CHAPTER II

REVIEW OF LITERATURE
I. PODOPHYLLACEAE:

The family is represented by about 12 genera which are mainly restricted to the temperate regions of the northern hemisphere. The taxa constituting the family have remained neglected in respect of a close scrutiny of the various aspects of their reproductive biology. No detailed information is available on their flowering phenologies, breeding systems, pollination mechanisms and resource allocation patterns. The information that has become available over the years regarding various aspects of the breeding systems at work in the members of the family is fragmentary and too meagre. The details are described below:
1) *Breeding System:*

Swanson and Sohmer (1976a) conducted some experiments to unravel the nature of the breeding system operative in *Podophyllum peltatum*. They observed that the species exhibits some degree of protandry and it does not set any seed through selfing or apomixis. The crosses performed between the plants of different populations resulted in more successful sexual reproduction compared to those of intrapopulational crosses. Most of the pollen produced was highly fertile and only up to 21.5% pollen exhibited sterility.

Continuing their studies on this species, Swanson and Sohmer (1976b) confirmed their earlier belief that *P. peltatum* is self-incompatible. They noticed that the successful transfer of pollen to the receptive stigmas in the species is largely mediated by *Bombus affinis*, and *B. vagans* although some other insects such as *Lasioglossum coriaceum* are also seen visiting the flowers of the species. These workers further report that the stigmas are receptive from the day of anthesis. The receptivity reaches its peak two days after anthesis and declines thereafter.

A year later, Sohn and Policansky (1977) determined the cost of reproduction in *Podophyllum peltatum*. 
They demonstrated that the sexuality can be predicted on the basis of the size of the rhizome internodes. The larger the ultimate internode, the greater is the probability of the future shoots to be sexual. The authors argue that the production of two-leaved flowering shoots require lot of energy resources which can be supplied only by a larger internode. The energy expenditure involved in the formation of a fruit is equal to that which would be required to produce one internode of a rhizome. Thus the sexual shoots which bear fruits as well, chanellize less of their resources towards the development of the rhizome system compared to the shoots which are only vegetative. From these observations the authors consider that in *P. peltatum* the reduction in the size of the rhizome has a consequent effect on the sexuality of the next year's shoots.

Recently, Smith *et al.* (1986) probed into the breeding behaviour of a related taxon, *Jeffersonia diphylla* and found it to be a facultative inbreeder. The selfed and outcrossed flowers produced almost equal number of seeds. The authors observed that the flower production in the species shows a significant positive correlation with the number of leaves borne by a plant. Thus plants with five or lesser leaves rarely produce a flower while those
with eight or more leaves produce well developed flowers. The authors report that some correlation exists between the leaf number and the production of ovules and seeds. However, neither the seed set nor the seed weight exhibit any correlation with the total number of ovules produced by a plant. It was demonstrated that the seed set and the seed weight are affected, if some leaves are removed from the plant after they have started flowering. These studies further revealed that nearly 96% of the total seeds in a population suffer from insect predation.

2. **Pollination System:**

In an attempt to understand the breeding behaviour of *Podophyllum peltatum*, Swanson and Sohmer (1976a) made some cursory observations on the pollination system of this species. The insects responsible for pollen transfer include *Bombus* spp. and *Lasioglossum coriaceum*. The frequency of their visitation is, however, quite low ranging between 0.0 - 0.066.

3. **Resource Allocation:**

Doust and Cavers (1982) studied the patterns of dry matter distribution to the different floral organs of four taxa including *Podophyllum peltatum*. The male:female
ratio is higher for outbreeders and lower for inbreeders. About half of the resources (44 - 66%) exist in the ancillary floral organs. It has been concluded that the outbreeders display higher resource allocation strategies towards the male rather than the female function compared to the self-fertilizing species. The authors opine that the pattern of resource allocation serves as a prelude in an understanding of the nature of the breeding system a species operates.

4. Karyology and Pollen Mother Cell Meiosis:

*Podophyllum* a well known genus of the family Podophyllaceae is represented by 10 species on the globe. These have been little worked out cytologically. Whatever has been done so far is mainly confined to the chromosome count alone (Mottier, 1897; Overton, 1905; Litardiere, 1921; Kaufmann, 1926; Langlet, 1928; Miyaji, 1930; Darlington, 1936; Delay, 1947; Newman, 1959; Fedorov, 1969). These studies reveal that the genus is dibasic having $x = 6$ or 8. All the species are diploid.

Detailed studies on karyology and pollen mother cell meiosis have, however, not been conducted on most of the species. The only exhaustive investigations that have become available so far pertain to *Podophyllum peltatum* (Newman, 1959). The author scrutinized the
chromosome complement of the species. Based on \( x = 6 \),
the complement comprises of 12 chromosomes which are:
metacentric, submetacentric and subtelocentric existing
in the ratio of 2:2:2. Anaphasic segregation is normal.
However, failure of one or two pairs of chromatids to
disjoin and occurrence of chromosome bridges and fragments
are certain rare cytological anomalies. Although a diploid
species, in few pmcs, a ring quadrivalent may be formed
at metaphase I. (** Please see page 40**)

Newman's study was immediately followed by that of
Muhling and Wilson (1961) who described the microsporo-
genesis and mitosis in the same species. They confirmed
the earlier findings that the haploid chromosome complement
of the species consists of 2 metacentric: 2 submetacen-
tric: 2 subtelocentric chromosomes. The authors also
observed satellites in one of the each type of chromosomes.
The total complement length of the species is about 60
microns. In somatic cells, the nucleoli vary from 1 to
3 per cell. These studies revealed the occurrence
of chromosome interlocking and various types of other
chromosomal aberrations in the tapetal cells.

II. RANUNCULACEAE:

Compared to Podophyllaceae, family Ranunculaceae
is a fairly large assemblage of angiosperm taxa based on
40 genera and about 1500 species. Despite such a large size of the family, majority of the members have remained unworked out for their reproductive biology. Only sporadic information is available regarding the breeding systems they follow and pollination mechanisms operative in them. As revealed by perusal of literature whatever little has been done so far in this direction is too scant and fragmentary.

1. Breeding System:

Epling and Lewis (1952) studied the adaptive ranges of several species of Delphinium and reported that all of them are primarily insect pollinated though self compatible. The authors observed that pollen and seed dispersal in these species are restricted. This is why, in nature, the populations are patchy. The reproductive modes are so adapted that the plants are able to adjust to severe climatic fluctuations. Thus, with the onset of unfavourable conditions, Delphiniums immediately undergo dormancy which may be initiated at any stage of plant's growth and is broken only in the following growing season. In some populations, several individuals undergo dormancy during their growing season while others do not. The authors opine that it is by virtue of this differential adaptedness of the genotypes
that the species of *Delphinium* are able to increase their adaptive ranges.

The pollen dispersal and the patterns of outcrossing in *Delphinium nelsonii* were determined by Price and Waser (1979). Plants growing at distances ranging from 1 to 1000m were outcrossed. The average seed set per flower was optimum when pollen came from intermediate distances. The seed set, however, decreased either by increasing or decreasing the outcrossing distance. The 1-10m range was thus found to be the optimal outcrossing distance for the species.

Brink (1980) investigated the modes of reproduction in *Aconitum columbianum* at California and concluded that the species reproduces sexually as well as vegetatively by producing tubers and bulbils. While the tubers are developed underground, the bulbils are produced in the axils of leaves and are mostly concentrated in the middle portion of the shoot. The author demonstrated that the depth of the nectaries changes in different geographically isolated populations and ranges between 3.4 - 9.4 mm. Plants with shallow nectaries are pollinated by short-tongued and long-tongued bees, but those having deep nectaries are adapted to pollination by long-tongued bees only. Nectary depths show a positive
correlation with bulbifery. Thus all the bulbiferous plants have shallow nectaries.

In a subsequent investigation, Brink (1982) studied the morphological variations of several species of *Aconitum* in the United States. These species were classified into two natural groups -- the "Western" and the "Eastern" aconites. The former is a polymorphic complex and displays significant interpopulational variability in the floral morphology and vegetative reproduction. This has been referred to as *Aconitum columbianum* complex. The "Eastern" *Aconitum* designated as *A.uncinatum* complex on the other hand does not exhibit much variation at the interpopulational level. While the former has contiguous parent and daughter tubers, in the latter, the tubers are separated by elongated connectives. The two groups also differ in foliar morphology and taste of their tubers.

A year later, Schmitt (1983) studied the individual flowering phenology and population flowering phenology, flower number, mortality and seed production in *Linanthus androsaceus*. The initiation of flowering registers a strong influence on the number of flowers and seeds produced per plant in the species. Thus plants which start flowering in the middle of the
growing season have a greater possibility of setting seeds than those in which flowering is initiated either early or late in the season.

Lubbers and Christensen (1986) analysed the variability in the ovule- and seed production of Thalictrum thalictroides. The initiation of flowering is closely tied to the number of flowers, ovules and seeds produced by a plant. Early bloomers produce more flowers, ovules and seeds while the seed production is much lesser in plants whose flowers anthesce late in the season. Plants which flower earlier continue to be in bloom for a longer period than those which start flowering either in the middle or late season. It was also observed that the lateral flowers open later than the central ones on the inflorescence and thus have a low seed set. Further, the authors contend that the seed output in the species is resource limited. Thus availability of light has a consequent effect on the seed set. Artificial shading of the plants resulted in the lowering of seed set and also decreased the probability of flowering in the next growing season.

Recently, Rendle and Murray (1988) investigated the breeding systems of 13 species of Ranunculus from
Newzealand. All these are self-compatible. During these studies, the authors have also studied the pollen germination. The data obtained are suggestive of the fact that there is no population effect to enhance the pollen germination in these species.

2. Pollination System:

Løken (1949) investigated in detail the behaviour of bumblebees on *Aconitum septentrionale* in Central Norway (Øyer). *Bombus consobrinus* and *B. hortorum* are the regular and consistent visitors of the species in the spruce zone. Other insects which make infrequent visits to the flowers of the species include: *Bombus distinguendus*, *B. mastrucatus*, *B. lucorum*, *B. agrorum*, *B. pratorum*, *B. balteatus* and *B. hypurorum*. Among these, however, only the first two bumblebees are the effective pollinators of the species. In the birch willow zone, *Bombus mastrucatus* and *B. balteatus* are the regular visitors to the flowers of the species. The author demonstrated that the altitude plays a significant role in shaping the pollination of flowers by specific insects. Before the commencement of flowering in *A. septentrionale*, several species of *Bombus* viz. *B. consobrinus* and *B. hortorum* etc. visit different flowering plants but show preference for *Glechoma hederacea*, *Carragana* sp. and *Aquilegia* sp. The
moment *Aconitum septentrionale* comes to bloom, both these bumblebees restrict their visits to the plant and are only rarely observed on the other plants. Similar observations have been made by the author in the birch willow zone where *B. mastrucatus* forages on *Vaccinium myrtillus* for sometime, thereafter disappearing from the area when the species ends flowering. However, the insect reappears in the area as soon as *Aconitum septentrionale* opens its flowers. The activities of the bumblebees are influenced by weather conditions and different day timings. Rain has little effect in the early summer but the effect is pronounced later on. Most of the bees appear around sunrise and disappear after 19.00 hours.

In the subsequent year, the author (Løken, 1950) reported the results of his similar studies in western Norway. The insects that visit the flowers of *Aconitum septentrionale* in this area include: *Bombus agrorum*, *B. balteatus*, *B. pratorum*, *B. consobrinus*, *B. hortorum*, *B. mastrucatus*, *B. hypcnorum*, *B. lapponicus*, *B. jonellus*, *B. soroeensis* and *B. lucorum*. Among these, *B. agrorum*, *B. balteatus* and *B. pratorum* are the major pollinators. This study revealed that while some bumblebees keep to the same plant species in a trip, others visit different
plants. For example, *B. jonellus* collects pollen from *Aconitum septentrionale* and nectar from *Geranium silvaticum* alternately. *Rubus idaeus* is a potential competitor for pollinators especially *B. pratorum*.

Macior (1966) found that *Aquilegia canadensis* is pollinated by a hummingbird (*Archilochus colubris*) and four species of *Bombus*. *B. affinis* perforates nearly 90% of the spurs for securing nectar while other bees obtain nectar normally through spur mouths. Foraging for pollen remains unaffected by changes in spur dimensions. The author has described and illustrated the behaviour of insects visiting the flowers of *A. canadensis*. Foraging for pollen on *Aquilegia* is uniform. The bees however, exhibit differential foraging behaviour for obtaining nectar, depending on the particular floral form and the position of a flower on the axis. Within a floral form, however, the foraging behaviour does not change.

Nine years later, Macior (1975) studied the pollination ecology of *Delphinium tricorne*. The form, colour and phenology of the flowers in the species are adapted to pollination by bumblebees and hummingbirds. The most abundant bumblebee pollinators include: *Bombus bimaculatus*, *B. nevadensis-auricomus* and *B. vagans*. Other
insects visiting the flowers of *D. tricorne* for pollen or nectar (but are not the pollinators) include bees such as *Anthophora ursina*, *Osmia bucephala*, *Ptilothrix bombiformis* and *Xylocopa virginica*, Lepidopterans like: *Amphion nessus*, *Danaus plexippus*, *Euphydryas clarus*, *Erynnis juvenalis*, *Hemaris thysbe*, *Papilio glaucus*, *P. philenor*, *P. troilus*, *Poanes zabulon*, *Vanessa atalanta*, *V. cardui* and the bee fly *Bombylius major*. The author has also analysed the floral colours of the species using reflectance spectrophotometry and UV photography. The behaviour of the pollinators has been recorded by cinematography and close-range stereophotography.

*Bernhardt* (1976) unravelled the pollination mechanism of *Hepatica acutiloba*. The insects foraging on the species include Coleoptera like: *Asclera ruficollis*; Diptera: *Bombylius major*, *Drosophila affinis*, *Gonia* sp., *Megaselia* sp., *Phormia regina*, *Polenia rudis*, *Syrphus ribesii*; Hymenoptera: *Andrena* spp., *Apis mellifera*, *Colletes thoracicus*, *Dialictus coerulus*, *D. imitatus*, *D. versatus* etc. Of these *Asclera ruficollis* was collected feeding on the carpels. Pollen loads of *Hepatica acutiloba* are mostly sternotribic in all these species. The plant reproduces predominantly through insect mediated xenogamy.
Miller (1978) studied the pollination ecology of two species of the genus Aquilegia namely *A. elegantula* and *A. caerulea*. *A. elegantula* has protogynous, red and yellow odourless flowers which produce nearly 44% of sucrose nectar. *A. caerulea* on the other hand produces mildly fragrant, protandrous, blue and white flowers which secrete about 26% of sucrose nectar. The seed set in response to pollinator exclusion treatments in the former (i.e. *A. elegantula*) is 12% and in the latter (*A. caerulea*) 39%. Allowed to open pollinate, the seed set increases respectively to 65% and 54% in the two species. *A. elegantula* is pollinated by a hummingbird—*Selasphorus platycercus* and some species of *Bombus* notably *B. occidentalis*. *Aquilegia caerulea* on the other hand is pollinated by a hawkmoth (*Hyles lineata*) and several species of *Bombus*; *B. occidentalis* being the most common.

Waddington (1981) focussed on the foraging behaviour of *Bombus americanorum* on *Delphinium virensens*. Nectar availability is reported to be a limiting factor for efficient pollen flow. The author noticed that when *B. americanorum* visits flowers with good amount of nectar, it also picks up more pollen but shifts to shorter distances than when it visits flowers with little nectar. Thus short flights are more effective for pollen
dispersal but the pollen flow is reduced.

The same year, Waser and Price (1981) commented on the various aspects of reproductive biology of *Delphinium nelsonii*. Two types of plants exist in the species, the normal deep blue flowered and the albinos. The frequency of the latter is quite low (0.00042 - 0.00103). These plants produce lesser number of seeds than the normal blue flowered ones notwithstanding the fact that the albinos produce slightly more number of flowers than the normal plants (blue flowered plants: $6.52 \pm 0.27$ flowers/plant; albinos: $6.61 \pm 0.30$ flowers/plant). The seeds produced as a result of hand pollination did not show any significant differences between the two groups of plants. In the normal course, it has been observed that the pollinators usually avoid albinos. In an artificial population also the visits per plant were $13.78 \pm 3.33$ for normal and only $10.53 \pm 2.27$ for plants with albino flowers. In this population, the albinos produced 20% lesser seeds than did the controls (control: $19.7 \pm 11.62$ seeds/flower; albinos: $15.3 \pm 1.23$ seeds/flower). The flowers of albinos and normal plants produce almost similar quantities of nectar. However, it takes slightly longer time for the pollinator to extract nectar from albinos and to fly between successive flowers on albino plants. Due to this discrimination of insects, the albino
Motten (1982) studied the modes of sexual reproduction and pollination in *Hepatica americana*. Sexual reproduction in the species is accomplished through autogamy as well as allogamy. Option for self-pollination is opened in case of the absence or scarcity of insect visitors. Flowers which were emasculated and caged, also produce viable seeds. The frequency of insect visitation varies widely during the blooming period of the species. The species faces a severe setback due to the scarcity of insect visitation at the time of full bloom. This is because, at this time, *Erythronium umbilicatum*, whose flowers are more attractive than the nectarless flowers of *H. americana*, offer stiff competition to the latter for pollinators. The competitive disadvantage in *H. americana* is, however, offset by resorting to autogamy. Nevertheless, allogamy is favoured by blooming earlier and producing protogynous flowers.

Zimmerman (1983) studied the effect of different water regimes on the nectar reward schedule and its consequent influence on the pollinator responses on flowers of *Delphinium nelsonii*. Watering of the plants resulted in more nectar production compared to the
plants which were not watered. The enhancement in nectar production lead to increased pollinator activity in the former. The bumblebees spent more time on nectar-rich flowers and foraged on more flowers in an inflorescence. Due to this efficiency in pollination, the watered plants produced more seeds per fruit. The author concludes that the "female component of the plant fitness is significantly increased by increase in the nectar production". In watered plants, the seed production averaged to 25.5 seeds/flower while the unwatered plants produced only 18.6 seeds per flower.

Gibula and Zimmerman (1984) conducted experiments to study the response of bumblebees (Bombus flavi-frons) to varying interplant distances in a population of Delphinium nelsonii. The visitations were frequent on flowers of small plants than on the flowers of large plants. Also, increase in the interplant distances increased the probability of visitation to a greater number of open flowers on a plant. On grounds of these observations, the authors conclude that a positive correlation exists between the plant to plant distance and distance of the bumblebee flights. The decrease in the interplant density resulted in a decrease in the flight distance of B. flavi-frons but the frequency of visitation was increased.
3. **Karyology and Pollen Mother Cell Meiosis:**

Aconitum is a larger genus comprising nearly 300 species distributed in different parts of the world. Perusal of literature reveals that of the 47 species known for their chromosome count, 23 are diploids having \(2n = 2x = 16\); 2 triploid (\(2n = 3x = 24\)); 16 tetraploid (\(2n = 4x = 32\)) 5 hexaploid having \(2n = 6x = 48\) and 1 octaploid having \(2n = 8x = 64\) (Schafer and La Cour, 1934; Fedorov, 1969; Mehra and Remanandan, 1972; Virjee et al., 1983, 1984). The genus is monobasic having \(x = 8\) and exhibits fairly high degree of polyploidy (Samuelsson, 1913; Langlet, 1927, 1932; Hagerup, 1928, 1941; Afify, 1933; Darlington, 1932; Tischler, 1934; Schafer and La Cour, 1934; Rohweder, 1937; Copeland, 1947; Knaben, 1950; Love and Love, 1948, 1956; Love, 1954; Mehra and Sobti, 1955; Kurita, 1959, 1960; Böcher, 1961; Sorsa, 1962, 1963; Love and Ritchie, 1966; Fedorov, 1969). These studies have mainly remained confined to chromosome count alone. The details of the chromosome complement and pairing behaviour are, however, still wanting for majority of the species. Schafer and La Cour (1934) studied the cytology of several species of the genus representing three sections, namely, Lycocotonum, Anthora and Eu Aconitum. The species belonging to the section Lycocotonum are uniformly diploid while those belonging to Anthora are
only tetraploids. However, section Eu Aconitum contains diploids, triploids, tetraploids, hexaploids and octaploids. From this break up, the authors deduce that in the genus Aconitum, the chromosome number is of classificatory value and enables a clear distinction between the three sections of the genus. On grounds of the preponderence of polyploidy, the authors ascribe speciation in the genus to polyploidy.

Mehra and Remanandan (1972) investigated the cytological details of 23 taxa of Ranunculaceae. These include three species of Aconitum namely A. lycoctonum, A. heterophyllum and A. kashmiricum. These three taxa are based on $x = 8$. Meiosis proceeds normally in all the three and the longer bivalents disjoining later than the smaller ones. In one species, namely A. kashmiricum, however, aberrations such as chain formation, occurrence of variable number of univalents, formation of pseudobivalents between non-homologous chromosomes, non-congression and non-orientation of bivalents, formation of laggards, micronuclei and bridge-fragment associations have been recorded.

Virjee et al. (1983, 1984) have put on record the hitherto unknown chromosome number of Aconitum moschatum and also confirmed the already known chromosome counts of
A. violaceum, A. heterophyllum and A. laeva. All the species are based on \( x = 8 \) and are diploid having \( 2n = 2x = 16 \).

III. ASTERACEAE :

Asteraceae is one of the largest families of the flowering plants and is based on 1,000 genera comprising 23,000 species. Notwithstanding the large size of the family, most of its constituent taxa are still unknown for their flowering phenology, breeding strategies, pollen-ovule ratio, pollination mechanisms, modes of propagation etc. Scrutiny of the literature reveals that only stray attempts have been made to analyse the reproductive biology of the members comprising the family. The few taxa that have been studied till date represent only a meagre proportion of the entire family. A brief summary of this work is given below:

1. Breeding System:

Lloyd (1972 a) studied the sex expression in the genus Cotula and identified five systems. These are: monocliny, gynomonoecy, monoecy, subdioecy and dioecy. More than one system is operative in many species. In
general, however, the extent of protogyny, brightness of flowers, degree of retraction of stigmas and anthers, floret length, head diameter, peduncle length and the number of pollen grains increases from gynomonoecious to monoecious to dioecious or subdioecious populations. The author has prepared a MAS (Measurements Associated with Sex Expression) index to predict the breeding behaviour of various species.

Subsequently, the author (Lloyd, 1972b) scanned populations of 17 monoecious species of the genus for their breeding system. On grounds of these studies he concluded that the different species display wide variation in the ratio of male and female florets. The differences between the different populations of a species are, however, not significant. For example, three widely separated populations of Cotula membranacea exhibit 63, 74 and 75% of the female florets and 2 populations of C. potentillina have 30 and 39% of these florets. In all the species studied, a negative correlation exists between the length of the florets and percentage of female florets. Although most of the species produce seed through outcrossing, there are some that undergo selfing as well. The seed set and subsequent seed germination in such cases is low. The author also noticed that the environmental differences
have little effect on the sex expression of a species.

Gibbs et al. (1975) investigated the breeding systems of several species of the genus *Senecio* and established a positive correlation between the breeding systems and the recombination indices in these species. They report that species such as *S. aetnensis*, *S. joppensis* and *S. squalidus* with low automatic selfing ability have large, showy capitula, high pollen output and low recombination indices. Conversely, species, Viz. *S. viscosus* and *S. vulgaris* with relatively inconspicuous capitula, low pollen output and high recombination indices have a high selfing ability. The differences in the recombination indices are mainly due to the fact that the selfing species are polyploids. The authors argue that, "high chiasma frequency and/or polyploidy may have a pre-adaptive value in facilitating the change from outbreeding to inbreeding in some species".

Stergios (1976) analysed the production and dispersal of achenes, germination of seeds and establishment of seedlings in *Hieracium aurantiacum*. These studies reveal interseasonal differences in the production of achenes. Thus the average number of achenes produced per head in June is more than the average number of achenes
produced per head during September. Evidently, the plants undergo a decline in the reproductive output as the season advances. The author noticed that nearly 82.7 to 94.9% of the achenes fell within 1m of the source patch. These were larger in size. However, the smaller achenes are carried to a distance of even 3m. These achenes show a low germinability and delayed germination. Plants growing towards the periphery of a population produce almost double the number of heads per scape compared to those growing towards the centre. The author demonstrated that the seed germination in the species is related to the time of seed collection. Thus seeds gathered in June, July, August and September show 66%, 28%, 18.5% and 13% germination respectively. Seedlings which appear early in the season have greater probability of survival than those which appear late. Further, the chances of seedling survival are higher within the source patch than outside the patch.

Five years later, Short (1981) worked out the breeding systems of several related taxa of Australian Gnaphaliinae (a subtribe of Asteraceae) such as Actinobole, Angianthus, Blennospora, Chrysocoryne, Chthonocephalus and Pogonolepis. The author observed that the outbreeders are diploids and have narrow
distribution ranges, tetrasporangiate anthers and pentamerous florets. Their inbreeding relatives, on the contrary, exhibit polyploidy, are widely distributed, have bisporangiate anthers and tri- or tetramerous florets. From these data he concluded that while the inbreeders are generally widespread in Australia, their outbreeding congeners are restricted to parts of western Australia and that there is a tendency from outbreeding to inbreeding behaviour in these taxa.

Lawrence (1985) studied the reproductive biology of 28 native and 4 exotic species of Senecio in terms of their breeding systems, longevity, habitat stability, seed size and number, dispersal potential and seedling establishment. Of these, nineteen are self-incompatible and the rest self-compatible. Nearly all of them occur in unstable environments and reproduce sexuality. Some viz., S.pectinatus, S. spathulatus and S. cunninghamii reproduce vegetatively as well. The author observed that the breeding systems in these species are related to their longevity. Thus while most of the self-incompatible species are perennial, the self-compatible ones are annual.

Clampitt (1987) studied the reproductive biology of Aster curtus. Seed germination in this species is
higher if the seed is obtained from insect pollinated plants and lower if the seed belongs to plants from which the insects are excluded. Seeds germinate on exposure to light. However, some seeds may germinate even in the total darkness. Percentage germination is higher if the seeds are stratified. Although the species has a wide ecological amplitude, yet the seedling recruitment is hindered to a great extent due to the competition offered by other species. The author has attributed the extirpation of the natural populations of the species to the loss of habitat due to agricultural and urban expansion and the natural conversion of grasslands to fir forests etc.

2. **Pollen-ovule ratio**:

Short (1981) determined the pollen-ovule ratio (P/O) of 24 species belonging to 13 genera of the sub-tribe Gnaphaliinae (Asteraceae). The autogamous taxa have significantly low pollen-ovule ratio than the allogamous ones. P/O ranges between 40 - 350 in the former and 1500 - 6000 in the latter. There are little interpopulational differences in the P/O unless otherwise associated with distinct morphological changes of the plants.
Likewise, $P/O$ of several species of *Senecio* was determined by Lawrence (1985). In case of self-incompatible species this ratio is in the range of 2252 - 5066. Self-compatible species on the other hand have much lower ratios ranging between 64 to 146 per capitulum. $P/O$ of the species exhibiting various habits such as ephemerals, annuals and perennials ranges from 2315 - 7008 per capitulum.

3. **Pollination System:**

Mogford (1974) examined the behaviour of the pollinators of two floral forms in *Cirsium palustre* - one having white and the other purple flowers. The pollinators discriminate between the two types of plants in a population. More frequent visits are made to the white flowered forms than the purple flowered ones. Since the flower colour polymorphism is found only in regions of low pollinator activity, the author concludes that the polymorphism may be an adaptation to compensate for less pollination activity. Different insects exhibit different responses to the flower colour polymorphism. Even different sexes (i.e., male and female insects) as seen in case of *Bombus lapidarius*, display a differential behaviour. However, *B. agrorum* is uniformly non-discriminative in all the populations of the plant.
These studies further reveal that the female insects are more discriminative than the males.

Pollination ecology of *Pyrrhopappus carolinianus* was studied by Estes and Thorp (1975). The species though cross pollinated is self-compatible as well. Pollination is affected by the female sweet bee (*Hemihalictus lustrans*). The males apparently visit the *Pyrrhopappus* heads only in search of females for mating. The female bee feeds on the pollen of the species before it is made available to the other insects. While collecting pollen, the insect ensures cross pollination of the florets. Breeding experiments indicate that the species can reproduce autogamously in the absence of the pollinating agents. The caged plants produced 85.1% seeds compared to 95.5% produced by the open pollinated ones.

4. Resource Allocation:

Harper and Ogden (1970) described the patterns of energy allocation in *Senecio vulgaris* and discussed the concept of 'strategy' and 'tactics' with reference to this species. The species was grown in pots of various sizes to ensure different stress conditions. Biomass allocation was measured throughout the life cycle of the species. Under high stress conditions the growth was
poor and flowering erratic. Reproductive effort of the species varied between 18 and 24%. The authors remark that these figures are well in agreement with the reproductive efforts of other annual composites.

Later, Abrahamson and Gadgil (1973) determined the reproductive efforts of four species of *Solidago* viz. *S. nemoralis*, *S. speciosa*, *S. rugosa* and *S. canadensis* growing in different communities. The authors report that with increase in the successional maturity of the community, the reproductive effort decreases in these species. Under low light conditions, less of resources are allocated in building the stem tissues and more towards the development of leaves. The authors further report that the flowering of different populations of a species is asynchronous. The asynchrony helps in maintaining the ecotypic differences in these species. These studies also record that the reproductive effort decreases in the order: *S. nemoralis* (dry), *S. speciosa* (dry), *S. canadensis* (wet), *S. speciosa* (hardwood) and *S. rugosa* (hardwood). Clearly, the RE decreases from dry through wet to hardwood communities with the exception of *S. speciosa*. It has also been demonstrated that the species of *Solidago* have a higher stem biomass in the wet meadow site than those growing in the hardwood area.
Species of hardwood communities exhibit a higher proportion of biomass in their leaves.

Ogden (1974) demonstrated the effect of different plant densities on the resource partitioning pattern in Tussilago farfara. Low levels of soil fertility are associated with increased dry matter allocation to the rhizomes in this species. The net resource accumulation is reduced at higher plant densities. Allocation of resources displays a shift towards the sexual component rather than the vegetative component of the plant with increase in the plant density in a population. The frequency of flower clusters, flower bud mortality and mean capitulum size are strongly influenced by different plant densities. Ogden found that the sexual reproductive effort, in the species ranges between 3 - 8%. The vegetative reproductive effort, however, shows significant variations and ranges between 4 and 23%.

Bradbury and Hofstra (1976) analysed the resource partitioning patterns in two populations of Solidago canadensis: one, a recently developed population and the other growing in a community at the late stages of secondary herbaceous succession. Reproductive efforts of the two populations are almost similar. Although the species reproduces exclusively by vegetative means in these populations, yet the proportion of resources
allocated to the production of rhizome is very small. The ratios of the allocation of resources between sexual and asexual reproduction works to 8.1 : 1 and 6.1 : 1 in the two populations. On a comparative basis, the size of the rhizome is more in the newly developed population rather than the established one. The number of shoots per clump and the density of shoots are, however, considerably higher in the established population rather than the invading one.

Bostock and Benton (1979) conducted a comparative analysis of the reproductive strategies of 5 perennial compositae namely: Achillea millefolium, Artemisia vulgaris, Cirsium arvense, Taraxacum officinale and Tussilago farfara. The studies revealed that the allocation of the resources to embryos, seed reproduction and vegetative reproduction in these taxa ranges between 0.3 - 4.3%; 2.3 - 26.1% and 8.9 - 26.0% respectively. Minimum seed reproductive capacity over a period of two years is found in Cirsium and maximum in Tussilago. The vegetative reproductive capacity is least in Taraxacum and maximum in Cirsium. The authors have discussed the effect of different types of habitats on the reproductive strategies of these species.

The same year, Brouillet and Simon (1979) reported
on the resource allocation patterns of two species of *Aster* and their hybrid. These include: *Aster acuminatus*, *A. nemoralis* and *A. X blakei*. Although *A. acuminatus* produces lesser number of leaves (13 per plant) compared to *A. nemoralis* (64 per plant) yet the biomass allocation to leaves is similar in all the three taxa. *A. nemoralis*, however, displays higher allocation towards the stem tissues compared to the other two taxa. The reproductive effort is minimum (4%) in *A. nemoralis*, maximum (14%) in *A. acuminatus* and intermediate between these two in their hybrid.

Subsequently, Pitelka *et al.* (1980) investigated the resource allocation patterns in seven populations of *Aster acuminatus*. The populations differ from each other in plant density and light levels. The authors report that the plant density has no significant effect on the allocation of resources in this herb. Vegetative reproductive effort also does not change under varying plant density and light levels. Sexual reproductive effort (SRE) and the size of the plants, however, vary significantly with different light levels. The authors have observed that the light effects the SRE indirectly by affecting the size of the plants; only large individuals are able to flower. The total reproductive effort (TRE) of the flowering plants is greater than the
Recently, Carpenter and West (1988) studied the reproductive allocation in *Artemesia tridentata* ssp. *vaseyana*. They observed that, different aspects of reproductive allocation are higher in plants grown singly than those grown in clumps. Plants grown in a regular pattern exhibit higher proportion of biomass in the achenes and the ratio of the total reproductive biomass to vegetative biomass is also increased. Reproductive effort increases by watering the plants. These studies also revealed that the allocation to the reproduction increases with increase in the age of the plants.

Simultaneously, Lapointe and Simon (1988) commented on the patterns of biomass allocation in two species of the genus *Aster* namely *A. acuminatus*, *A. nemoralis* and their natural hybrid, *A. X blackei*. *A. acuminatus* has a higher allocation strategy towards foliage and higher RE compared to the other two taxa. On the other hand, *A. nemoralis* has more biomass accumulation in the stem and rhizome.

5. **Karyology and Pollen Mother Cell Meiosis:**

One of the largest genera of the family
Asteraceae, *Saussurea* comprises nearly 400 species distributed all over the world. Cytologically, these are little known and most of the studies made so far are restricted to chromosome count alone.


Recently, Virjee et al. (1983, 1984, 1985) worked out the chromosome numbers of four Himalayan species namely *S. atkinsonii*, *S. candolleana*, *S. lappa* and *S. bracteata*. Of these the chromosome count of *S. bracteata* is recorded for the first time. Based on $x = 13$ or $16$ all these are diploid.

** In his further studies on the same species, the author (Newman, 1966, 1967)* reported numerous meiotic anomalies which include translocation and inversion heterozygosity, incomplete homologous and non-homologous pairing, formation of univalents and asymmetric bivalents, bridge-fragment associations at anaphase I and non-disjunction at anaphase II in a large number of clones. The author concludes that there is a possibility of widespread occurrence of some translocations in the species.

These two reprints were received from the author while the manuscript was in its final stages of preparation.