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SPORE DISPERSAL IN THE DESERT SPECIES OF *MARSILEA*

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Observations of the desert species of *Marsilea* have shown large scale weevil larvae infection of the sporocarps of such species as *M. aegyptiaca* & *M. rajasthanensis* which assists in sporocarp burst and spore dispersal in these species. Distribution and spread of Marsileaceae particularly the genus *Marsilea* in desert regions is discussed with special reference to such factors as prolonged spore viability and frequency of parthenogenesis/apogamy and microsporal aberrations in this family of amphibious ferns.

The sporocarp of Marsileaceae is indeed an unique and unparalleled structure in the plant kingdom. It has been at the center of debates in so far as its homologies are concerned and as yet there seems to be no agreement on its morphological nature. There is no doubt however, that the sporocarp adds to many unfern like attributes of Marsileaceae so much so that Meeuse (1961) has even suggested Marsileaceae to be surviving representatives of the fossil Glossopteridales. The present contribution relates to the uniqueness of sporocarp as a reproductive unit which seems to be specifically adapted for a group of plants of the amphibious habitats and which in course of evolution had to encounter extremes of environment. One of the genera of this family, namely *Marsilea* happens to be widely represented and diversified as observed by Kornas (1985) in the course of his studies of the African Marsileas. Retaining its amphibious moorings the family Marsileaceae and in particular the genus *Marsilea* has a very wide ecological amplitude providing for a facile exploitation of both the aquatic and xeric ecological niches, especially the latter largely because of the peculiar organisation of its sporocarp.

The present study describing some hitherto unreported modes of sporocarp and spore dispersal in *Marsilea* is based on investigations for over two decades on the spread and survival of this genus in desert habitats of Rajasthan in India and also in the middle east. The most important biological characteristic of *Marsilea* and which is so well known and recorded in the literature is of particular relevance to this study and that is the almost indefinite viability of both mega- and microspores of various species of *Marsilea*. These viability records as found in literature and also based on my personal observations extend to more than a hundred years and are presented in Table 1.

There are two points requiring special attention in context of the spore viability in Marsileaceae : (i) it is mostly the xeric taxa of the genus *Marsilea* inhabiting desert regions which possess such extended viability periods. In case of such species as *M. quadrifolia* which is primarily a subtemperate species, the long winters provide rather extended periods of hibernation for the sporocarp. My own observations of nearly 50-60 species show that such hydric species as *M. polycarpa* and *M. mutica* possess attenuated and shorter periods of spore viability. (ii) The intergeneric differences in respect of spore viability in the family Marsileaceae also confirm to this pattern in that *Pilularia* comes next in this respect. I could obtain germination of both mega-microspores only once in a sample of the subtemperate *P. globulifera* from an eighty two year old sporocarp. Spores of *Regnellidium diphyllum* possess a short period of viability in comparison.

The impact of this factor of spore viability in regard to the spatial distribution of Marsileaceae may be considered now. It will be pertinent here, however, to consider features of sporocarp structure providing for this long period of spore viability. Our studies suggest that it is the stark protection provided by the sporocarp wall which is primarily responsible for this attribute of *Marsilea* spores which are additionally protected by the gelatinous matrix and mucilaginous material so richly present in the sporocarp and which surrounds the mega- and microspores individually as

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Table 1. Spore viability in Marsileaceae

Sr. No.	Species	Years Spores known to be viable		Germination observed for micro-, or mega-spores or both
1.	*M. aegyptiaca*	96	Bhardwaja, Pers. Obs.	Both
2.	*M. cornuta*	113	"	Both
3.	*M. crenata*	65	"	Only microspores
4.	*M. diffusa var.*	103	"	Both
5.	*M. diffusa var.*	60	"	Only megaspores
6.	*M. drummondii*	71	"	Both
7.	*M. macrocarpa*	41	"	Both
8.	*M. minuta*	130	"	Both
9.	*M. pubescens*	130	"	Both
10.	*M. quadrifolia*	100	"	Both
11.	*M. uncinata*	123	"	Both
12.	*M. vestita*	80	"	Both
13.	*M. burchellii*	131	(Bhardwaja, 1980)	
14.	*M. fournieri*	61	(Allsopp. 1952)	
15.	*M. minuta*	68	(Allsopp, 1952)	
16.	*M. quadrifolia*	80	(Bloom, 1955)	
17.	*M. crenata*	71	(Johnson, 1985)	
18.	*M. mollis*	89	(Johnson, 1985)	
19.	*M. oligospora*	100	(Johnson, 1985)	
20.	*M. vestita*	77	(Johnson, 1985)	
21.	*Pilularia globulifera*	82	(Bhardwaja, Pers. Obs.)	Both

Remarks : Personal observations based on material at Herbarium BGBM, Berlin.

well in comparison to the sporocarp and spores of both *Pilularia* and *Regnellidium*. This protection is so rigorous in *Marsilea* that sporocarps preserved in FAA/Alcohol/poisoned herbarium sheets would germinate with both mega-and microspores forming respective prothallia and gametes. The wall of the sporocarp is thus the toughest in *Marsilea* and is able to check the entry of any external material and fluids notwithstanding pits and stomata being abundantly present on its surface. This is presumably done by the special layer of elongated cells under the sporocarp epidermis containing the 'Linea Lucida' (Tournay, 1951) and which is conspicuous by its absence in both *Pilularia* and *Regnellidium* sporocarp. Studies of comparative wall structure of the sporocarp of these three genera carried out by Mahabale (1956) also corroborate this. The interspecific differences in spore viability period in *Marsilea* also seem to be related to differences in sporocarp wall structure since such 'hydric' species as *M. polycarpa* do not exhibit a strongly developed 'Linea Lucida' and the gelatinous/mulcilaginous matter is also poorly developed compared to the 'xeric' species. The presence of a sorophore which fills the sporocarp completely in *Marsilea* and which is rich is globular carbohydrates and fibrous polysachharides (Bilderback, 1978) also contributes to the spore viability factor in Marsileaceae since this structure is absent in both *Pilularia* and *Regnellidium*. My study of the sporocarp germination process in various species of *Marsilea* also indicates that sorophore is rather poorly developed in the hydric species like *M. polycarpa* which grow in areas with abundant humidity and moisture throughout the year.

This viability of *Marsilea* spores can now be considered with particular reference to the observations made by field collectors of this genus and which Launert (1970) mentions as the unusually erratic 'behaviour' or *Marsilea* populations particularly in the arid regions when an entire stand of *Marsilea* will disappear for any length of time from a particular locality to reappear again as mysteriously as it disappeared (Singh & Bhardwaja, 1977, Soni, 1987). Similarly new stands at far disjunct localities would spring up quite suddenly, specially in the arid regions around temporary water storage areas formed during the rainy spell. Soni's observation on West Rajasthan species of *Marsilea* (Ph.D. Thesis, 1987) are especially relevant in this latter connection. He notes that in the long dry and hot season *M. aegyptiaca*, a typical desert species of this area, would dry up completely and form balls containing hard, dry sporocarps. And sand storms, so common in this desert region especially during summers and before the advent of rains blow up these sporocarp balls over fairly long distances. Added to this is the factor of cattle grazing, especially sheep migrations over long distances when vegetation is drying up during summers with a lot of grazing pressure around ponds and tanks. The sporocarp balls are carried by the grazing cattle from one locality to other. And lastly, it is the anthropogenic activities such as digging of smooth bottom soil of desert tanks during summers for brick making purposes which is very common in this west Rajasthan area which loosens the sporocarp balls for dispearsal by sand storm currents. And sporocarps lying buried for long, long years may germinate on chance exposure to favourable conditions prevailing during the rainy season giving rise to *Marsilea* eruptions at newer localities.

It is at this point that an observation made by Loyal & Kumar (1979) assumes particular relevance to sporocarp opening and spore dispersal in nature in the genus *Marsilea*. These authors observed that sporocarp contents of north western populations of *M. minuta* were destroyed by weevil larvae belonging to the genus *Echinocnemus* Schonherr. These larvae had bored holes and punctured the sporocarp wall. This prompted us to look for such larval attacks in the W. Rajasthan *Marsilea* populations, particularly *M. aegyptiaca* sporocarps. Our observations did show that sporocarps of this species had a big percentage of punctured sporocarp walls due to insect larval attacks and this was found to be a regular feature in our surveys of the desert localities along Bikaner Jaisalmer Road.

This occurrence of larvae attacked sporocarp populations of *M. aegyptiaca* becomes considerably important in the context of the toughness of the sporocarp wall in such desert species. it is a well known practice for all experimental work on spore germination in *Marsilea* that the sporocarp wall is scarified for entry of water resulting in swelling of the sorophore causing sporocarp burst for spore dispersal. But for this the sporocarp will not open otherwise due to the tough wall which is resistant even to avian digestion processess as observed by Malone & Procter (1965) when they demonstrated that *M. vestita* sporocarps would pass intact through digestive tracts of the wood duck *Aix sponsa* Linnaeus. This becomes particularly relevant to sporocarp opening and spore dispersal in desert species like *M. aegyptiaca* with extremely hard sporocarps as a result of enduring high soil temperatures of desert summers. Sporocarps of *M. aegyptiaca* with walls punctured due to weevil attacks and where the spore contents had not been destroyed completely by the larvae were found to burst open dispersing spores on being placed in water leading to both mega- and microspore germination.

It is difficult to say at this point if this is a regular mode of dispersal of spores in all species of *Marsilea* but it seems to be a common feature in the xeric taxa. It may be emphasized here that this weevil assisted dispersal of spores is singular and unparalleled in ferns. Additional features relevant to this observation in the desert taxa are : (1) the xeric and desert species of *Marsilea* do possess a much higher ratio of megasporangia/sours with abundance of microsporal aberrations (Bhardwaja, 1966) compared to the hydric species. The sporocarps of the xeric species thus contain a larger percentage of megaspores gorged with food reserves attracting these weevil larvae attack (2) it is these xeric taxa which are known for a greater frequency of parthenogenesis/apogamy compared to hydric species (Bhardwaja & Abdullah, 1972) providing for apomictic sporelings. And megaspores are reported to be diploid in species producing sporelings apogamously (Strasburger, 1907; Haberlandt, 1922). This zoogenic dispersal of spores is thus a significant factor in the survival and spread of the desert species like *M. aegyptiaca,* being a consequence of a sturdy sporocarp wall and which seems to provide apparently a basis of the prolonged viability of spores in *Marsilea.* Moreover, the abundance of megaspores with their stored food reserves apart from attracting weevil larvae also enhances species survival potential since the rainfall often gets delayed in these desert regions. At the same time eating up and elimination of the megaspores should the rains be excessively delayed must contribute to the sudden disappearance of *Marsilea* stands so often seen in these desert localities. To sum up, the present observations have focussed on a hitcherto unemphasized aspect of spore dispersal and spread of the amphibious fern *Marsilea* in desert regions.

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