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A Review on Reproductive Strategies in Ferns

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ABSTRACT

Reproductive strategies in ferns include biological discussion of all reproductive methods i.e. sexual, asexual, vegetative and other unusual special methods which leads to the development of new generations. In ferns, there are various works in different fields of reproductive biology, such as in mating system of ferns-populational, ecological, genetic adaptation in different types of apomixes i.e. apogamy, apospory, agamospory, vegetative reproduction and vivipary etc. A brief overview of the reproductive strategies taken by the ferns in different climatic and experimental conditions is represented here.

INTRODUCTION

From the point of view of reproductive strategies, the extant pteridophytes can be categorized in two major groups-homosporous forms and heterosporous forms. Heterosporous pteridophytes consist of eight living genera,such as *Selaginella, Isoetes, Stylites, Marsilea, Pilularia, Regnellidium, Azolla and Salvinia*. The life cycle of heterosporous pteridophytes is analogous genetically to the seed plants than to the rest of the pteridophytes. Megasporangia give rise to megaspores, which develop into endosporic female gametophytes bearing archegonia, while microsporangia give rise to microspores which develop endosporic male gametophytes and form antheridia and antherozoids respectively. Thus, maximum amount of inbreeding (self fertilization) that can occur in such a way that a plant is the fusion of egg and sperm coming from sib gametophytes. In contrast, ferns have sporangia, which form spores having the capacity to give rise to gametophytes that are exosporic and hermaphroditic. Union of two gametes produced by the same gametophyte, resulting in a zygote that is completely homozygous. Therefore, homosporous ferns have the capacity to form fully homozygous zygotes in one generation of selfing.

The pioneer works in the field of modern of reproductive strategies in ferns were done by Edward J Klekowski Jr. in the middle of 1960s (Klekowski & Baker, 1966; Klekowski & Lloyd, 1968). Since that time numerous studies had appeared on a variety of species and phenomena by a limited number of works (Cousens & Horner, 1970; Duckett, 1970, 1972; Ganders, 1972; Holbrook-Walker & Lloyd, 1973; Klekowski, 1969a, 1969b, 1970a, 1970b, 1970c).Due to the complexities, which are possible in fern reproductive biology, very specific terminology has been derived to describe various levels of crossing and selfing that are possible in ferns. Selfing can be defined

as the fusion of gametes from gametophytes derived from the same parental sporophytes, but due to the possibility of forming hermaphroditic gametophytes two levels of selfing are possible i.e. the fusion of gametes produced by the same gametophytes and the fusion of gametes produced by sib-gametophytes. The probability of a genotype being homozygous for a given gene where selfing is a result of the fusion of gametes formed by sib-gametophytes is half (1/2), where as the possibility that a gene locus is homozygous where the gametes originate from the same gametophyte is one (1).An additional point is that the zygote resulting the fusion of the gametes coming from the same gametophyte is homozygous at every gene locus, where as the probability of completely homozygous zygote occurring, where the gametes come from sib-gametophytes is $(1/2)^n$, where n=number of heterozygous loci in the parental sporophyte genotype. The following types of selfing, crossing and mating are found in pteridophytes.

1. **Intragametophytic selfing:** The fusion of sperm and egg from the same gametophyte. Normally this results in a completely homozygous zygote.
2. **Intergametophytic selfing:** The fusion of sperm and egg from gametophytes with both genotypes being sib i.e. originating from the same parental sporophyte. This is analogous to the self-fertilization of a seed plant.
3. **Intergametophytic crossing:** The fusion of sperm and egg from different gametophytes with each gametophyte originating from a different parental sporophyte. This is analogous to cross-fertilization of a seed plant.
4. **Intergametophytic mating:** The fusion of sperm and egg from different gametophytes with the origin of gametophytes not specified.

Although the genetic consequences of selfing of a gametophyte have been long recognized (Lang, 1923), previous discussion of evolution in ferns have emphasized hybridity (interspecific) and have assumed that intragametophytic selfing is of little consequence in nature (Manton, 1961). This opinion regarding intragametophytic selfing still held many pteridologists and is based primarily upon a kind of "Fern Chauvinism" against homozygosity.

MATING SYSTEM IN FERNS:

A. POPULATIONAL:

Homosporous ferns offer a particular interesting comparison with seed plants. They differ from higher vascular plants in producing highly dispersible haploid spores, which generate free-living potentially bisexual gametophytes. Thus mating systems in ferns are quite different from those of angiosperms and gymnosperms and similar in some ways to those of bryophytes. In fact, three types of mating are possible (Klekowski, 1969; Lloyd, 1974 a).

1. **Intergametophytic crossing:** the cross-fertilization of gametophytes produced by different sporophytes.
2. **Intergametophytic selfing:** the cross-fertilization of gametophytes produced by a

single sporophyte.

3. **Intragametophytic selfing:** the self-fertilization of a single gametophyte.

Intergametophytic crossing is genetically equivalent to outcrossing (cross fertilization) in seed plants and Intergametophytic selfing is genetically equivalent to selfing in seed plants.

As archegonia and antheridia are borne on the same thallus it has long been maintained that Intragametophytic selfing is predominant mode of reproduction in natural population of Homosporous pteridophytes (Klekowski and Baker, 1966; Klekowski, 1973). This would have major implications for the genetic structures of these populations, because Intragametophytic selfing results in the production of completely homozygous sporophytes by act of fertilization. Experimental evidence indicates that some ferns like *Botrychium virgianum, B. dissectum* and species of *Asplenium* reproduce predominantly by self-fertilization (Soltis and Soltis, 1986).

Majority of the adaptations, which influence the breeding systems of ferns are aspects of the gametophytic generation. There are sporophytic adaptations, which can play a prominent role. An example of this is the reproductive biology of *Mettuccia struthiopteris*. This fern begins to shed their propagules in January and continue to do so until March. If snow is collected from beneath these fronds in January, it is found to contain full, unopened sporangia rather than spores, whereas collection of snow in March will contain spores and sporangia. The sporangia contain viable spores, which will germinate within the sporangium and rupture it, resulting in a cluster of male and female gametophytes. Thus in this fern two kinds of propagules are formed, sporangia that are distributed when the snow melts and the wind disseminated spores. The reproductive biology of sporangia is genetically analogous to an inbreeding seed plant (the predominant level of mating is between sib-gametophytes, Intergametophytic selfing, Klekowski, 1979).

Gametophytic adaptations also influence the nature of fern mating system (Lloyd, 1974). The adaptations include the gender, ecology, distribution of gametangia, longevity of the gametophytes, capacities for vegetative reproduction and polyembryony (Klekowski, 1969).The basic morphological syndrome or characteristic which leads to a predominance of Intragametophytic selfing is a uniform gametophyte population with respect to gender, the differentiation of antheridia initially and the later attainment of the hermaphroditic condition by differentiation of the archegonia with the continued proliferation of antheridia and a relatively short-lived gametophyte generation with limited capacities for vegetative reproduction and simple polyembryony. Such a mating system often characterizes weedy fern species, which rapidly colonize open, recently disturbed habitats (Lloyd, 1974b). *Pteridium aquilinum* and *Ceratopteris thalictroides*), which is aggressive weed in the respective environments, have capacities for extensive multiplication and antheridogen system, which can promote Intergametophytic mating (Schedlbauer and Klekowski, 1972). It is

interesting to note that amount of genetic variability in the populations of these four weedy species varies greatly and only *Pteridium aquilinum* populations consistently have genetic load (Klekowski, 1972).

No prior evidence was found regarding genetic self-incompatibility system present in homosporous ferns with free-living hermaphrodite gametophytes. Wilkie (1956) hypothesized that a genetic self-incompatibility system was present. Tryon (1941) did not support 'Wilkies hypothesis'. All the hybridization data could be explained best by assuming that sporophytes of this species are heterozygous for various combinations of recessive sporophytic lethals (genetic load) and that occasionally a spore sample is obtained that forms a trans heterozygote for a pair of closely linked lethal alleles Ab/aB. The spores of such a sporophyte will be ½ Ab and ½ aB and isolated gametophytes will not form viable homozygous sporophytes upon Intragametophytic selfing. If the gametophytes are paired randomly the following expectations will be realized – ¼ (Ab x Ab), ½ (Ab x aB), ¼ (aB x aB). Thus only 50% of the random pairs will be heterozygous at both loci and form sporophytes (Ab x aB). Crossing over will generate two recombinant spore genotypes (AB and ab) of which one (AB) will form viable sporophytes upon intragametophytic selfing. It should be noted that the above genetic load model accounts for all the hybridization data for a sporophyte heterozygous for a pair of self-incompatibility alleles S^1S^2 (Klekowski, 1979).

A population of isolated gametophytes will not yield viable homozygous sporophytes upon selfing (as their genotypes would be S^1S^2 or S^2S^2) and population of random pairs of gametophytes (were capable of forming a viable homozygous sporophytes upon) will result in 50% of the combinations being heterozygous (S^1 x S^2) yielding sporophytes. Wilkie (1956) found that a low frequency of gametophytes were capable of forming a viable homozygous sporophytes upon Intragametophytic selfing, this phenomenon is not accounted for the genetic self-incompatibility hypothesis, but readily explained under the genetic load hypothesis.Genetic load and self-incompatibility systems are closely related and one readily can envisage the evolution of such genetic incompatibility system from trans-heterozygotes for recessive sporophytic lethal. The tightening of the linkage relationships between such loci could well be a consequence of such evolution. The distinction between two phenomena, genetic load and genetic self-incompatibility for a species is based upon the ubiquity of sporophyte genotypes in the populations, which yield spore samples that are self-incompatible i.e. from gametophytes which fail to form viable homozygous sporophytes upon Intragametophytic selfing.

Among homosporous ferns three types of reproductive strategies can be found-

1. Those in which syngamy is eliminated and sporophytes originate apogamously.
2. Those which promote Intragametophytic mating, and
3. Those which promote Intergametophytic

mating.

Genetically apogamy results in the least genetic variability in the species, and Intergametophytic mating results in the greatest degree of genetic variability.

B. ECOLOGICAL:

Correlations between ecology of the species and length of the gametophyte generation discussed by Klekowski (1972, 1979), suggests that ferns occupying habitats less favourable to the survival of their gametophytes for a longer duration are expected to undergo predominantly Intragametophytic selfing, and these species would be characterized by shorter gametophytic generation time (Lloyd, 1974 a, b), indicates that the colonizing species may possess a shorter gametophyte phase. Moreover, considering the significance of polyploidy in the homosporous ferns as intimately related to homothallism of their gametophytes (Klekowski, 1973, 1979). Intragametophytic selfing might be expected to be more common in present day polyploids as compressed to the diploids. Masuyama (1979, 1986) has documented such a correlation with respect to 2X and 4X forms of *Phegopteris decursivepinnata*, where the diploid is favoured toward Intergametophytic mating and tetraploid toward Intragametophytic selfing.

Guillon and Raquin (2002) studied the environmental sex determination in Horsetails (*Equisetum*). Horsetails are Homosporous and sexual differentiation of *Equisetum* gametophytes is under the influence of environmental conditions. Still the environmental cues responsible for sex determination of *Equisetum* gametes *invitro* and in wild conditions have remained elusive. Here we show that significantly different sex ratios are obtained when gametophytes are grown on media with or without sugar.

C. HORMONAL:

A careful observation by Dopp (1950) led to the discovery of a specific organ-inducing substance in ferns. Dopp (1950) observed that juvenile gametophytes of *Pteridium aquilinum* bore antheridia. He thought that the induction to be mediated by the substance elaborated by older gametophytes and it has been found that the extract from mature prothalli of bracken fern hastened the onset of antheridium on newly formed gametophytes. This substance was organ specific, but not species specific. Naf (1959) rediscovered the biologically active factor, a natural metabolite specifically concerned with induction of antheridia. The "Pteridium factor" was designated as "Antheridogen". It has been found to be active in the members of Pteridaceae, Dryopteridaceae (Dopp, 1950), Gymnogrammaceae (Dopp, 1959), Aspleniaceae (Naf, 1959).The antheridogen either induce the formation of antheridia under conditions in which control plants do not form them, as in *Osmundasensibilis* or hastens the onset of antheridium formation. Extremely small amount of substance required for antheridial development. Investigations on fern reproductive biology revealed that, unresponsive to antheridogen led to the formation of a substance that controls antheridium formation in *Anemia phyllitidis*. The substance however is inactive towards

plants or gametophytes which respond to "Pteridium factor" (Naf, 1959). In *Lygodium japonicum* antheridium formation seems to be controlled by a second substance A_2 (=Antheridogen in *Lygodium*). From these studies it is apparent that antheridium formation is controlled by different substances in different groups of ferns.

Schraudolf (1962) introduced a new control of antheridial differentiation by Gibbarelic Acid (GA). GA induces antheridium formation in *Anemia phyllitidis, Anemia rotundifolia* and *Lygodium japonicum* in exactly same manner as "Anemia factor". GA_3 has been found to be active in all members of Schizaeaceae (Voller and Weinberg, 1969). Among non-Schizaeaceous species, GA induces antheridia on *Dryopteris filix-mas*. The antheridia formed in response to GA_3 quite normal. Voller (1964) has shown that seven gibberellins GA_1, GA_3, GA_4, GA_5, GA_7, GA_8 and GA_9 are capable of inducing antheridia *Anemia phyllitidis* (Schraudolf, 1967).

Relative information about archegonial initiation in ferns is lacking except that the conditions favourable for growth, favour femaleness and fast growing prothalli are female and later become hermaphrodite. Schizaeaceaeous ferns are especially suitable for studies on sexuality as the native antheridogen is replaceable by giberellin. In polypodiaceous ferns indole auxins are known to inhibit the formation of antheridia (Dopp, 1962), but this was imperative in Schizaeaceae. However, in *Lygodium flexuosum* auxin, 2,4-D hastened three-dimentional growth, inhibited the formation of antheridia and instead archegonia appeared first (Rashid, 1970). These gametophytes rapidly initiated antheridia on transfer to auxin deficient medium. Antheridia formation was also suppressed when auxin and gibberellins were supplied together. Therefore, the prothalli, which are initially archegoniate, are to be looked for either high auxin content or inhibitor of antheridium inducing substances.

The genetic mechanism of regulation of antheridogen activity has been worked out in *Ceratopteris* by (Banks *et al*., 1993, Banks 1994, 1997). The epistatic pathway is interplay of two master regulatory genes that regulate the sexual phenotype of the gametophyte. The transformer gene (TRA), which when active simultaneously promotes femaleness and suppresses maleness. While, the feminization gene (FEM) when active promotes maleness and suppresses femaleness. The factor that determines which of these two master sex-regulatory gene is expressed is determined on the presence or absence of A_{ce} (Ranker & Geiger, 2009; Mukhopadhyay, 2009).

D. GENETIC:

Genotype of homosporous ferns contains the necessary genes for the development of both the haploid gametophyte and diploid sporophyte. It is expected that a considerable portion of the genotype is expressed only in the sporophyte generation. Physiological and genetic evidence supports the hypothesis that many of the genes in the Homosporous fern genotype are expressed primitively in either one or other generation (Mohr and Barh, 1962;

Mohr, 1971; Klekowski, 1972). This compartmentalization of the genotype allows the development of viable gametophytes inspite of recessives, which are lethal when homozygous in sporophyte generation. Various techniques developed by (Klekowski, 1973; Dobzhanski, 1970; Wallace, 1970) for studying phenomenon of genetic load in fern populations. The fundamental question asked in these studies is whether a given sporophyte genotype is heterozygous for deleterious genetic combinations, which when present in the haploid gametophyte or diploid homozygous sporophyte generations, decrease the viability of that generation.

Genetic load studies have two functions-

a. They allow an estimate to be made of the nature and extent of this component of genetic variability in fern populations.

b. They led to accumulations of gametophytes clones bearing interesting mutations.

The former function yields information of an evolutionary nature, specifically the extent to which the various gametophytic and ecological adaptations have resulted in a genetically heterozygous population structure and the later results in interesting mutation for ontogenetic and developmental studies.

Masuyama (1986) revealed that gametophytes of diploid plants of *Phegopteris decursive-pinnata* have a low capability for Intragametophytic selfing. Chiou et al (1998) worked out on the reproductive biology of the genus *Elaphoglossum*. Fixed heterozygocity in *Elaphoglossum palaeaceum* suggests that sporophytes of this species are polyploidy, but at least some outcrossing occurs. High genetic loads determined from a single gametophyte cultures of *Elaphoglossum califolium* and *Elaphoglossum crassifolium* indicate two probabilities of successful Intragametophytic selfing.

Sequence and duration of gametangia formation:

Sequence and duration of gametangia formation in gametophytes of ferns is a significant behavior for reproductive strategies. Klekowski (1969) conceived the classification of the ontogenetic sequence of gametangia on meristic-prothalli. In his classification most of the Homosporous ferns belongs to the category with the initial formation of antheridia followed by a prolonged hermaphroditic phase, which led to the notion that the Homosporous fern life cycle is largely tuned for intragametophytic selfing. Masuyama (1975 a, b) proposed a revised classification of the sequence of gametangia. Masuyama (1975 a, b) concluded that features of gametangial sequence (type, A, B, C of table-1) are species specific and do not vary under experimental conditions, whereas the three patterns of gametangial sequence on meristic prothalli recognized by Masuyama (1975 a, b) characterize most of the ferns and these may be regarded as the basic patterns. Accordingly, Verma (1985, 1989,2003), Verma et al. 1987, 2000; Ganguly and Mukhopadhyay (2005, 2009) added two more new types to Masuyama's classification and visualized finally eight different types. From this classification, intraspecific variation for

gametangial sequence may be explained particularly in all such species committed to versatility in mating and there would always be sufficient deviation within species in the pattern of gametangia production to provide flexibility in reproductive strategies.

Antheridial area and its correlation:

Distribution of antheridia on bisexual gametophytes plays a significant role in breeding system of Homosporous ferns (Nayar and Kaur, 1971; Atkinson and Stokey, 1964). Masuyama (1975 a, b) recognized four basic locations of antheridia on monoecious-prothalli-

1. Antheridia on the lower part of the body (L).
2. Antheridia on the lower half of the wing (LW).
3. Antheridia on the lower half of the margin (LM)
4. Antheridia on the upper half of the central cushion (UC).
5. Antheridia on all along the margin (M).

Masuyama (1975a) observed that a striking correlation between the four types of antheridial area (L, LW, LM, UC) and three types of (A,B,C) of gametangial sequence. The location of antheridial area restricted to the lower part of the gametophyte (L-position) was formed to be associated more often or generally with type-A gametangial sequence, which lack antheridium formation during archegonial phase, essentially ensures Intergametophytic mating. The type B sequence of gametangia, where indefinite and simultaneous formation of antheridia and archegonia, capable of intragametophytic selfing, was associated often with antheridial location as UC and LM. Moreover, the type A occurred more frequently among diploid species, whereas type B sequence commonly in the polyploids (msuyama, 1975 b, 1979). These correlations tend to suggest that the ancestral kind of mating in homosporous ferns as exemplified by the present day diploid is Intergametophytic mating, contrary to the view of habitual gametophytic self-fertilization (Klekowski and Baker, 1966; Klekowski, 1969, 1979).

As concluding remarks, it may stated that, the initial bearing of antheridia on eventual monoecious prothalli together with the location of antheridia in the lower part of the gametophyte (location L)cannot be taken as conditions predisposing such species to Intergametophytic selfing (Klekowski, 1969). Instead, the co-occurrence of the L-type location of antheridia commonly with the type A sequence of gametangia (lack of antheridium formation during the subsequent archegonial phase, i.e. protandry) suggests an adaptation for Intergametophytic mating.

ASEXUAL AND VEGETATIVE REPRODUCTION:

Departures from a normal sexual life cycle of a fern result in the customary cytological and or morphological alteration of generations being interrupted or modified. Such events include apospory, apomixes and vegetative reproduction.

1. APOGAMY:

Apogamy involves the production of sporophyte

from a prothallus without the intervention of oogenesis or fertilization. Like apospory this may occur or be induced sporadically, but is also found as a recurrent event in the obligatory apomictic alteration of generations, which characterizes many ferns.Apogamy was first reported by Farlow (1874) in *Pteris critica*. Apogamy occurs in nature and has also been induced under experimental conditions. It is common and widespread phenomenon in ferns. In some species of ferns apogamy appears to be a necessity and is a regular process. It is perhaps due to the inherited constitution of the plant. Natural apogamy is common in *Dryopteris, Pteris, Adiantum, Asplenium, Athyrium* etc.

Reasons for Apogamy:

Regarding the casuses of apogamy, several explanations have been put forwarded. Lang (1889) induced the formation of sporophytic buds, roots, sporangia and tracheids in the various fern prothalli, by avoiding watering of the prothalli. Brown (1923) summarized regarding the induction of apogamy by avoiding fertilization. The following conditions are thought to favour apogamy:-

1. Culture in bright light and at the higher temperature (Solni, 1900).
2. By lowering the vitality of the prothallus by fungal and algal infection and various unfavourable nutritional environments.
3. Willams (1938) suggested that in addition to the environmental factors there must also be some internal factors, such as the nature of inherent susceptibility due to abnormal nuclear composition and behavior, which bring about apogamy.
4. Ageing of the prothallus has also been regarded as one of the factors influencing apogamous development on the prothalli of some ferns.

Evans (1964) has reported an interesting case of apogamy in a species of *Polypodium*. He reported the formation of 32 mitospores in the sporangia. The sporangia have 16 spore mother cells, which do not undergo meiosis, but instead divide mitotically into 32 spores. This spore is reniform in shape and occurs in diads rather than tetrads. He reported this sequence to occur regularly in all sporangia. The spores germinate readily to form prothalli, which bear numerous apogamous sporophytic buds. The prothalli bear stomata, but produce no sex organs.

2. APOSPORY:

In apospory, gametophytic tissue is produced by the sporophyte without intervention of spores. The prothalli so produced are usually functional, although they may differ somewhat in morphology from those of the same species produced by spores. Apogamy only occurs sporadically in ferns, but it can be induced. Aposporous prothalli customarily bear normal sex organs and since they have the same chromosome number as the parental sporophytic tissue, they provide a means of inducing polyploid series. For example, production of triploid (3n) and tetraploid (4n) *Osmunda* without use of cochicine (Manton, 1950).Induced apospory in a normal sexual species cannot be repeated indefinitely from

generation to generation, because this would involve doubling of chromosome number in each fertilization. The phenomenon of apospory was recorded by Druery (1884) in fern called *Athyriumfilix-fomina* var *clarissima*. Bower (1885) reported apospory in two species of *Trichomanes*.

Reasons for Apospory:

Several factors seem to influence the aposporous development of gametophytes from vegetative tissues of sporophyte.

- Bristow (1962) demonstrated that minimal nutrition is responsible for the formation of prothalli from callus tissue obtained from the sporophytes of *Pteris critica*. When he supplied sucrose to such callus tissue it develops into sporophytes.
- Lawton (1932) and Beyerle (1932) demonstrated that there is a pronounced relation between the stages of development of sporophytic cells and kind of organs regenerated. They observed that in *Ceratopteris thallictroides* aposporous gametophyte development on decapitated young sporophytes with one or two leaves where as in older sporophytes only shoot bud developed.

3. AGAMOSPORY:

In some fern species apogamy may be repeated from generation to generation and from a regular method of reproduction. In such cases, it is accompanied by diplospory, involving certain well-defined cytological events during a modified sporogenesis such that the chromosomal number remains the same in both generations. It forms a major type of recurrent apomixes met within the ferns and described as apogamy by Love and Love (1977). During sporogenesis in sexuality reproducing ferns, the initial archesporial cell in a developing sporangium divides four times by meiosis resulting in 16 spore mother cells. Meiosis occurs, giving rise to 64 spores with half the original chromosome number. In agamosporous ferns modifications of either mitosis or meiosis occur, resulting in the production of viable spores, but which have the sporophytic instead of the reduced chromosome number. Dopp (1932, 1939) originally described the course of events in *Dryopteris remota* and the process was further amplified and fully illustrated by Manton (1950). This system is described as Dopp-Manton system. In the Dopp-Manton system, two main types of cytological behavior are shown-

- In one case the archesporial cell divides four times by mitosis to give rise to 16 spore mother cell and then meiosis occurs, just as in sexual species. However, meiosis is irregular and consequently only abortive spores are produced, whilst these events are of no reproductive significance, they are scientifically important in that the true chromosomal homologies are demonstrated and therefore can be used in experimental analyses of agamosporous species.
- In other type of behavior shown, a compensation mechanism occurs, resulting in regular meiosis and the production of viable spores. Here three mitotic divisions have given rise to cells. A further mitotic division starts

normally, the chromosomes move to the equation and divide, but there is no separation towards the poles and restitution nuclei are formed. As there is no cytoplasmic division involved during this mitosis the result is the formation of eight spore mother cells, each with double the original chromosome number, following meiosis. As a result 32 diplospores are produced which have the same chromosome number and genotype as the sporophyte.

Braithwaite (1964) described another type of agamospory in *Asplenium aethiopicum*, here only one type of sporangial development occurs. Here, the archesporial cell undergoes four normal mitotic divisions to produce 16 spore mother cells. At the first meiotic division the chromosomes move towards the equator without pairing. The cytoplasm fails to divide and restitution nuclei are formed with the result that there are still 16 without any alteration in chromosome content. The second meiotic system is normal, giving rise to up to 32 viable diplospores, arranged in diads and having the original sporophytic chromosome number. Evans (1963) independently described a method of agamospory in *Polypodium dispersum* and mentioned that it was an ameiotic process.

4. VIVIPARY:

The function of aphlebiae as vegetative propagules developing young sporophytes viviperously is reported in *Dennstaedtia scabra*. This type of alternative means of reproduction is an ecological adaptation, which is not unlikely in a situation where development of sexuality produced sporophytes, seems difficult in a snowy coverage. Detachment of aphlebiae as propagating organ seems possible, as the vascular tissue of aphlebiae is not continuous with the parent plant (D'Rozario *et al.,* 2005). Vivipary is a common phenomenon observed in mangrove plants such as *Rhizophora* and is considered as an ecological adaptation to halophytic habit. It is also noted in some ferns like *Asplenium*, *Woodwardia*, *Adiantum*, *Camptosorus, Cystopteris, Diplazium, Tectaria* and specially in plants growth on rocks in the sheltered areas in moist forests to overcome the unfavourable environmental condition. In these species, frond architecture is typically such that gemmae are brought easily into contact with the substrate, either during the life of the parent frond or by its eventual decay.

D'Rozario *et al* (2001) suggested that aphlebiae could function as vegetative propagules.Some *Dennstaedtiascabra* plants were found to bear aphlebiae on their leaves during winter. The most interesting part of this observation is that the development of some young sporophytes from the surrounding surface of these aphlebiae. Aphlebiae have been reported earlier from fossil coenopterids *Stauropteris* and in some Cyatheoid ferns.

5. VEGETATIVE:

In addition to the sexual gametophyte-sporophyte life cycle, some pteridophytes have developed various vegetative means of propagation to increase the extent and the number of their population. This is advantageous where seasons are favourable, or the environment is otherwise not conductive to gametophyte production and in some cases it

may just be advantageous to generate numerous genetically identical individuals.A number of quite unrelated species produce vegetative buds or bulbils that are capable of producing roots and new plants. The bulbils are leaves derived structures and are produced in leaf axis or at various places on the leaf surface. Plants may chain along as successive bulbils produce roots, establish themselves and produce fronds and bulbils of their own. Proliferating bulbils can be found in *Asplenium*, *Camptosorus*, *Diplazium*, *Polystichum*, *Ampelopteris*, *Huperzia* etc. proliferation is possible from root stolons, tubers and similar structures. This occurs in some species of *Nephrolepis* and *Blechnum*. More of the survival strategies than a means of propagation, some ferns of arid areas are able to dry out almost completely without actually dying. Crisp and brittle to touch, they resuscitate rapidly when rain comes and continue their growth. A number of species of *Cheilanthes* behave in this way.

Special reproductive strategies in some epiphytic Polypodiaceae:

Genetic load estimates from sporophyte production by isolated gametophyte cultures indicate mating systems of intragametophytic selfing in *Campyloneurus angustifolium*, *C. phyllitidis*. Polyploidy characterizes the intragametophytic selfing species; whereas the intragametophytic mating taxa are diploid. The duplicate loci of polyploidy taxa may mitigate the expression of recessive lethal alleles caused by intragametophytic selfing; whereas genetic load probably maintains the mating system of intergametophytically mating taxa. Enzyme electrophoresis patterns of fixed heterozygosity suggest allopolyploids origin of *C. phyllitidis* and *Polypodium leuceanum* and confirm their intragametophytic mating systems. Antheridogen present in both groups may promote Intergametophytic mating in diploids through promotion of the early development of the male plants in gametophyte populations and bisexuality in isolated gametophytes of polyploids of the gametophytes delay or do not attain insensitivity to their own antheridogen. In the poliploids, antheridogen may also alleviate low genetic variability through promotion of occasional outcrossing. The perennial clone forming habit of epiphytic Polypodiaceae increases the duration and the physical space occupied by derivatives of a single spore, thus expanding, the chances of interaction with a later migrant. Genetic load, duplicated genes and antheridogen together with a perennial and clone forming gametophytes growth habits interact to produce successful breeding strategies of the epiphytic species.

Several fern species are known to exist over parts of their ranges as gametophytes only, without development of the sporophyte stages of their life cycle. Gametophytes of *Hymenophyllum wrightii* have been collected from several places along the pacific coast. Farrar (1967) has demonstrated the occurrence of populations of *Trichomanes* gametophytes in England over 800 km from any known sporophytes of the genus.In this case the gametophytes have the characteristic capacity to produce gemmae by which they maintain

local populations vegetative and independently of the sporophyte generation. Species of *Vittaria* also have gemmae producing gametophytes. In peninsular Florida *Vittaria lineata* produce both sporophytic and gametophytic stages. Here gametophytes produce the gemmae characteristic of the genus but also produce sporophytes in normal sexual life cycle (Farrar, 1974). In Appalachian Mountain plataue region of the eastern US, a third species of *Vittaria* is represented by the gametophytes only. This species is known as *Vittaria appalachiana* (Farrar and Mickel, 1991).

CONCLUSION

The gametophyte generation of Homosporous ferns is the most delicate part of the life cycle and the sporophyte generation would be at the mercy of their gametophytes to the extent that latter expresses any portion of the genome they convey (Mukhopadhyay, 2013; Ganguly, 2013).

Homosporous ferns produce sporophytes intragametophytic selfing, Intergametophytic mating or apogamy, gametangium ontogeny, genetic load and polyploidy affects the mating system of each species. Gametangium ontogeny causes different sexual expressions and may permit or prohibit intragametophytic selfing. Only in the situation, which the male and female gametangia on the same gametophyte mature at the same time and release sperms, is intragametophytic selfing likely to occur. Genetic load is a measure of the effect of deleterious genes on fitness. The lower the genetic load, the higher the probability of intragametophytic selfing. As the genetic load increases, so does the frequency of Intergametophytic mating. Intragametophytic selfing is a characteristic feature of polyploidy species, whereas most diploid species reproduce by Intergametophytic mating. Antheridogen promotes antheridium and male gametophyte formation. Thus Intergametophytic mating is more frequent and more successful in those species with high antheridogen production. In addition to sexual reproduction some ferns produce sporophytes by apogamy. Each reproductive strategy is favourable for creating a new population (intragametophytic selfing, apogamy), increasing genetic diversity (Intergametophytic mating) or produce offspring's in drier habitats (apogamy).

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