

Studies on Reproductive aspects of *Willisia selaginoides* (Podostemaceae), an endemic species from Kerala

Leleeka Devi M.¹, Uniyal P.L.^{1*}, Mann N.², Kumari P² & Sanavar³

¹Department of Botany, University of Delhi, Delhi – 110007, India

²Department of Botany, Daulat Ram College, University of Delhi, Delhi – 110007, India

³Department of Botany, Kalindi College, University of Delhi, Delhi– 110008, India

*Email: uniyalpl@rediffmail.com

Abstract: The present study deals with some aspects of reproductive biology of an endemic and endangered aquatic angiosperm, *Willisia selaginoides* (Bedd.) Warm. ex Willis (Podostemaceae) restricted to the Western Ghats of India. Due to its occurrence in the challenging habitats, there is limited information available on its reproductive biology. *Willisia* possesses a small tuft of shoots with triangular thick scales and terminal flowers. The horizontal thallus arising after seed germination is considered as primary shoot and the vertical shoots arising on the dorsal surface of the thallus are considered as secondary shoots. The gummy substance exudes from the lower elongated surface cells (rhizoids) of the shoots and holdfast help in firm attachment to the shoots to rocks in fast flowing water. The flower is enclosed in spathe and represented by a pistil with bilobed stigma and a pair of dithecous anthers. Initiation of flower buds and subsequent development occurs in submerged conditions but flowers open only after the water level lowers down after monsoon. Pollination occurs when the flowers are just exposed to air after lowering of water level at the air-water interface. Co-occurrence of stigma receptivity with anther dehiscence and the close proximity of two organs seem to promote self-pollination. The pollen:ovule ratio (32:1) and ovule:seed ratio (6:5) suggest that even after relatively low pollen:ovule ratio, chances of high seed set occur. It clearly indicates the best possibility of self-pollination.

Keywords: Endemic, germination, Podostemoideae, self-pollination, thallus.

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Introduction

Podostemaceae are a large family of aquatic dicots with ca 60 genera and 340 species (Cook & Rutishauser, 2007; Koi *et al.*, 2012) of which 30 species occur in India and 24 of them are endemic to India (Krishnan *et al.*, 2019). As the vast majority of aquatic plants exhibits the combination of sexual and clonal reproduction, podostemads are solely dependent on sexual mode of reproduction (Philbrick & Novelo, 1997; Khosla *et al.*, 2001). Life-cycle events in the Podostemaceae are closely linked with seasonal variations of the water level in the river. Periodic phases of dry and wet periods underline the life history of podostemads. The plants remain vegetative when they are submerged and flowering occurs only when the water level recedes (Koi *et al.*, 2022; Cook & Rutishauser, 2007). They are thalloid rheophytes, restricted to tropical and subtropical riverine habitats all over the world. Podostemaceae are different from a typical angiosperm in their morphological, anatomical, embryological, and developmental attributes, and show higher rates of endemism (Philbrick & Novelo, 1997). Despite the large size of the family (~340 species), information on the reproductive systems and modes of pollination is available for nearly 30 species. The probable reasons are their unprocurable habitats and miniature size of the flowers.

Various studies indicate that Podostemaceae predominantly follow the mode of self-pollination (Philbrick, 1984; Khosla *et al.*, 2000, 2001; Okada & Kato, 2002; Cook & Rutishauser, 2007; Khosla & Sehgal, 2009; Sehgal *et al.*, 2009; Khanduri *et al.*, 2014; Silva-Batista *et al.*, 2020). Reports of cross-pollination by bees have been described in *Mourera fuviatilis* Aubl. and *Weddellina squamulosa* Tul. (Sobral-Leite *et al.*, 2011; Silva-Batista *et al.*, 2020). Besides entomophily, wind pollination has also been reported in a few taxa (Cook, 1988; Philbrick & Novelo, 1998). Consequently, the breeding system in the family varies from allogamy to autogamy (Rutishauser, 1997; Philbrick & Novelo, 1998; Sobral-Leite *et al.*, 2011; Khanduri *et al.*, 2024).

Unlike in majority of angiosperms, the embryo sacs in Podostemaceae are only 4-nucleate cells. Antipodals are absent and development of embryo sac corresponds to the podostemum type. There is no double fertilization and no endosperm formation, although two male gametes reach an incipient embryo sac having an egg and a central cell. Presence of pseudo embryo sac/nucellar plasmodium is characteristic feature of this family. It is believed that nucellar plasmodium nourishes the developing embryo as endosperm because real endosperm is absent and protects it from desiccation (Went 1908; Razi 1949; Mukkada, 1969; Mukkada & Chopra, 1973; Arekal & Nagendran, 1975). There is comparatively short span of time available for pollination and because the dehisced anthers are not able to retain pollen for longer duration due to fast flowing water. So, self-pollination appears to ensure the sexual reproduction but still the natural seed set found to be high in them. As there are certain floral features in podostemads that indicate the chances of self-pollination but possibility of out crossing cannot be over ruled through wind pollination (Cook, 1988; Philbrick & Novelo, 1997).

Willisia is represented by only two species *Willisia selaginoides* (Bedd.) Warm. ex Willis.

and *W. arekaliana* Shivam. & Sadanand. Both are critically endangered and endemic to Kerala, India and represented by only 1 or 2 populations (Shivmurthy & Sadanand, 1997; Uniyal & Mohan Ram, 2001). Although earlier there were doubts about delimitations of these two species (Cook & Rutishauser, 2007) but recent phylogenetic analysis revealed that two taxa are distinct (Koi *et al.*, 2012, Khanduri *et al.*, 2015). Morphologically these two species differ from each other in terms of their length of floral shoots, arrangement of flowers, size and arrangement of leaves, number of pollen grains to ovule and their shape and size of fruits (Khanduri *et al.*, 2014). The morphology and seed germination of *Willisia selaginoides* were studied by Uniyal and Mohan Ram (2001) and the reproductive biology of *W. arekaliana* was studied by Khanduri *et al.* (2014). The present study was focused on the reproductive aspects of *Willisia selaginoides* including floral anatomy and embryology.

Willisia selaginoides grows in a fast-flowing rivers in Kerala, India. The plants were found attached to the rocks with the help of rhizoids and haptera. The seed germination and vegetative growth occur under submerged conditions during rainy season and with the retreat of monsoon, water level in rivers lowers down which elicits flowering (Leleeka *et al.*, 2016). The plant body is characterized by tufts of long, erect shoots arising from the thalloid body. The flowers are zygomorphic, bear tepals, petals, and only ovary and stigma covered by a hard spathella. Seeds are minute and non endospermous, enclosed in a fruit which is a capsule (Uniyal & Mohan Ram, 2001).

Material and Methods

Willisia selaginoides was collected from Companywadi, Pooyamkutty dam site, Ernakulam district, Kerala, India (latitude of 76° 46.36' N and longitude of 10° 9.37' E), in the month of December (Fig.1, 2a). Flower buds, open buds and fruits at various stages of development (Fig. 2 b–f) were collected from the rocks and fixed

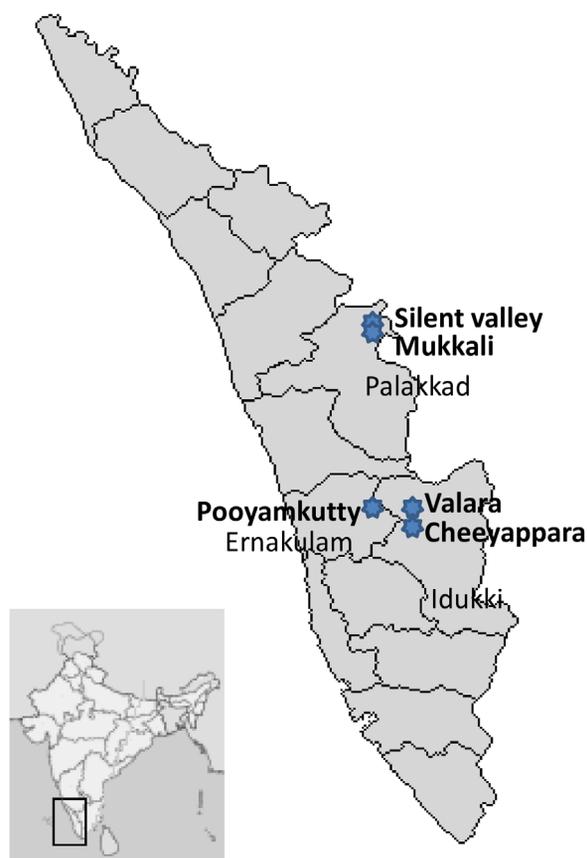


Fig. 1. Map of Kerala showing the collection localities.

in FAA (5% formalin, 5% glacial acetic acid, 50% ethyl alcohol) for 24 hours, then transferred to 70% alcohol. Various stages of buds and flowers were also fixed in 3% Glutaraldehyde for 24 hours and transferred to 0.2M phosphate buffer for scanning electron microscopy. Flowering phenology was recorded in the field. Nearly 100 flowers were examined at random to note the details of flower development and conditions of stigma and stamens using hand lens. The morphological details of flowers (*c.* 200) were observed and a comparison was made in their sizes, shape, and number of floral parts. Different stages of flower development were recognized on the basis of morphological parameters and in relation to environmental conditions for analysis.

Fixed floral buds were processed through series of 2-methoxyethanol, ethanol, *n*-propanol, and *n*-butanol for one day each, infiltrated and embedded in a monomer prepared from glycol

methacrylate, PEG and Azobisisobutyronitrile. The embedded plant material was then serially sectioned at 3 μ m using glass knives and then stained with 0.05% Toluidine Blue O prepared in benzoate buffer (pH 4–5), the observations were recorded with the help of Trinocular Microscope Zeiss Primostar, Canon Power shot G10 camera. For scanning electron microscopy (SEM), the fixed material was subjected to critical point drying, mounted on aluminum stubs, coated with gold palladium alloy and scanned using a Carl Zeiss EVO 40 Scanning Electron Microscope at 20 KV level.

Results

Flowering phenology: The plant consists of small crust like thallus closely attached to the surface of the rocks. With the development of tuft of secondary shoots, the thallus decay and shoots become attached to the substratum. The plant begins to flower at the end of October under submerged conditions and become exposed to air in December (Fig. 2b). A terminal solitary floral bud appears on each shoot in submerged water and opens only when the water level in the river recedes exposing them in the air. A mature flower bud measures *c.* 6 mm in length and *ca* 3mm in width. The flower buds (Fig. 2d) are enclosed by a spathella. The tip of the spathella has two projections indicating the fusion of leaves during development. Flowers are pedicellate (Fig. 3b, e), pedicel measuring 2–3 mm in young bud but increased up to nearly 16 mm during maturation (Uniyal & Mohan Ram, 2001).

Mature Flower: On removing spathella, the flower bud shows a laterally placed ovary and two stamens which are basally united into a thick, short filament forming a Y-shaped andropodium (Fig. 3a–c). A pair of tepal, *c.* 5 mm in length, arises at the base of the filament (Fig. 3d). The pistil consists of an elliptical-shaped ovary, a bifid stigma but lacks a distinct style (Fig. 3b). The stigmatic lobes lie close and bent over the ovary surface (Fig. 3e, f). The anthers when young, are pressed against the ovary

wall and lie below the stigma. The filaments are c. 1.5mm in young buds. At the time of pollination, the filament elongates nearly 6–8 mm, curve inward and bring the anther to the same level of the stigma. Further the andropodium elongates and the anthers extend beyond the stigma. The

spathella which enclosed the flower bud ruptures laterally exposing the stigma and anthers. After pollination the anthers are shed and the shrivelled andropodium persists at the base of the ovary. The surface of the ovary develops four longitudinal ribs along the wall (Fig. 3i, j)



Fig. 2. *Willisia selaginoides* (Bedd.) Warm. ex Willis: **a.** Habitat in nature (5×); **b.** Shoots above the water level (5×); **c.** Flower buds and fruits (5×); **d.** A close portion of the flower bud with leaves and spathe (10×); **e.** Dry plants bearing the fruits growing on the rock (5×); **f.** An enlarged portion of dry plant with the capsules (10×).

Pollen grains: Anthers are tetrasporangiate, introrse, dorsifixed. The wall of the mature anther is composed of three layers of cells. The endothecium shows wall thickenings. Pollen grains are released in pairs and called dyads (Fig. 3g, h). It has two layers exine and intine. The surface of the pollen shows microechinate ornamentation. A single flower produces nearly ± 8135 pollens grains ($n = 100$) (Table 1). It measures about \pm

$29.04 \mu\text{m}$ polar diameter and has an equatorial diameter of $\pm 19.35 \mu\text{m}$. Pollen tube appears from both of the pollens of a dyad that were found to bear the potential nuclei.

Pistil: Spathella is non-vascularised lamina and consists of 3–4 layers of cells (Fig. 3f). SEM of pistil shows a bifid stigma that curved towards the ovary surface. In a bud the two lobes of the stigma lie close to each other, which start to straighten when

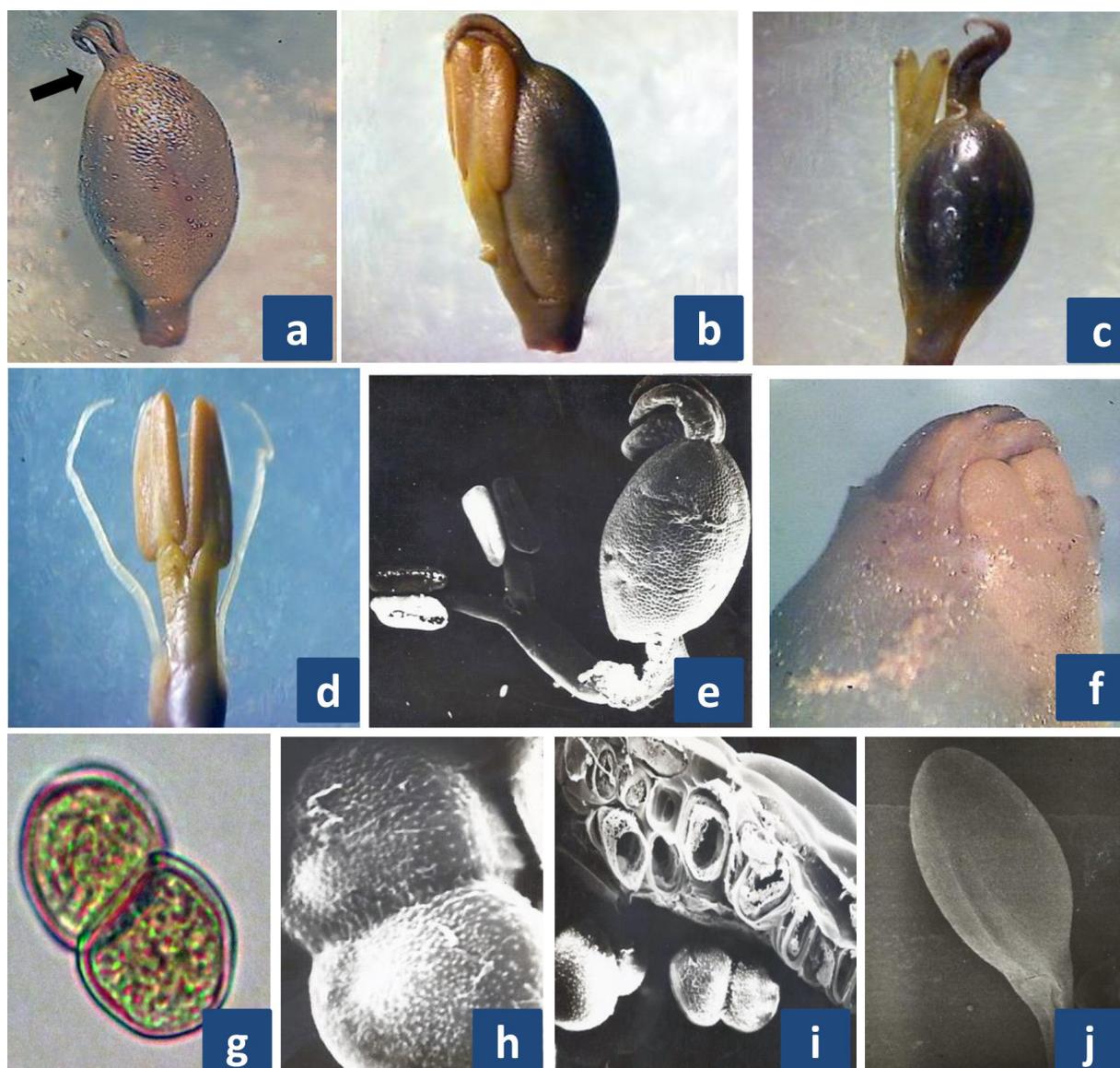


Fig. 3. *Willisia selaginoides* (Bedd.) Warm. ex Willis: **a.** A single ovary with the bifid stigma (10 \times); **b.** A flower where the spathe has been removed to show the essential organs. The anthers are closely appressed to the stigma (10 \times); **c.** The anthers have already dehisced and the formation of fruit has started (10 \times); **d.** The two stamens with a pair of tepals. The filaments of the two stamens are fused at the base (10 \times); **e.** SEM of a flower showing the bifid stigma and the two stamens (40 \times); **f.** A portion of the flower where the tip of the spathe has been ruptured (40 \times); **g.** whole mount of a single dyad showing the exine and intine layers (40 \times); **h.** SEM of a single dyad pollen. The surface of pollen has echinate ornamentation (40 \times); **i.** The SEM of dehiscent anther releasing the pollens (40 \times); **j.** SEM of a mature fruit showing two ribs (40 \times).

the buds are exposed to air. Receptive time is in the forenoon. Tepals are linear-shaped and made up of loose parenchymatous cells and lack vascular tissue and they are emerged, one at each side of the andropodium base. Longitudinal section of the pistil shows that the stigma lobes are unequal. Ovary is bicarpellary, syncarpous, bilocular and produce ovules in an axile placentation. About 252 ovules are produced per ovary. Placenta is located at the middle of the septum and rich in starch grains. Ovary wall is eight cells thick. The inner epidermis and adjacent cells are filled with some dark brown carbohydrate. The layer next to it is narrow and radially elongated cells. The outer epidermis and the two subjacent layers consist of large, thin-walled cells which contain starch granules.

Pollen-ovule ratio and Ovule-Seed ratio: The pollen:ovule ratio is found to be 32:1. A fruit produces about 184 seeds and so the ovule:seed ratio is found to be 6:5.

Pollination events: Pollen:ovule ratios of flowering plants are generally indicative of the chances of pollen reaching the stigma ensuring maximum seed set and thus determining their

breeding system. The low pollen:ovule ratio and high seed set suggest the possibility of self-pollination (autogamous) (Wang *et al.*, 2004; Bochynek & Burd, 2024). Autogamy ensures the maximum seed production, which is highly significant because asexual reproduction has not been reported in Podostemaceae (Philbrick & Novelo, 1997). Podostemaceae in general represents an example in which all reproductive energy seems to have been channelized into high seed production, replacing asexuality with sexuality.

Development of Embryo sac: Present study in *Willisia selaginoides* revealed that the megaspore mother cell (mgc) occurs in the micropylar region of the nucellus (Fig. 4a). When meiosis starts, epidermis and central column of nucellar cells (nc) with dense cytoplasm below the megaspore mother cell enlarge and stretch, persisting in this way during all the meiotic process (Fig. 4b). The nucellar plasmodium completes its development by the time of embryo sac formation due to the cell wall degradation of both the central column and lateral (epidermal) layers of nucellar cells. Later,

Table 1. Floral parameters of *Willisia selaginoides*.

Fruit	Length (mm)	± 3.7
	Width (mm)	± 1.5
	Number of ribs on the fruit	04
	Number of seeds per fruit	± 184
Seed	Length (mm)	± 274.5
	Width (mm)	± 206.6
Number of dyads per flower		± 8135
Size of pollen dyad	Polar diameter (µm)	± 29.04
	Equatorial diameter (µm)	± 19.35
Number of ovules per ovary		± 252
Pollen: ovule ratio		32:1
Ovule: seed ratio		6:5
Pedicel length in mature fruit (mm)		± 16.0

the integuments show a considerable increase in length and the outer integument, composed of three cell layers forms the micropyle and contain numerous starch grains.

Megasporogenesis and embryo sac: Longitudinal section of mature ovary shows numerous anatropous, tenuinucellate and bitegmic ovules in an axile placenta. The micropyle is formed by the outer integument only as the

inner one lags behind the former. Megasporecyte (megaspore mother cell) differentiates in an ovular primordium. The megasporecyte is large with a conspicuous nucleus and dense, non-vacuolate cytoplasm. The megaspore mother cell divides meiotically (Meiosis I) to produce two uninucleate dyads cells (Fig. 4c). The upper or micropylar dyad cell degenerates soon but persists as a dark cap over the developing embryo (Fig. 4d,

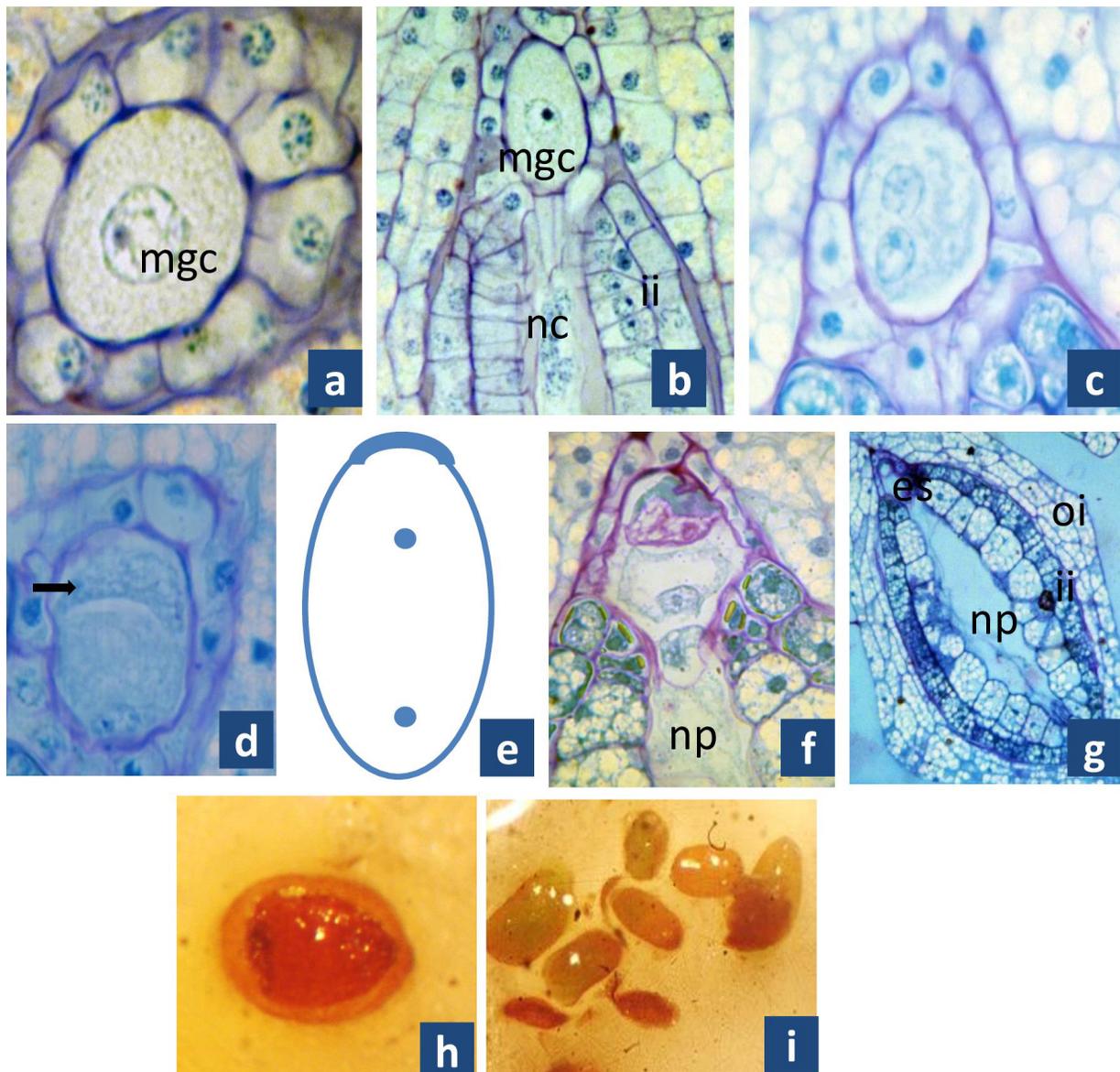


Fig. 4. *Willisia selaginoides* (Bedd.) Warm. ex Willis: **a.** Longitudinal section of a young ovule showing megaspore mother cell (mgc) (100×); **b.** Megaspore mother cell (mgc) just before division and the nucellar cells below (nc) (40×); **c.** The megaspore mother cell divides and form two nuclei. (100×); **d.** The degenerated micropylar dyad cell (arrow) (100×); **e.** Diagrammatic representation of embryo sac where the chalazal nucleus divide and form two nuclei; **f.** Organize embryo sac with two synergids at micropylar end, a median egg and a polar cell at chalazal end can be seen (100×); **g.** Longitudinal section of an ovule showing embryo sac (es), outer integument (oi), inner integument (ii) and nucellar plasmodium (np) (40×); **h & i.** Seeds after soaking in medium for a day. Note the gum surrounding the seed (10×).

e). The dyad cell at the chalazal end undergoes the second meiotic division resulting in the formation of two nuclei. These two nuclei divide resulting in formation of four nuclei that participate in the formation of the embryo sac. The embryo sac consists of two synergids at the micropylar, an egg cell and a polar cell at the chalazal end (Fig. 4f, g). The sequence of the development of the embryo sac corresponds to the *Podostemum* type (Battaglia, 1971; Sehgal et al., 2011; Chaudhary et al., 2014). Female gametophyte follows a monosporic development to form 4-nucleate/4-celled embryo sac. The antipodals, triple fusion and endosperm are found to be absent.

Fruits and Seeds: The fruit is oval-elliptical in shape and measures c. 4 mm length and width of c. 3 mm. SEM of the fruit shows two slightly prominent longitudinal ribs (Fig. 3j) along the wall of one side of the fruit. Fruit dehiscence occurs by two valves. A single fruit produces about 184 seeds and each seed measures (n=100) about $\pm 274 \mu\text{m}$ in length and $\pm 206 \mu\text{m}$ in width. The seeds are ovoid in shape (Fig. 4 g, h).

Discussion

We observed that the reproductive features significantly favour the self-pollination, as earlier speculated (Uniyal & Mohan Ram, 2001). Self-pollination occurs in podostemads in different manners as studied in *Podostemum ceratophyllum* Michaux, *Griffithella hookeriana* (Tul.) Warm. & *Hydrobryopsis sessilis* (Willis) Engl. Under submerged conditions (Philbrick, 1984; Khosla et al., 2001; Sehgal et al., 2009), self-pollination also have been reported in the flowers of *Polypleureum stylosum* (Wright) Hall., *Indotristicha ramosissima* (Wight) van Royen (Khosla et al., 2000; Khosla & Sehgal, 2009), and *Podostemum subulatum* Gardn. (Khanduri et al., 2024). Self-pollination in *W. arekaliana* occurs at the air-water interface by their partial emergence from spathella (Khanduri et al., 2014). Such diversity in the mode of self-pollination represents different degrees of adaptation to uniform ecological settings indicating the intimate

relation between their functional floral morphology and pollination biology.

In the present study, it appears that only the tip of spathella separates to avoid any contact with water and to minimize wastage of pollen grains. Exposure to air provides the necessary desiccation for anther dehiscence that is supported by the emergent anthers and endothelial bands of anther wall. Stigma emerges from spathella for pollen reception.

Self-pollination has been reported as a predominant mode of pollination in various members of Podostemaceae (Sobral-Leite et al., 2001) although cross pollination cannot be ruled out completely because studies in flowers of *Polypleureum stylosum* and *Indotristicha ramosissima* (Khosla et al., 2000; Khosla & Sehgal, 2009) also leads to seed set. Even various studies in the chasmogamous flowers of *Mourera fluviatilis* Aubl. and *Marathrum rubrum* Novelo & C.T.Philbrick showed the autogamous nature. Thus, a shift in the breeding system seems to have occurred in Podostemaceae from allogamy/autogamy in chasmogamous flowers to complete autogamy in cleistogamous flowers (Khosla et al., 2001).

Experimental studies also suggest that *Willisia selaginoides* is a self-compatible species that is typically self-pollinated. A low pollen/ovule (P/O) ratio is also an indication of obligate autogamy (Cruden, 1977, Okada & Kato, 2002). In the present study pollen/ovule ratio have been found significantly low (32:1), suggesting its self-pollinated nature, but even then, the seed set was found high. Podostemads usually bear high seed numbers compared with other aquatic plants (Rutishauser, 1997; Philbrick & Novelo, 1998). The maturation of floral organs at the same time is also a favourable step for the success of self-pollination. The compound pollen units (dyads) are also proved as efficient means to increase self-pollination (Kress, 1981; Knox & Kenricks, 1983). Occurrence of dyads is also helpful in rapid flow of water current that facilitates deposition

of greater number of pollen grains to stigma. Field experiments indicated mere chance of any cross pollination in *Willisia selaginoides* even the morphology of floral structure excludes the possibility of hydrophily or anemophily. Application of molecular markers may help in elucidating the possibility of natural out crossing in this species. *Willisia selaginoides* showed relatively high natural seed set by channelizing most of its resources to reproduction and perpetuate them by manifestation of self-pollination to ensure survival of this plant. Under unfavorable conditions reproductive success usually became uncertain but self-pollination offers a adaptive strategy in plants under ecological conditions that could be compensated by cross pollination.

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