Podostemaceae pass through extreme conditions of high force and depth of water. Podostemaceae are the largest family of submerged aquatic angiosperms that exclusively grow on rocks and pebbles in fast flowing freshwaters and spend a part of their life under inundated conditions. They flower annually in abundance and produce a large number of seeds (Willis, 1902; Philbrick & Novelo, 1995). Although a high incidence of flowering has long been recognized in the family Podostemaceae, empirical data on seed production and seed biology for most of its species are meagre. Factors that influence seed production, dispersal or germination, in addition to recruitment of seedlings, remain poorly understood.

Strange habitat versus unique plant morphology

The family Podostemaceae is often called the 'River Weed Family' and consists of unique thalloid rheophytic angiosperms restricted to the tropical riverine habitats all over the world. The Podostemaceae represent features of significant morphological and evolutionary interest. Preliminary field observations on Indian Podostemaceae were recorded by various authors (Willis, 1902; Nagendran, 1975; Mathew & Satheesh, 1997; Mohan Ram & Sehgal, 1997; Uniyal, 1999, 2001; Uniyal & Suman, 2005; Sanavar *et al.*, 2005). The Podostemaceae are different from typical angiosperms in morphological, anatomical, embryological and developmental features and consequently remain an evolutionary enigma. The members have a thalloid plant body (**Fig. 1a,b**) usually dorsiventral, resembling algae, lichens or bryophytes. Their plant morphology deviates so markedly from the classical root-shoot (CRS) model typical of angiosperms that morphological

Fig. 1. a. Thalloid plant body in *Polypleurum stylosum*; b. Funnel-haped plant body of *Griffithella hookeraina*; c. Rhizoids from the ventral surface of the thallus of *Willisia selaginoides* [arrows indicate the secretion of a gum at the tips of rhizoids]; d. Haptera (arrow) at the base of the shoot of *Indotristicha tirunelveliana*; e. Waterfall under which Podostemads grow; f. Turbulent stream water under which Podostemads are found; g. *Polypleurum munnarense* growing attached to a rock; h. Dry thalli with fruits of *Zeylanidium lichenoides* during post monsoon period, part of the rock with plants still splashed with water.

connotations such as stem root and leaf cannot be precisely applied. The plants grow tenaciously attached to submerged rocks by means of unicellular adhesive hairs and haptera that secret a gummy substance for firm fixation (**Fig. 1c,d**). The basic elements of plant structure in Podostemaceae seem bizarre and have defied interpretation (Jäger-Zürn, 1992; Mohan Ram & Sehgal, 1992; Rutishauser, 1997). The names of many species in the family reflect their 'non-angiospermic' appearance, e.g., *Apinagia fucoides* (Mart. & Zucc.) Tul. (resembling a brown alga *Fucus*), *Zeylanidium lichenoides* (Kurz) Engl. (resembling a lichen), *Willisia selaginoides* (Bedd.) Warm. ex Willis (resembling the heterosporous fern-ally *Selaginella*).

All members of the Podostemaceae inhabit moving water such as rapids and waterfalls and hill streams **(Fig. 1e,f)**. Podostemads grow attached to rocks **(Fig. 1g)**, but occasionally may be seen growing upon water-worn logs of wood or other objects like stones. The rocks along river are more or less overgrown with Podostemaceae, wherever they are covered by water during weather. These plants grow only in regions where water is turbulent and in constant motion, and never in stagnant water. They even flourish on the rocks at the sides of waterfalls, with furious currents drowning them. A great variety of species of these plants grow where water is most turbulent. These plants carry out their life-cycle firmly attached to the rocks in torrential currents of river rapids and waterfalls. When the level of water decreases any time and the plants become exposed to air they perish leaving behind tidemark on the rocks **(Fig. 1h)**. This mark indicates the average level to which the water rises during the growing season, above which it may temporarily rise during heavy rain, or below which it may sink during severe dryness.

Number of ovules

The number of ovules borne in an ovary varies among species of Podostemaceae. The ovule number varies from 35 in *Podostemum ricciiforme* (Liebm.) P. Royen to 996 in *Marathrum rubrum* Novelo & C.T. Philbrick (Philbrick & Novelo, 1997). The ovule number per ovary in *Willisia selaginoides* was reported to be 270(± 20) and the corresponding seed number was 200(± 20) with an ovule:seed ratios of 9:7 (Uniyal & Mohan Ram, 2001). The number of ovules in *Polypleurum stylosum* (Wight) J.B. Hall varies from 363(± 27) to 400(± 20) (Khosla *et al.*, 2000). There is a significant difference between ovule number for annual species and perennial species (Philbrick & Novelo, 1997). Annual species produce significantly greater number of ovules than perennial species. This corresponds to the general pattern observed in other angiosperms (Richards, 1986). The riverweeds produce seed in abundance (**Table 1**) and seed yield may even reach tens of millions per population.

Seeds

Seeds of Podostemaceae are generally minute (average size 0.25 mm) and are produced copiously (*c.* 200) in a capsule **(Fig. 2a**; **Table 1**). Seeds lack morphological and anatomical structures that enable them to stay afloat, thus do not seem specifically adapted for water transport (Willis,

Table 1. Quantitative morphological fruit characters of Indian Podostemaceae

Taxon	Length of fruit excluding the stalk (in mm)	Length of stalk (in mm)	Number of ridges on fruit	Number of seeds per fruit	Length of seeds (in mm)
Subfamily: Tristichoideae					
Dalzellia ceylanica (Gardner) Wight	2	10	9	250 (± 30)	0.18
Indotristicha ramosissima (Wight) P. Royen	2	12	9	139 (± 20)	0.18
I. tirunelveliana B.D. Sharma *et al.*	2	7	9	100 (± 20)	0.5
Subfamily: Podostemoideae					
Farmeria indica Willis	1.5	2	Smooth	25 (± 5)	0.16
Griffithella hookeriana (Tul.) Warm.	1.6	15	2	260 (± 70)	0.34
Hydrobryopsis sessilis (Willis) Engl.	1	0	Smooth	46 (± 15)	0.20
Podostemum barberi Willis	3	40	8	20 (± 10)	0.30
P. subulatum Gardner	2	20	8	70 (± 10)	0.20
Polypleurum dichotomum (Gardner) J.B. Hall	2.7	20	8	255 (± 30)	0.38
P. munnarense Nagendran & Arekal	3	12	6	100 (± 20)	0.32
P. stylosum (Wight) J.B. Hall	2.5	38	8	245 (± 20)	0.20
Zeylanidium johnsonii Engl.	1	?	4	20 (± 5)	0.13
Z. lichenoides Engl.	1.8	2	Smooth	130 (± 20)	0.16
Z. olivaceum Engl.	3	4	Smooth	70 (± 10)	0.19
WIllisia arekaliana Shivam. & Sadanand	3	14	Smooth	200 (± 20)	0.2
W. selaginoides (Bedd.) Warm. ex Willis	4	25	2	210 (± 20)	0.39

1902). Podostemaceae seeds possess an outer mucilaginous seed coat (Willis, 1902; Accorsi, 1953; Grubert, 1980; Philbrick & Novelo, 1997), which represents the remains of the outer integument of the ovule. This sticky seed coat plays a crucial role in the establishment of a young plant, as it is the primary means by which the seeds initially become attached to the substratum (Gessner & Hammer, 1962; Grubert, 1976; Philbrick, 1984; Uniyal, 1999, 2001). When seeds are shed from the capsule, the cells of the outer integument are dry and collapsed. These cells hydrate rapidly when wetted with the first shower of monsoon, expand and become mucilaginous and sticky **(Fig. 2b)**. Based on the studies of *Mourera fluviatilis* Aubl. (Grubert, 1970, 1980), it is inferred that the adhesive strength of the mucilage far exceeds the shearing force of the water current. Successful natural recruitment requires that seed attachment be followed by seedling establishment. Seeds of podostemads germinate readily when supplied with light and water. After the emergence of radicle from the seed coat, the hypocotyl bends towards the substratum. The end of the radicle then flattens against the substratum and attaches itself with the aid of rhizoidal hairs **(Fig. 2c)**. This stage of hypocotyl attachment is the period when seedlings are most likely to be washed away by the current (Grubert, 1975).

Seed production

Seed production is generally prolific in Podostemaceae (**Table 1**). Capsule dehiscence leads to the release of tiny (<0.5 mm long) dry seeds. The Mexican species *Oserya coulteriana* Tul. and *Marathrum rubrum* produce 14,000 and 70,000 seeds per 5 cm^2 area, respectively. Seed production per plant may range from 2360 to 1,020,000 (Philbrick & Novelo, 1997). Seed count per capsule varies in different species: 2000–2400 in *Mourera fluviatilis* (Rutishauser & Grubert, 1994), ± 590 in *Apinagia multibranchiata* (Matthiesen) P. Royen, ± 720 in *Rhyncholacis penicillata* Matthiesen (Grubert, 1974) and 278 (± 52) in *Indotristicha ramosissima* (Vidyashankari, 1988). Seed production in both annual and perennial Podostemaceae is notable because it contrasts with the general pattern among aquatic angiosperms for reduction in flowering and seed production (Sculthorpe, 1967; Barrett *et al.*, 1993; Les & Philbrick, 1993; Philbrick & Les, 1996). These examples illustrate that podostemads have a high reproductive potential.

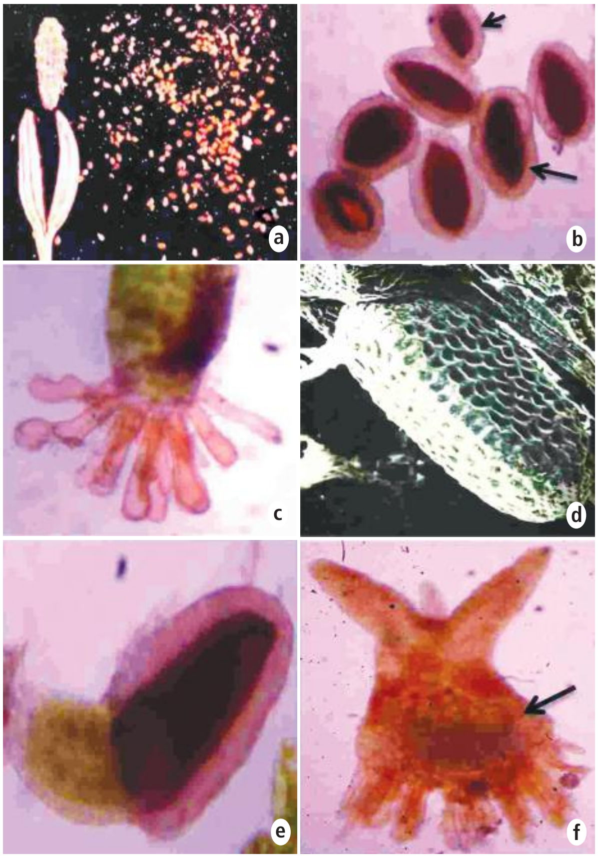

Fig. 2. **a.** Fruit of *Polypleurum stylosum* with placenta and dispersed seeds; **b.** Seeds imbibed in water showing thick mucilage layer (arrow) around the seed coat; **c.** Rhizoids emerged from the base of seedling; **d.** Electron micrograph of a seed of *Zeylanidium lichenoides* showing reticulate ornamentation; **e.** Emerged radicular pole from the seed coat; **f.** A 23-days old seedling of *Willisia selaginoides* showing the expansion (arrow) of the hypocotyl which will form the prostrate thallus.

Ovule:Seed ratios

In nature, all ovules of a plant do not mature into seeds. In fact, many plants produce substantially more ovules than mature seeds. Ovule:seed ratios of flowering plants are generally indicative of ensuring maximum seed-set and thus determining their breeding systems. The ovule:seed ratios varied in different species: *Indotristicha tirunelveliana* B.D. Sharma *et al.* was 3:2 (Uniyal, 1999), *Griffithella hookeriana* (Tul.) Warm. was 3:1 (Khosla *et al.*, 2001), *Polypleurum stylosum* was 4–8:1–5 (Khosla *et al.*, 2000), *Willisia selaginoides* was 9:7 (Uniyal & Mohan Ram, 2001) and *Indotristicha ramosissima* (Wight) P. Royen was 2:1 (Khosla & Sehgal, 2009). This high ovule:seed ratio points to a breeding system comprising mostly autogamy in the family. This is a significant observation, as asexual reproduction has not been reported in Podostemaceae (Philbrick, 1997), in contrast to other aquatic plants (Arber, 1920; Sculthorpe, 1967; Cook, 1996).

Seed structure and size

Seed structure in Podostemaceae is relatively uniform. The seeds are generally small, ovate and somewhat flattened **(Fig. 2b)**. There are no projections like papillae or hooks in the seeds, which can give stability on the substratum. Electron micrographs show that the seed has reticulate pattern/ornamentation of the seed coat surface **(Fig. 2d)**. Seed coat is made up of two distinct layers; the inner layer develops from the inner integument of the ovule and seems to serve the protective function of a typical seed coat. Upon wetting, the outer integument expands and the overall seed dimensions increase. The outer integumentary layer develops into an outer region of large somewhat mucilaginous layer. This outer layer is transparent. A straight embryo is present inside the seed with two cotyledons and a suspensor but without endosperm.

The recorded seed size in *Polypleurum stylosum* showed a length of 214–283 µm, a width of 121.9–147 µm (Khosla *et al.*, 2000). Dry seed width ranged from 160 µm for *Marathrum tenue* Liebm. to 302 µm for *Podostemum ceratophyllum* Michx. and wet seed width ranged from 218 µm in *Oserya coulteriana* to 389 µm in *P. ceratophyllum* (Philbrick & Novelo, 1997). Dry seed length range extended from 246 µm in *Vanroyenella plumosa* Novelo & C. Philbrick to 574 µm in *Podostemum ceratophyllum* and wet seed length range from 294 µm in *Vanroyenella plumosa* to 638 µm in *Podostemum ceratophyllum* (Philbrick & Novelo, 1997).

Seed dispersal

Capsule maturation and dehiscence occur in podostemads aerially. The capsule is a valve-like structure, which dehisces from the wall during dry period usually during January–February. Seeds are very light and are easily blown by the wind. Subsequent dispersal may occur through biotic (e.g., birds, insects) or abiotic (wind, water) agents. Birds are likely the dispersers of seeds between rivers (Willis, 1902). Birds are seen commonly on rocks around water-rapids where Podostemaceae occur. It seems that insects may also play an important role in the seed dispersal in Podostemaceae. It is conceivable that birds walking on rocks where seeds have been shed could pick them up on their feet. The sticky outer coating of the wet seed may aid in attachment to the birds feet. However, large amount of seeds are transported by the water splashes with the onset of showers in the monsoon.

Angiosperms follow various mechanisms for their seed or fruit dispersal by water, and seeds of the Podostemaceae being tiny become 'trapped' with the surface tension of water (Pijl, 1972). Upon wetting, these seeds 'hang' from the underside of the surface film of water. It appears that the mucilaginous layer helps in hanging the seeds beneath the surface film. Differences in seed characteristics (e.g., size, shape) may affect the dispersal potential. Heavy seeds are fixed to the substratum quickly and do not disperse over distances. However, lighter seeds are carried away to distant places by water, wind or birds. Therefore, the species with lighter seeds are widely distributed (*Indotristicha ramosissima, Zeylanidium lichenoides*). The seeds are transported by water and then trapped in the wood or rock crevices, dry thalli of older plants and some are thrown on the higher rocks and banks of streams, where they stick to the substratum and germinate. They require only a hard substratum for germination and establishment. A thorough study is needed to conclude on seed dispersal and the possible locations of a seed bank for Podostemaceae.

Seed viability

In nature, seeds of Indian Podostemaceae remain viable for 5 to 15 months. According to Vidyashankari & Mohan Ram (1987) and Philbrick & Novelo (1994), the seeds of Podostemaceae remain viable for 18 months when stored dry at room temperature (25°C ± 2°C). The duration of seed viability may exceed in *Griffithella hookeriana* (Vidyashankari & Mohan Ram, 1987) and *Podostemum ceratophyllum* (Philbrick, 1984) by 6 and 16 months, respectively. Seeds of *Marathrum schiedeanum* Cham. and *M. rubrum* retained their viability for at least 2 years in suboptimal storage conditions (Hong & Ellis, 1996). But the percentage of germination gradually decreases with time. When the seeds are stored at room temperature the percentage of seed germination falls from 89% to 30.5% after one year in *Griffithella hookeriana.* However, in seeds of the same species stored at 4°C germination was reduced from 93% to 83% after one year. This suggests that unlike some other exclusively aquatic plants, seeds of podostemads retain viability for considerable periods when dry. Seeds show no dormancy and germinate after dispersal if they find a suitable habitat. This aspect of seed biology suggests a terrestrial ancestry to the podostemads than their current aquatic existence.

Seed germination

The dispersed seeds remain trapped in the crevices of rocks and dried thalli until the concurrence of subsequent monsoon. These substrata become wet during the rainy season. Germination starts within the first couple of weeks after the showers arrive when the water level rises. Seeds imbibe water and mucilage comes out from the seed coat, which helps in sticking them to a hard substratum. After 3 or 4 days, a green radicular pole comes out by rupturing the seed coat **(Fig. 2e)**. The epidermal cells of the radicular pole elongate and secrete a gum and that helps in their further adherence to the substratum. This special kind of gum is found abundant in the basal cells, which plays an important role in the establishment of the plant **(Fig. 2b)**. This has often been described as an adaptation to fasten the seedlings to the rocks.

The germinating seeds and seedlings become submerged in the water for 1 to 2 m, owing to continuous rain and rise in water level. Such conditions promote the vegetative growth. Seed germination and seedling growth of *Zeylanidium lichenoides* were observed under a waterfall, where the velocity of the flowing water was recorded as 4 m/sec. Seeds of some Indian podostemads had been reported to germinate in petri dishes (Nagendran, 1975), the seedlings were unable to sustain their growth beyond 30 days. Seeds of *Griffithella hookeriana* are reported to germinate readily in petri dishes lined with wet filter paper but the seedlings fail to grow beyond 5–6 days (Philbrick, 1984; Vidyashankari & Mohan Ram, 1987). Seeds of *Marathrum schiedeanum* and *M. rubrum* reached high germination percentage when in direct contact with the wet surfaces (Reyes-Ortega *et al.*, 2009). Seeds of *Polypleurum stylosum* quickly germinate in nutrient medium, the radicular pole becomes visible in four days, and several unicellular rhizoids develop from it (Sehgal *et al.*, 1993). Seed germination increased to 50% in 5 days, 89% in 6 days and reached 95% in 7 days in the Mexican Podostemaceae (Philbrick & Novelo, 1994). The germination percentage in podostemaceae reaches its peak within 8 or 9 days after soaking. In seed cultures, it is evident that nutritional requirements vary species to species. The plumular apex produces 3 or 4 leaves and ceases to grow further. However, a meristem is activated in the hypocotylar region, which grows in horizontal direction and produces the prostrate body, thallus (**Fig. 2f**) . The location of meristematic activity may vary from species to species (Mohan Ram & Sehgal, 1997).

Water quality

Podostemaceae generally occur in low nutrient water and no other plant associates have been observed with them except for some algae. A river in Mexico lacked detectable levels of nutrients, but harboured nearly 17 podostemads (Quiroz *et al.*, 1997). *Vanroyenella plumosa* and *Marathrum rubrum* are reported to occur in rivers that lacked detectable levels of nutrients (Quiroz *et al.*, 1997). River biota are highly threatened by anthropogenic factors (Allan & Flecher, 1993). Tropical rivers represent one of the most heavily polluted aquatic habitats (Sioli, 1986). In the Indian habitat of Podostemaceae, the temperature of water varies from 17°C to 26°C, and the temperature of rocks reaches to 33°C, where plants are found dry and with mature capsules, and this temperature is suitable for the busting of capsules to disperse the seeds. The pH of water ranged from 7.1 to 7.9 where podostemads are found. The dissolved oxygen was 20–23 ppm. Most of the rivers with detectable levels of nutrients are reported to have obvious anthropogenic impacts, e.g., domestic or industrial sewage or agricultural activity.

Addition of pollutants, water-level manipulation, and siltation via runoff from agricultural practices and canopy gap via deforestation may have adverse impact on river-weed communities. Some species of Podostemaceae can tolerate notable levels of pollution (e.g., nutrients) for at least short periods of time. But prolonged exposure to pollutants may cause detrimental impact and death of populations. Populations of the temperate *Podostemum ceratophyllum* in New Hampshire, USA were decimated after apparent industrial waste disposal in the early 1970s (Philbrick & Crow, 1983). A population of *Hydrobryopsis sessilis* has disappeared in Karnataka, India due to change in water levels and developmental activities in the Killoor stream (Uniyal, 2001). Siltation increases turbidity of water and decreases light levels available to submerged plants. Higher light intensity seems especially crucial to river-weeds during the early growth stages as well as for initiation of flower buds. Silt deposition on rocks compromises initial seed or seedling attachment. The seedlings of Venezuelan species of *Rhyncholacis*, *Mourera* and *Apinagia* are reported to be susceptible to being washed from the rock by the water current during the initial seedling attachment (Grubert, 1974); the presence of a silt layer at the time of seed/seedling attachment is thus severely detrimental to their perpetuation.

Distribution pattern and role of seeds

Numerous authors have recorded a high level of local endemism in Podostemaceae (Royen, 1951; Cusset, 1973, 1980; Philbrick & Novelo, 1995; Cook, 1996; Sanavar *et al.*, 2005). Several species are known only from small geographical areas or a single river (Cook, 1996). *Angolaea fluitans* Wedd. occurs only in the Quanza river in Angola (Baker & Wright, 1909; Cook, 1996); *Marathrum rubrum* is confined to the Horcones rivers in Mexico (Philbrick & Novelo, 1995). *Podostemum ceratophyllum* occurs in northeast America. *Willisia selaginoides*, *W. arekaliana* and *Indotristicha tirunelveliana* are represented by a single population of each in southern India (Sanavar *et al.*, 2005). On the other hand, *Tristicha trifaria* (Bory ex Willd.) Spreng. has the widest distribution range in the whole family found in both Old World and New World.

Restricted distribution of Podostemaceae may be due to the following possible reasons:

a) When the seeds are shed upon rocks, many are washed away by the water, and only those, which are retained by cracks or crevices in the rock, or the old thalli of podostemads seem to have a chance of germination. Once carried off by the stream, there is little chance of a seed reaching an ecologically safe site to grow. It must have a rocky substratum, in a rapid stream of water, and it has no adaptation of its own, other than small size, to enable it to retain a position in such a place.

b) The nature of the substratum and water chemistry may be important in limiting the distribution of Podostemaceae. Ameka (2000) while studying distribution of Podostemaceae in Ghana, concluded that the availability of appropriate substratum, in addition to adequate light, was important than water chemistry.

c) It is likely that different species have different ecological requirements that dictate their specific local distribution.

d) The seeds of Podostemaceae remain viable for a very limited period of about 18 months. The germination percentage reduces with time.

e) It is also possible that the seeds of a particular population that germinate readily and abundantly in one season may have lower potential to germinate in the next season.

No vectors are known for the dispersal of seeds. Moreover, the overall seed shape is relatively uniform; generally ovate and somewhat flattened. There are no projections (e.g., papillae, hooks) that could help the seeds in dispersal. It is worthwhile to conduct population studies to determine their stability and evolutionary trend in the family. The microhabitat variation leading to distribution of species in a river is little understood. There is a need to introduce some methods to store the seeds in low temperature to retain their viability for a longer period. Laboratory-grown seedlings can be introduced to new sites and to explore their ability to adapt and establish.

Podostemaceae are scientifically interesting, evolutionarily enigmatic and insufficiently investigated family (Mohan Ram & Sehgal, 1992). There is much need for a thorough study of these plants in view of their vulnerable habitats and conservation.

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