INTRODUCTION

Ever since Lesjczyc-Suminski (1848) worked out the fern life cycle, there has been several searching efforts to offer causal explanations for the alternation of generations in ferns, beginning with Hofmeister (1851), Lang (1909) and Blackman (1909) to the modern period of experimentation (see De Maggio 1961, 1963; Mehra 1972; Bell 1979). The major breakthrough in the understanding of ferns, after the trilogy of Bower (1923-28), was the stimulating contribution by Manton (1950) on the "Problems of cytology and evolution in the pteridophyta" that revolutionized the entire concept of fern systematics and evolution (Lovis 1977). The enormous data accumulated on the chromosome numbers in the pteridophytes (Löve et al. 1977) reveal a very striking feature, first pointed out by Klekowski and Baker (1966). The homosporous pteridophytes as opposed to heterosporous ones are characterized by high gametic chromosome numbers based on high basic numbers (mean X = 37.5), and that 40-60% of the cytologically investigated species of homosporous ferns are polyploid on the present day high base numbers (Klekowski 1972b, 1979; Löve et al. 1977; Walker 1979, 1984). The mean basic chromosome number for the heterosporous members, as calculated (Klekowski 1972b) comes to 12.7 and 12% heterosporous taxa are polyploid. A search into the probable evolutionary significance of high polyploidy in the homosporous pteridophytes was made first by Klekowski and Baker (1966),
who suspected an intimate correlation with the sexual strategies of homosporous taxa.

Homosporous ferns constitute the bulk of extant pteridophytes, and their sexual life cycle has at least two distinctive features. Firstly, there is a cyclical alternation of two independent generations, the short-lived haploid gametophyte and the usually perennial diploid sporophyte. Secondly, the gametophyte generation is considered to be commonly monoecious, and most often hermaphroditic (Atkinson and Stokey 1964; Momose 1967; Nayar and Kaur 1971; Mehra and Gupta 1986). Barring self-incompatibility (Wilkie 1956), the simultaneous occurrence of antheridia and archegonia on the same prothallus raises the possibility of intragametophytic selfing, which would yield completely homozygous sporophytes. The homosporous ferns display, therefore, an unparalleled situation in the archegoniatae, which is also without a parallel in the angiosperms (Klekowski 1972b). Thus, if intragametophytic selfing would be the habitual or the predominant mating system in homosporous ferns, owing to the presumed hermaphroditism of their monoecious prothalli, the basic advantages of sexual reproduction may appear to be negated (Lewis and John 1963).

Klekowski and Baker (1966) were the first to emphasize that fern populations were characterized by greater homozygosity. They correlated the suspected high frequency of haploid selfing in homosporous ferns with their high chromosome numbers and
higher frequency of polyploids. They postulated that polyploidy with its manifestation of unlinked duplicated loci provided the means to maintain inter-locus heterozygosity, and release of such variability could occur via occasional homoeologous chromosome pairing and recombination. The hypothesis as elaborated later by Klekowski (1972a,b, 1973a,b, 1979) envisaged all homosporous ferns to be essentially polyploid in origin and their meiotic system was so modified as to allow the chromosomes to pair within homoeologous sets while restricting pairing to form only bivalents. There is some evidence in support of the hypothesis (Hickok and Klekowski 1973; Klekowski and Hickok 1974; Klekowski 1976a, 1979; Hickok 1978a,b; Verma 1978a) despite the criticism against its evolutionary significance (Lovis 1977; Walker 1979).

It may be pointed out that Klekowski's stimulating hypothesis is based on two main assumptions, namely i) fern gametophytes are usually hermaphrodite, and ii) intragametophytic selfing occurs commonly. Both of these assumptions are debated, and in recent years there has been an upsurge in this field of study. It may be said that almost all of the studies devoted to the gametophyte generation of ferns have been concerned primarily with general morphology and ontogeny, and their contribution in systematics and the related problems of evolution (Atkinson and Stokey 1964; Nayar and Kaur 1971; Momose 1967; Nayar 1971, 1981; Mehra and Gupta 1986). The
contributions on the gametophyte generations of ferns referred to in these works are deficient in information relevant to reproductive biology. Fresh investigations are desired therefore toward understanding the sexuality of gametophytes and their influence on the mating system.

The current interest in the gametophyte generation of ferns is particularly directed toward their sexuality both in laboratory cultures and in the nature. During the last 15 years, or so, a number of researches have been carried out on the reproductive biology of a number of homosporous ferns which reveal a complex situation (Klekowski and Lloyd 1968; Klekowski 1969a,b, 1972a,b, 1973a,b, 1976a,b 1979, 1984; Verma 1969; Ganders 1972; Hickok and Klekowski 1973; Lloyd 1974a,b; Klekowski and Hickok 1974; Saus and Lloyd 1976; Lovis 1977; Cousens 1979; Nester and Schedlbauer 1981; Haufler and Soltis 1984). It is being increasingly realized that not all of the homosporous ferns can undergo intragametophytic selfing habitually. Rather, there are several kinds of adaptations or strategies that tend to favour or disproportionately increase the probability of intergametophytic mating. In the very first case of Onoclea sensibilis, Klekowski and Lloyd (1968) argued in favour of low probability of intragametophytic selfing, and some genetic load was documented in the sample implying heterozygous nature of the source sporophyte. This was supported
later by Sans and Lloyd (1976). Studies on the reproductive biology of several members of family Blechnaceae by Klekowski (1969b) showed that most of the species possessed a female to hermaphrodite gametangial sequence and longer duration of the prior pure archegonial phase favoured intergametophytic mating. The contributions made by Klekowski and his collaborators (cited in Klekowski 1979; Lloyd 1974a, b; Verma 1969; Verma and Kapur 1972; Verma and Bala 1979) have emphasized that fern species are equipped with several different types of adaptations of their gametophyte generation that tend to reduce the chances of intragametophytic selfing.

Studies on the reproductive biology of Indian ferns were initiated by Verma (1969) utilizing the common maiden hair fern Adiantum capillus-veneris, and later similar studies were extended to several other species of ferns from the W. Himalaya (Verma and Dhir 1971, 1972; Verma and Kapur 1972; Verma 1978a, b, 1983, 1984, 1986; Verma and Bala 1979; Verma and Sharma 1980; Verma et al. 1983, 1984, 1986; Sharma 1986) following basically the methodology outlined by Klekowski (1969a, b). These authors documented evidence in favour of adaptations that promote or ensure intergametophytic mating. Other investigators from India, namely Singh (1977), Singh and Roy (1977), Khare (1977), Khare and Roy (1977), Niranjan and Roy (1978), Khare and Kaur (1979), Sinha (1983), examined some fern species for their mating system. But many
of these studies have not reported on the sexuality of prothalli with reference to the sequence, position and duration of gametangia on monoecious prothalli, and on the sexuality and sporophyte-bearing on gametophytes in isolation and in pairs.

The number of species studied so far, particularly from the Himalaya, are few and most of them have been sampled from one or two sporophytes. Obviously, there is a need to undertake studies on the reproductive biology of homosporous ferns from the Himalaya, for an understanding of their predominant mating system. As pointed by Masuyama (1975a,b) the duration of the antheridia production on the monoecious prothalli requires a serious consideration, and this aspect has been carefully analysed in this study, besides incorporating the criteria laid down by Klekowski (1969a). The special circumstance of the bisexuality of fern gametophytes allows, firstly, the testing of their ability to undergo intragametophytic selfing, when isolated. And secondly, whether the ensuing homozygote reveals or not the presence of recessive sporophytic lethals/subvitals. The observation and estimation of such genetic load in spore samples, together with features of sexuality, are important in determining the predominant mating system of a fern species.

Presently, reproductive biology of 24 species of homosporous ferns from the Himalaya have been studied from
laboratory grown gametophytes. The predominant mating system has been assessed from ontogenetic sexual structure of gametophyte populations, the position, sequence and duration of gametangia on monoecious prothalli, and sporophyte bearing in the population, isolates and pairs. Since the cultural conditions are known to affect gametophyte development, form and sexuality (Miller 1968), the data on each species are obtained under similar conditions for two or more years, so that the data reveal the relative sexual strategies of the different species. Each of the different spore samples originated from a single sporophyte, and in addition to the cultures raised on nutrient solution, gametophytes were raised on earthenware pieces to simulate, as far as possible, the natural conditions. Besides, investigating these ferns for their predominant mating system, the aim of the present study is to discover any correlation of the predominant mating system with polyploidy, and also with the colonizing or non-colonizing habit.