CHAPTER V

DISCUSSION
I. DISTRIBUTION:

The present study is based on three taxa namely *Podophyllum hexandrum*, *Aconitum heterophyllum* and *Saussurea lappa* representing three phylogenetically different genera belonging to families Podophyllaceae, Ranunculaceae and Asteraceae. Of these three genera, *Podophyllum* is the smallest genus comprising nearly ten species, while *Aconitum* and *Saussurea* are fairly large genera based respectively on 300 and 400 species. A look at their global distribution reveals that *Podophyllum* and *Aconitum* are confined to the temperate regions of northern hemisphere. On the contrary *Saussurea*, which among the genera under reference is by far the largest, exhibits a much wider distribution and grows allover the world.
The taxa presently investigated are, however, unique in that they are restricted only to parts of central Asia and western Himalayas, thus obtaining a critically low world-wide representation (Fig. 123 : Table 68). While *P. hexandrum* is restricted to the Himalayas, Pakistan, Afghanistan and Yunan and Szechwan in south west China; *A. heterophyllum* and *S. lappa* are localized to western Himalayas including Kashmir and Pakistan. Both these species are believed to be endemic to this region (Dhar and Kachroo, 1983).

In Kashmir Himalayas the three species inhabit high altitude montane habitats which may be temperate, sub-alpine and alpine (Table 1 and 68). Placed as they are at an altitude of 2100 - 4000 m above sea level, these sites experience severe climates and are too inaccessible. The species constitute thinly scattered populations in these areas and usually the plants are sporadically distributed even in these small populations. It seems

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Taxon</th>
<th>World Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.</td>
<td><em>Aconitum heterophyllum</em></td>
<td>Endemic to West Himalaya.</td>
</tr>
</tbody>
</table>
Fig. 123: The world distribution of the three taxa under discussion.
that these taxa have a greater endurance to extreme environments but have stringent ecological requirements. At lower altitudes, however, these requirements are not fulfilled which probably accounts for their absence from the low lying lands of the valley. The specific ecological preferences these species have, seem to act as barriers preventing them from further invasion and exploitation of the newer habitats with the result their populational representation in this region is far too limited.

The distribution pattern is not only known as an important factor in speciation, it also provides clues regarding the status of a species whether rare, threatened, vulnerable, endangered, extinct or abundant. Numerous workers viz., Du Mond, 1973; Johnston, 1974; Read, 1976; Copper et al., 1977; Rhoades and Williams, 1977; Coddington and Field, 1978; Siddall et al., 1979; Ward, 1979; Ayensu, 1981 etc. have formulated the assessment criteria for determining the status of angiosperm taxa with reference to the aforementioned categories. These criteria are based among other factors, on the distribution pattern of a taxon at the global level and/or at the level of the restricted areas they inhabit. From this standpoint one could conclude that the distribution patterns followed by the presently investigated taxa in Kashmir Himalayas and the neighbouring regions are quite revealing. As mentioned earlier also, *A. heterophyllum* and *S. lappa* are
believed to be endemic to western Himalayas and as such are confined to a fairly narrow geographical region of the globe. *P. hexandrum* most likely seems to have migrated from the neighbouring regions of central Asia which are believed to represent the primary gene centre and the original source of Kashmir Himalayan flora (Koul and Wafai, 1981). Three fourths of this flora are akin to the flora of Afghanistan and central Asia (Sharma and Kachroo, 1981). Once introduced into this part of the Himalayas the species remained confined to higher reaches due to strict ecological needs.

While on the one hand, these species are restricted in distribution, they are heavily exploited for medicinal purposes on the other. Endemic nature, limited distribution, thin populational representation and indiscriminate commercial usage are some important factors that seem to be contributory to their rarity and insecure future in this part of the Himalayas.

Here it is pertinent to refer to Ward (1979), IUCN (see Synge, 1981) and Jain (1983) who designate the species that exist in the form of small populations localized within a restricted geographical region or habitat or thinly scattered over a more extensive range and potentially at risk as "rare". Those in which most
of the populations are decreasing because of over-exploitation, massive depletion of the habitat or other environmental disturbances and are likely to become endangered in the near future should the causal factors now at work continue to operate are referred as "threatened". Viewed from this standpoint the species under discussion genuinely qualify for both these categories. This is the reason why earlier also many workers namely, Arora and Nayar (1983); Gaur and Semwal (1983) and Siddique et al. (1987) have enlisted these species among the rare and threatened taxa of the western Himalayas.

II. PHENOTYPIC VARIABILITY:

Variations may be developmental, environmentally induced or genetic. Of these, only the latter are of long term evolutionary consequence and provide the raw material not only for the natural selection to operate but also for exploitation in the selection of superior genotypes at the hands of a breeder. It is in this context that the intraspecific variations assume great significance. The taxa presently under discussion were explored from this standpoint for their morphological variability in the natural populations. In Kashmir Himalayas, these taxa inhabit high altitude temperate through alpine zones ranging between 2100 – 4000 m. These sites experience severe micro climates. In response
to the diverse ecological stresses prevailing in these localities, the species have developed a spectacular diversity in their morphological characters and are highly variable in respect of the dimensions of the underground perennating organs, stature of the plants, foliar characters such as the number of leaves per plant, lobing pattern of the leaves and leaf size; floral density, floral spread and fruit dimensions etc. The results reveal a great body of variability in these characters among plants growing in the same population and, therefore, essentially in the same environment. From population to population also there is a noticeable difference in the pattern of variability. The details are discussed separately for the three taxa as under:

**Podophyllum hexandrum** :

The species has been explored for six characters namely the plant height, number and arrangement of leaves, lobing pattern of the leaves, leaf area, floral spread and fruit dimensions. The details are discussed below:

1. **Plant height** :

The height of the aerial shoots varies remarkably from population to population and plant to plant within a population. The tallest individual may be double or even seven times the size of the smallest
one in some populations. Plants comprising Naranag, Sargergloo and Tangmarg populations depict maximum variability in this parameter as indicated by the coefficients of variability computed in Table 69.

Harper (1977) argued that variation in the size of the individuals of one and the same population is quite advantageous for the long term survival of a taxon as it "influences most aspects of an individual's ecology. With a few exceptions large plants endure more environmental stress, survive better, produce more seeds, tolerate greater herbivore damage and are better competitors". In the presently investigated sample, maximum frequency of such plants is encountered in Gratnar I population where at least 50% of the individuals are tall and attain a height ranging between 31 - 40 cm. This population is in a moist shady environment; the soil is humus rich and being a relatively protected one, the plants are allowed an undisturbed growth. Evidently, therefore, an environment such as this seems to be quite congenial for the luxuriant growth of the species in Kashmir Himalayas.

The variability is no less pronounced even at the interpopulational level. Plants of Gratnar I population are distinctly large sized while those growing at Sargergloo are the shortest. The mean values of the plant heights of the two populations therefore, are in
Table 69: Mean values and coefficients of variability of five quantitative characters of *P. hexandrum*.

<table>
<thead>
<tr>
<th></th>
<th>Plant height</th>
<th>Leaf area per plant</th>
<th>Floral spread</th>
<th>Fruit length</th>
<th>Fruit diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gratnar I</td>
<td>* 35.5 ± 1.67</td>
<td>825.6 ± 34.30</td>
<td>3.25 ± 0.14</td>
<td>5.74 ± 0.30</td>
<td>3.59 ± 0.15</td>
</tr>
<tr>
<td></td>
<td>** 19.93</td>
<td>13.13</td>
<td>16.11</td>
<td>18.84</td>
<td>15.06</td>
</tr>
<tr>
<td>Ahrbal</td>
<td>* 32.62 ± 1.79</td>
<td>505.0 ± 48.39</td>
<td>2.77 ± 0.12</td>
<td>4.74 ± 0.24</td>
<td>3.19 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>** 22.62</td>
<td>27.10</td>
<td>14.36</td>
<td>16.01</td>
<td>13.87</td>
</tr>
<tr>
<td>Tangmarg</td>
<td>* 28.53 ± 1.48</td>
<td>748.6 ± 41.14</td>
<td>2.80 ± 0.18</td>
<td>5.26 ± 0.45</td>
<td>3.36 ± 0.24</td>
</tr>
<tr>
<td></td>
<td>** 31.12</td>
<td>17.37</td>
<td>18.18</td>
<td>24.19</td>
<td>20.20</td>
</tr>
<tr>
<td>Naranag</td>
<td>* 26.94 ± 1.66</td>
<td>576.6 ± 80.65</td>
<td>2.93 ± 0.09</td>
<td>5.21 ± 0.26</td>
<td>3.44 ± 0.16</td>
</tr>
<tr>
<td></td>
<td>** 36.45</td>
<td>34.25</td>
<td>11.07</td>
<td>15.78</td>
<td>14.70</td>
</tr>
<tr>
<td>Gulmarg I</td>
<td>* 24.75 ± 1.08</td>
<td>477.7 ± 65.62</td>
<td>2.68 ± 0.10</td>
<td>4.70 ± 0.16</td>
<td>3.12 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>** 19.02</td>
<td>36.34</td>
<td>11.79</td>
<td>11.29</td>
<td>10.63</td>
</tr>
<tr>
<td>Sangergloo</td>
<td>* 23.40 ± 1.53</td>
<td>446.1 ± 42.4</td>
<td>2.63 ± 0.04</td>
<td>4.0 ± 0.32</td>
<td>2.74 ± 0.23</td>
</tr>
<tr>
<td></td>
<td>** 35.81</td>
<td>25.14</td>
<td>5.48</td>
<td>22.62</td>
<td>23.74</td>
</tr>
<tr>
<td>Gulmarg II</td>
<td>* 20.05 ± 0.86</td>
<td>320.2 ± 12.44</td>
<td>2.56 ± 0.09</td>
<td>2.80 ± 0.17</td>
<td>2.2 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>** 16.04</td>
<td>10.27</td>
<td>8.61</td>
<td>12.14</td>
<td>7.27</td>
</tr>
</tbody>
</table>

* ± S.E.; ** C.V.
the ratio of 1.5. These differences in the mean values of plant height among different populations are statistically significant as depicted by Analysis of Variance (Table 70).

Table 70: Analysis of Variance of five quantitative characters of *P. hexandrum*.

<table>
<thead>
<tr>
<th></th>
<th>Plant height</th>
<th>Total leaf area/plant</th>
<th>Floral spread</th>
<th>Fruit length</th>
<th>Fruit diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>F value</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed</td>
<td>13.635</td>
<td>123.231</td>
<td>8.85</td>
<td>76</td>
<td>30</td>
</tr>
<tr>
<td>tabulated</td>
<td>2.46</td>
<td>2.60</td>
<td>2.46</td>
<td>2.46</td>
<td>2.46</td>
</tr>
<tr>
<td>SE diff.</td>
<td>2.066</td>
<td>25.552</td>
<td>0.107</td>
<td>0.15</td>
<td>0.10</td>
</tr>
<tr>
<td>CD (0.05)</td>
<td>4.338</td>
<td>53.660</td>
<td>0.23</td>
<td>0.31</td>
<td>0.22</td>
</tr>
</tbody>
</table>

It may be pointed out here that the aforementioned populations have an altitudinal gradient of more than 600 m being placed respectively at 2350 m and 3000 m. Evidently, the plant height seems to be inversely related to the increase in the altitude in this species. This is understandably so because the high altitude populations experience severe climates which have a drastic effect on the overall growth and development of the plants. Gulmarg II population being exposed to ruthless trampling is, however, an exception. Despite being at a lower altitude than Sangergloo population, the plants of this population are the smallest.
2. **Number and arrangement of leaves in a plant:**

The plant produces 1 - 3 leaves, the two leaved shoots, however, preponderate in all the populations. Single leaved vegetative shoots are readily distinguishable from single leaved flowering shoots by the presence of a distinct knob in the latter which perhaps represents the vestige of a second leaf. Whether a plant bears two or three leaves may be genetically determined.

In the two and three leaved shoots, the two bigger leaves usually appear to be positioned opposite to each other; the floral bud occupies the stem apex where the two petioles originate or is borne on one of the petioles. The same holds true for a related species *P. peltatum* as reported by Porter (1877) and Holm (1899). These workers, however, argue that the two leaves in this species are alternate rather than opposite in origin. The placement of the leaves and the flower on shoots of these species are in general alike (Figs. 124 - 125) which speaks of parallelism in their variation pattern.

3. **Lobing pattern of the leaves:**

Mature leaves in the species are variously lobed. A look at the overall variability in the lobing pattern of the leaves (Figs. 6 - 8) suggests a tendency towards increase in the leaf insertions from low to high altitude.
Figs. 124 - 125: Natural variability in two congeners of *Podophyllum*.
populations in this taxon. Thus plants growing at higher elevations (e.g., Sangergloo population) exhibit maximum foliar dissection. Earlier some workers viz., Taylor (1975) and Sohn and Policansky (1977) noticed this tendency even in *P. peltatum* and they regard it to be an adaptive response to reduce the effect of environmental stresses such as the heat load, wind resistance, rain damage and also the rate of spread of the rust on the species. The present observations lend further support to this contention on grounds of the fact that the plants which exhibit maximum degree of foliar insertions in the present sample are exposed to diverse environmental stringencies such as the increased cosmic fallout believed to be very high at higher altitudes as compared to the lower altitudes (see Shah and Yadav, 1970); high wind velocities and torrential rains etc.

4. **Leaf area**

The species also exhibits considerable leaf to leaf, plant to plant and population to population heterogeneity in the leaf area (Tables 69, 70). The two leaves of an individual may be almost equal sized (\( L_1 = 212 \text{ cm}^2 \), \( L_2 = 200 \text{ cm}^2 \)) and differ by a margin of over 250 \( \text{ cm}^2 \) (\( L_1 = 483 \text{ cm}^2 \), \( L_2 = 219 \text{ cm}^2 \)).

Compared to the two leaved shoots, the variability is much more pronounced in the three leaved ones. This is
attributable to the extremely small sized third leaf which in some individuals is more than five times smaller than the largest leaf $L_1$ ($L_1 = 559 \text{ cm}^2$, $L_2 = 102 \text{ cm}^2$). Both the types of individuals occur freely in all the populations. In general the total leaf area is more in the three leaved shoots compared to the two leaved ones (Table 5).

Individuals of Gratnar I population have the biggest leaves, hence maximum leaf area as compared to those of Sangergloo population which display the minimum leaf area per plant. The results are quite commensurate with those regarding the plant height. The increased leaf area of plants in some populations is possibly a response to competition for light in the light-limited conditions of these populations. As already pointed out the plant grows as a forest undergrowth and is densely shaded not only by the associated shrubs like *Viburnum foetens* etc. but also by the overhead tree canopy which allows only a small proportion of light to reach the leaves of this species. In response to this limitation, the species is urged to increase the photosynthetically active surface so that maximum use of the available solar energy is ensured. Abrahamson and Gadgil (1973) also point out that plants respond to shading by allocating more biomass to leaves in order to intercept maximum available solar energy. This hypothesis receives ample support by
the present observation that plants growing in partially shaded/exposed habitats such as those at Sangergloo have comparatively lesser total leaf area than those inhabiting moist and shady habitats. As shown earlier, reduced total leaf area per plant is also attributable to a high degree of leaf insertions in this population. The plants comprising Gulmarg II population depict minimum leaf area per shoot. Being under heavy biotic interference which tells upon their overall growth, these plants stand an exception.

While some of the populations are alike in their total leaf area on a per plant basis, others exhibit statistically significant differences as indicated by the Analysis of Variance test (Table 70).

5. Floral spread:

The diameter of the flower varies from 2 – 4 cm in these populations. The variability is well pronounced within and between different populations. Plants of Tangmarg and Gratnar I populations exhibit maximum degree of variability (Table 69). Individuals of Gratnar I Population produce the largest, (3.25 ± 0.14 cm) and those of Sangergloo the smallest (2.63 ± 0.04 cm) flowers. The differences between the mean values of the floral spread of various populations are statistically significant (Table 70). This goes hand in hand with the pattern of variability exhibited by the species in the
characters discussed earlier. Obviously, plants with more vigour and larger photosynthetically active surface area possess large flowers.

6. **Fruit dimensions**:

The length and diameter of the fruit are important parameters as they have a great bearing on the seed production of a species. Fruits of the plants from various populations scanned for variability in their size show clearly discernible differences. The length of the fruit varies from 2.4 - 7.8 cm and the diameter from 2.0 - 4.4 cm in these populations. Individuals growing at Tangmarg and Sangergloo exhibit maximum variability in their fruit dimensions (Table 69). Biggest fruits (5.74 x 3.59 cm) are borne by the plants constituting Gratnar I population and the smallest (4.0 x 2.74 cm) by those growing at Sangergloo. The mean length and diameter of the fruits of these populations are in the ratio of 1.43 and 1.31 respectively. A.O.V. test indicates that these differences in the mean values are significant (Table 70). Whether the fruit size in the species is determined by genotype, age of the plant or some other environmental factor(s) is not clear. Sohn and Policansky (1977), however, report that in *P. peltatum*—a close congener of *P. hexandrum*, the allocation of materials to fruit is modulated by the number of fertilized ovules. It follows from this that the more the number of fertilized
ovules (hence the more the efficient fertilization), the more will be the resources channelled into the developing fruit and the larger will be the fruit size. These workers also observed that the material used in fruit and rhizome formation is produced in the current season; previously stored material is not of primary importance. From these comments one can infer that the leaf area may be playing an important role in fruit development of the species. The larger leaves offer large photosynthetic area and produce more assimilates than the smaller ones. This inference draws support from the present observations on *P. hexandrum* which reveal that the individuals comprising Gratnar I population (having distinctly increased leaf area in the sample investigated now) produce larger fruits than those of Sangergloo population which bear much smaller leaves.

It is apparent from the above discussion that the plants of Gratnar I population excel those of the other populations in all the phenotypic characters. On the contrary the plants comprising Sangergloo population are meak and less vigorous. Placed at a higher altitude, the alpine population of Sangergloo experiences severe climates all the year round which do not seem to favour the luxuriant growth of the species. The relatively lower altitudes (temperate - subalpine zone) with moist shady environments and humus rich soils are, however, most congenial for the species to thrive.
Correlation Studies:

In order to understand the variation patterns of the aforementioned characters in relation to each other, coefficients of correlation have been worked out between them and the results are discussed below (Table 71).

Table 71: Coefficients of correlation between the morphological traits of _P. hexandrum_.

<table>
<thead>
<tr>
<th></th>
<th>No. of leaves/plant</th>
<th>Fruit length</th>
<th>Fruit dia.</th>
<th>Total leaf area/plant</th>
<th>Floral spread</th>
<th>No. of seeds/fruit</th>
<th>Seed size</th>
<th>Leaf area of L_1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total leaf area/plant</td>
<td>0.329</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>0.201</td>
<td>0.261</td>
<td></td>
</tr>
<tr>
<td>Plant height</td>
<td>0.521</td>
<td>0.424</td>
<td>0.472</td>
<td>0.801</td>
<td>0.036</td>
<td>0.092</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruit length</td>
<td>0.822</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td></td>
<td>0.621</td>
<td>0.018</td>
<td></td>
</tr>
<tr>
<td>Fruit diameter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.104</td>
<td>0.372</td>
<td>0.094</td>
</tr>
<tr>
<td>Seed size</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.421</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf area of L_2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.820</td>
</tr>
</tbody>
</table>

* Significant at 5% level.

i) Relationship between the leaf area of L_1 and L_2:

Leaf area of the two leaves (L_1 and L_2) of an individual plant bears a positive correlation (r = 0.820). Hence increase or decrease in the dimensions of L_1 are associated with a corresponding change in the dimensions of L_2. The two leaves, therefore, exhibit parallel variation in their surface area.
ii) Relationship between the leaf area of $L_2$ and $L_3$ :

As holds true of $L_1$ and $L_2$, the leaf area of $L_2$ and $L_3$ in the three leaved individuals also bears a positive correlation ($r = 0.801$) and any variation in the size of one is invariably accompanied by a proportionate change in the dimensions of the other.

(iii) Relationship between the number of leaves and total leaf area per plant :

The three leaved shoots have more leaf area per plant compared to the two leaved ones. Thus the total leaf area per plant bears a positive relationship with the number of leaves it produces ($r = 0.329$).

(iv) Relationship between the leaf area and fruit size :

leaf area is significantly correlated with fruit length ($r = 0.428$) and fruit diameter ($r = 0.375$). Hence, plants with increased leaf area usually bear large fruits.

(v) Relationship between the leaf area and flower diameter :

The surface area of the leaves also seems to be positively correlated with the size of the flower. Therefore, plants with large leaves tend to have large flowers ($r = 0.479$).
(vi) **Relationship between the plant height and floral spread:**

The correlation coefficient $r = 0.801$ indicates that plant height is positively correlated with the floral size in this species. Therefore, variation in the vigour and stature of the plants is associated with corresponding changes in the floral size.

(vii) **Relationship between the plant height and fruit dimensions:**

The length and diameter of the fruits bear a significant positive relationship ($r = 0.521$ and 0.424 respectively) with the overall size of the plant. Obviously, therefore, larger plants produce bigger fruits and hence more seeds.

(viii) **Relationship between the length and diameter of the fruit:**

The length of the fruit is positively correlated with its diameter ($r = 0.822$). Thus increase in fruit length is accompanied by a proportionate increase in its width. This is the reason why, the outline of the fruit generally remains the same despite alterations in actual fruit dimensions.

(ix) **Relationship between the fruit size and the number of seeds per fruit:**

The size of the fruit is positively correlated with the number of seeds it produces ($r = 0.621$, 0.372).
Hence the larger fruits, usually bear more seeds.

\[(x) \text{ Relationship between the number of seeds per fruit and seed size:}\]

While on the one hand, the number of seeds a fruit produces is positively correlated with the fruit size, it bears a negative relationship with the seed size \((r = -0.421)\). This explains why in a fruit the large sized seeds are produced in lesser number and smaller ones in large numbers.

\[\text{Aconitum heterophyllum:}\]

Twelve quantitative characters namely the length and girth of the tubers, plant height, number of leaves per plant, length and breadth of the basal most and apical leaves, floral density, height and depth of the hood, and length of the pendant sepal have been analysed in this species. The results are discussed below:

1. **Tuber dimensions:**

   The underground tubers serve as a means of perennation for the species. Usually a plant produces a single tuber annually. The tubers vary in size from 1.6 \(\times\) 1.8 - 4.8 \(\times\) 3.8 cm in the five populations presently investigated. The populations are not uniform in this regard since the length and the girth of the tubers vary from plant to plant within a population. The mean values and coefficients of variability have been presented populationwise in Table 72.
Table 72: Mean values and the coefficients of variability of the quantitative characters of Kashmir Himalayan A. heterophyllum.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Ahrbal</th>
<th>Gratner</th>
<th>Sangerloo</th>
<th>Korabhal</th>
<th>Razahani-pass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuber length</td>
<td>3.61 ± 17.15</td>
<td>3.54 ± 15.15</td>
<td>3.26 ± 14.70</td>
<td>2.85 ± 18.24</td>
<td>2.76 ± 16.31</td>
</tr>
<tr>
<td></td>
<td>0.14</td>
<td>0.12</td>
<td>0.11</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>Tuber girth</td>
<td>3.0 ± 12.90</td>
<td>2.81 ± 14.32</td>
<td>2.7 ± 19.37</td>
<td>2.4 ± 15.0</td>
<td>2.6 ± 17.32</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>0.09</td>
<td>0.12</td>
<td>0.09</td>
<td>0.13</td>
</tr>
<tr>
<td>Plant height</td>
<td>99.14 ± 35.50</td>
<td>100.27 ± 21.95</td>
<td>53.29 ± 26.82</td>
<td>66.72 ± 18.68</td>
<td>22.4 ± 20.08</td>
</tr>
<tr>
<td></td>
<td>4.75 ± 7.59</td>
<td>2.35 ± 2.23</td>
<td>2.17 ± 0.90</td>
<td></td>
<td>8.45 ± 17.15</td>
</tr>
<tr>
<td>No. of leaves/plant</td>
<td>9.58 ± 10.04</td>
<td>9.06 ± 19.15</td>
<td>9.05 ± 18.81</td>
<td>10.47 ± 9.05</td>
<td>8.45 ± 17.15</td>
</tr>
<tr>
<td></td>
<td>0.21</td>
<td>0.37</td>
<td>0.23</td>
<td>0.23</td>
<td>0.29</td>
</tr>
<tr>
<td>Length of the basal leaf</td>
<td>6.9 ± 9.96</td>
<td>7.9 ± 17.78</td>
<td>6.5 ± 22.45</td>
<td>7.6 ± 19.74</td>
<td>6.3 ± 23.01</td>
</tr>
<tr>
<td></td>
<td>0.15 ± 0.30</td>
<td>0.24 ± 0.32</td>
<td>0.32 ± 0.24</td>
<td></td>
<td>0.29 ± 0.29</td>
</tr>
<tr>
<td>Breadth of the basal leaf</td>
<td>6.0 ± 10.69</td>
<td>6.4 ± 21.18</td>
<td>5.2 ± 26.54</td>
<td>6.6 ± 14.88</td>
<td>5.5 ± 35.26</td>
</tr>
<tr>
<td></td>
<td>0.14 ± 0.23</td>
<td>0.23 ± 0.24</td>
<td>0.24 ± 0.24</td>
<td></td>
<td>0.39 ± 0.29</td>
</tr>
<tr>
<td>Length of the apical leaf</td>
<td>4.2 ± 19.63</td>
<td>4.7 ± 20.69</td>
<td>3.8 ± 24.01</td>
<td>4.6 ± 12.49</td>
<td>3.9 ± 21.79</td>
</tr>
<tr>
<td></td>
<td>0.18 ± 0.21</td>
<td>0.23 ± 0.24</td>
<td>0.24 ± 0.24</td>
<td>0.14 ± 0.17</td>
<td>0.17 ± 0.17</td>
</tr>
<tr>
<td>Breadth of the apical leaf</td>
<td>3.2 ± 14.14</td>
<td>2.6 ± 14.21</td>
<td>2.9 ± 12.49</td>
<td>2.7 ± 10.65</td>
<td>2.9 ± 11.98</td>
</tr>
<tr>
<td></td>
<td>0.10 ± 0.08</td>
<td>0.06 ± 0.07</td>
<td>0.07 ± 0.07</td>
<td></td>
<td>0.07 ± 0.07</td>
</tr>
<tr>
<td>No. of flowers/plant</td>
<td>14.2 ± 49.55</td>
<td>12.4 ± 73.00</td>
<td>28.8 ± 59.70</td>
<td>13.12 ± 40.39</td>
<td>10.3 ± 42.85</td>
</tr>
<tr>
<td></td>
<td>1.54 ± 1.93</td>
<td>2.83 ± 2.83</td>
<td>1.06 ± 1.06</td>
<td></td>
<td>0.99 ± 0.99</td>
</tr>
<tr>
<td>Hood height</td>
<td>23.12 ± 16.34</td>
<td>22.82 ± 16.03</td>
<td>25.31 ± 16.12</td>
<td>22.12 ± 14.10</td>
<td>22.87 ± 10.75</td>
</tr>
<tr>
<td></td>
<td>0.63</td>
<td>0.61</td>
<td>0.68</td>
<td>0.52</td>
<td>0.41</td>
</tr>
<tr>
<td>Hood depth</td>
<td>8.57 ± 27.30</td>
<td>8.09 ± 20.76</td>
<td>9.62 ± 21.20</td>
<td>8.18 ± 18.33</td>
<td>9.52 ± 22.68</td>
</tr>
<tr>
<td></td>
<td>0.39</td>
<td>0.28</td>
<td>0.34</td>
<td>0.25</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>0.26</td>
<td>0.23</td>
<td>0.31</td>
<td>0.30</td>
<td>0.22</td>
</tr>
</tbody>
</table>

Note that in majority of the characters the five populations exhibit almost a uniform magnitude of variability.

*: X ± SE; ** : CV.
Plants of the Ahrbal population produce the largest tubers while those of the Razdhanipass population the smallest. The mean values of these differ significantly as shown by A.O.V. test (Table 73).

Table 73: Analysis of Variance of five quantitative characters of *A. heterophyllum*.

<table>
<thead>
<tr>
<th>Character</th>
<th>Ahrbal</th>
<th>Razdhanipass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuber length</td>
<td>32.34</td>
<td>12.03</td>
</tr>
<tr>
<td>Tuber girth</td>
<td>5.54</td>
<td>2.03</td>
</tr>
<tr>
<td>Plant height</td>
<td>41.98</td>
<td>35</td>
</tr>
<tr>
<td>No. of leaves/plant</td>
<td>3.95</td>
<td>0.54</td>
</tr>
<tr>
<td>No. of flowers/plant</td>
<td>12.03</td>
<td>2.75</td>
</tr>
</tbody>
</table>

The Ahrbal and Razdhanipass populations exhibit wide spatial as well as temporal isolation in their growth behaviour and are located at an altitude of 2450 and 3000 m respectively. Expectedly the differences in the altitudinal range which amount to over 500 m are associated with changes in the soil architecture and the microclimate. Put together, these factors affect the overall growth and development of the plants. Tubers of plants at lower altitudes which generally experience relatively favourable climates tend to be larger than those of the plants at higher altitudes.
2. **Plant height**:

The height of the plants is a highly variable character in the species at intra- as well as inter-populational levels as depicted by higher coefficients of variability (Table 72) and ranges between 12 - 190 cm in the present sample. This is a fairly wide range. As holds true of the tuber size, even the stature of the plants is minimum towards higher altitudes and maximum at comparatively lower elevations. The differences exhibited in the mean values of the plant height of these populations are statistically significant (Table 73).

The plant height in the species seems to be inversely related to the increase in the altitude. The reduced plant heights towards higher elevations may be an adaptive response to avoid dessication and injury due to high velocity winds so characteristic of the alpine habitats of the valley. There are indications that the height of the plants in this species is influenced more by the environmental factors than the genotype of the individuals (Shah and Yadav, 1970).

3. **Number of leaves per plant**:

To begin with, the juvenile shoots are supported by mother tubers and subsequently nourished by the short lived basal leaves. The photosynthetic function is then taken over by cauline leaves which range in number from
4 - 10 per plant. The number of leaves per plant depicts greater variability at the intrapopulation rather than at the interpopulational level (Tables 72 & 73).

4. **Foliar dimensions**:

Plant to plant and population to population variations are discernible even in the leaf size. The largest leaves are found in the plants constituting the Gratnar population and the smallest in those growing at Razdhanipass and Sangergloo. This goes hand in hand with the variation pattern exhibited by the plant height. The size of the leaves seems to be greatly affected by the variations in the altitude of the populations. The higher the altitude the lesser is the leaf size and vice versa. Shah and Yadav (1970) also observed a marked increase in the foliar dimensions when plants of this species drawn from a high altitude population (3660 m) were grown at a lower altitude (1677 m).

5. **Floral density**:

Floral density is an index of the reproductive potential of a plant species and, therefore, constitutes an important parameter in selecting plants for efficient reproductive capacity. In the species under reference, the flowers are borne on the main inflorescence and 1 - 8 lateral inflorescences. The species displays maximum variability in flower production both at intra - as well
as interpopulational levels in the natural habitats of Kashmir Himalayas (Table 72). Plants of the lower altitude populations bear maximum number of flowers while those growing at higher elevations bear the minimum number. These observations are quite in tune with the findings of several workers (Billings and Mooney, 1968; Johnson and Cook, 1968; Bliss, 1971; Hickman, 1975) who reported a decrease in the floral density and biomass allocation to sexual tissues in species with increase in altitude. Plants growing at Sangergloo, however, stand an exception. Although located at an altitude of 3000 m the plants when compared with the equally high altitude Razdanipass population, produce much larger number of flowers. High floral density in this population appears to be a result of undisturbed growth of the plants since the population is well protected against various kinds of biotic interference. Otherwise, plants of this population may represent a variant of the species.

6. Floral dimensions:

The height and depth of the hood provide an index of the floral dimensions in the species. These parameters depict little variability within a population as well as between different populations. Therefore, flower dimension is relatively a more conservative trait. It may be noticed here that the flowers of *Aconitum* are zygomorphic and specialised for the peculiar behaviour of insect
vectors, their landing on the flower and obtaining pollen and or nectar from the concealed nectaries. Any altera­tions in the floral morphology of such a flower, could affect the pollinator efficiency; hence are not tolerable in nature. This is the reason why Brink (1980, 1982) found that populations of *Aconitum* have similar floral morpho­logies over large geographical regions in the United States.

**Correlation Studies:**

Correlations were worked out between the various quantitative characters of the species. While some of these show significant relationship, others vary independent of each other (Table 74). Details of only the significant correlations are discussed as under:

1) Relationship between the tuber length and plant height:

The significant positive correlation ($r = 0.621$) between the tuber dimensions and plant height indicates that the large tubers produce large plants and vice-versa. Thus the size of the mother tubers affects the overall growth performance of the future shoots.

ii) Relationship between the diameter and length of the tubers:

The length and the thickness of the tubers are strongly correlated with each other ($r = 0.301$). Therefore,
variation in any dimension is associated with a proportionate change in the other. This explains why the shape of the tuber in the species remains the same despite wide variations in its length and thickness.

Table 74: Coefficients of correlation between various quantitative characters of *A. heterophyllum*.

<table>
<thead>
<tr>
<th></th>
<th>Tuber length</th>
<th>No. of leaves/ plant</th>
<th>No. of flowers/ plant</th>
<th>Length of basal leaf</th>
<th>Length of apical leaf</th>
<th>No. of flowering branches/height</th>
<th>Hood depth</th>
<th>Length of basal leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height</td>
<td>0.621*</td>
<td>0.428*</td>
<td>-0.091</td>
<td>0.328*</td>
<td>0.287*</td>
<td>0.029</td>
<td>0.070</td>
<td>-</td>
</tr>
<tr>
<td>Tuber diameter</td>
<td>0.301*</td>
<td>0.241</td>
<td>-</td>
<td>0.293</td>
<td>0.302</td>
<td>0.281</td>
<td>0.043</td>
<td>0.013</td>
</tr>
<tr>
<td>Breadth of basal leaf</td>
<td>0.271</td>
<td>-</td>
<td>0.001</td>
<td>0.721</td>
<td>-</td>
<td>0.021</td>
<td>0.042</td>
<td>-</td>
</tr>
<tr>
<td>Breadth of apical leaf</td>
<td>0.022</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.528*</td>
<td>0.004</td>
<td>0.012</td>
<td>-</td>
</tr>
<tr>
<td>No. of flowers/ plant</td>
<td>0.072</td>
<td>0.201</td>
<td>-</td>
<td>0.022</td>
<td>0.030</td>
<td>0.824</td>
<td>0.021</td>
<td>-</td>
</tr>
<tr>
<td>No. of leaves/ plant</td>
<td>0.321*</td>
<td>-</td>
<td>-</td>
<td>0.010</td>
<td>0.002</td>
<td>0.004</td>
<td>0.001</td>
<td>-</td>
</tr>
<tr>
<td>Hood depth</td>
<td>0.003</td>
<td>0.021</td>
<td>0.022</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.625</td>
<td>-</td>
</tr>
<tr>
<td>Length of apical leaf</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.521</td>
<td>*</td>
</tr>
</tbody>
</table>

* Significant at 5% level.
iii) Relationship between the tuber diameter and leaf size:

The two parameters bear a positive correlation (Table 74). The healthy and vigorous plants with larger leaves, hence greater leaf area, produce more metabolites to be transported into the tubers which act as metabolic sinks. Thus larger the leaves, more will be the food reserves available for storage in the tubers.

(iv) Relationship between the plant height and leaf size:

The size of the leaves is positively correlated with the plant height (r = 0.328, 0.287). Therefore, the taller plants invariably possess larger leaves.

(v) Relationship between the plant height and the number of leaves per plant:

The plant height and the number of leaves a plant produces, bear a strong positive correlation (r = 0.428). Hence, the taller plants usually bear more leaves.

(vi) Relationship between the size of the tubers and the number of leaves per plant:

The size of the tubers has a great bearing on the number of leaves a plant produces. Therefore, plants producing more leaves always have large tubers (r = 0.321).

(vii) Relationship between the length of the basal and the apical leaves:

Plants with large basal leaves usually
produce larger apical leaves ($r = 0.521$). The two leaves, therefore, exhibit parallel variations in their dimensions.

(viii) Relationship between the length and the breadth of leaves:

The length and breadth of the basal leaves are positively correlated with each other ($r = 0.721$). Thus, any increase or decrease in the length is accompanied by a proportionate change in their breadth. This is the reason why the basal leaves in the species are always broader in outline. These two dimensions, however, exhibit a negative relationship with each other in respect of the apical leaves which are, therefore, somewhat lanceolate.

(ix) Relationship between the number of flowering branches and the number of flowers per plant:

Plants with more lateral inflorescences produce more flowers. This is indicated by a significant positive correlation between the two parameters ($r = 0.824$). Thus, the plants possessing only the main inflorescence produce about $6.87 \pm 0.40$ flowers per plant while those bearing as many as eight laterals produce $56.5 \pm 8.48$ flowers per plant which means a ninefold increase. Hence, increase in the production of lateral inflorescences has a positive effect on the overall reproductive fitness of the species.
(x) Relationship between the height and the depth of the hood:

The height and the depth of the hood determine the shape of the flower. Both these floral dimensions are strongly correlated with each other (r = 0.625). Any alteration in one is, therefore, accompanied by a corresponding change in the other. This explains why the shape of the hood in this species remains unaltered despite variability in its size. This correlation obtains great importance in *A. heterophyllum* whose flowers are highly specialised for insect visitation.

*Saussurea lappa*:

The species has been explored for several quantitative characters viz., plant height, number of leaves per plant, length and breadth of the basal and apical leaves and number of capitula produced per plant in four natural populations namely, Gratnar I, Gratnar II, Sangergloo and Gunasnar. The data reveal that the characters investigated, vary a great deal at intra- and interpopulational levels. The coefficients of variability for each character computed populationwise are presented in Table 75.

1. **Plant height**:

The species depicts a high degree of variability in plant height both at intra- as well as interpopulational levels. Thus the tallest and the smallest individuals differ by a margin of nearly 109 cm. Plants of Gratnar I population
outnumber all others in respect of plant height while those constituting the Sangergloo and Gunasnar populations are short stunted (over 50 cm shorter than those of the former population). The average values of the plant height of these populations show statistically significant differences.

The data obtained, reveal that the plant height registers an increase in the shady environments compared to the habitats which are exposed to direct sunlight (such as Sangergloo and Gunasnar). The increase in the overall stature of the plants towards shady situations seems quite advantageous for the species as it provides access to maximum possible solar energy in these habitats. Numerous angiosperm taxa growing in situations where they have to compete for light are known to adopt such strategies (Abrahamson and Gadgil, 1973).

2. Number of leaves per plant:

The number of leaves per plant shows a definite plant to plant variability in different populations and ranges from 5 - 16. The populations, however, behave almost uniformly in this respect. This explains why the average number of leaves per plant remains almost the same in these populations.

3. Foliar dimensions:

The size of the leaves, however, depicts
Table 75: Mean values and coefficients of variability of various quantitative characters of *S. lappa*.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Gratnar I *</th>
<th>**</th>
<th>Gratnar II *</th>
<th>**</th>
<th>Sangerllo **</th>
<th>**</th>
<th>Gunasnar *</th>
<th>**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height</td>
<td>164.6 ± 10.68</td>
<td>2.44</td>
<td>124.7 ± 10.06</td>
<td>2.01</td>
<td>114.5 ± 10.32</td>
<td>1.87</td>
<td>112.1 ± 11.84</td>
<td>1.98</td>
</tr>
<tr>
<td>No. of leaves/plant</td>
<td>9.3 ± 22.74</td>
<td>9.31</td>
<td>9.0 ± 15.26</td>
<td>0.22</td>
<td>9.2 ± 21.87</td>
<td>0.32</td>
<td>9.6 ± 23.73</td>
<td>0.34</td>
</tr>
<tr>
<td>Length of basal leaf</td>
<td>33.66 ± 12.83</td>
<td>1.08</td>
<td>28.0 ± 10.00</td>
<td>0.70</td>
<td>22.25 ± 22.93</td>
<td>1.67</td>
<td>22.5 ± 30.02</td>
<td>1.29</td>
</tr>
<tr>
<td>Breadth of basal leaf</td>
<td>28.66 ± 23.02</td>
<td>1.65</td>
<td>23.75 ± 22.56</td>
<td>1.34</td>
<td>18.0 ± 19.45</td>
<td>2.12</td>
<td>18.5 ± 47.11</td>
<td>0.9</td>
</tr>
<tr>
<td>Length of apical leaf</td>
<td>17.5 ± 18.74</td>
<td>0.82</td>
<td>17.5 ± 20.57</td>
<td>0.90</td>
<td>15.5 ± 18.35</td>
<td>0.75</td>
<td>15.75 ± 19.35</td>
<td>0.73</td>
</tr>
<tr>
<td>Breadth of apical leaf</td>
<td>13.75 ± 18.61</td>
<td>0.64</td>
<td>12.0 ± 31.00</td>
<td>0.93</td>
<td>12.5 ± 17.60</td>
<td>0.55</td>
<td>12.5 ± 17.60</td>
<td>0.55</td>
</tr>
<tr>
<td>No. of capitula/plant</td>
<td>7.03 ± 23.59</td>
<td>0.23</td>
<td>6.48 ± 28.91</td>
<td>0.30</td>
<td>6.30 ± 26.04</td>
<td>0.28</td>
<td>6.97 ± 18.28</td>
<td>0.19</td>
</tr>
</tbody>
</table>

* *x ± CE; **: CV.
considerable variability; the differences being more obvious at the interpopulational rather than at the intrapopulational level. Thus the largest leaves are observed in plants of Gratnar I and the smallest in those of Sangergloo population. These observations are quite commensurate with those on plant height. A marked increase is registered in foliar dimensions of plants growing in shady situations at comparatively lower altitudes such as those of Gratnar I. On the contrary, plants located in more or less exposed high altitude habitats bear relatively smaller leaves. From these data it becomes apparent that in its natural home, the species thwarts the shade stress not only by increasing the plant height but also by enhancement of the total photosynthetically active surface.

4. Capitula and floret production:

Floral density has a great bearing on the reproductive efficiency of a species. Hence, the greater the floral density of an individual, the higher should be the seed set. In the species under discussion, the individual shoots produce varying numbers of capitula ranging from 3 - 10. However, plants with 5 - 8 capitula preponderate in all the populations. Individuals within a population exhibit different degrees of variability in this respect (Table 75). At interpopulational level, however, all the four populations presently investigated, are alike and the differences in the number of capitula per plant between
these populations are statistically not significant. The total number of florets produced per plant, in the species, depends upon the number of capitula a shoot bears and to some extent the distribution of capitula within a shoot. Thus, the plants with more heads aggregated at the top produce greater number of florets than those with most of the heads scattered all along the shoot.

Plants bearing different numbers of heads grow side by side in one and the same population; hence essentially the same environment. This suggests that the environment may have little or no role in determining the number of heads an individual produces.

Correlation Studies:

Correlations were drawn between the quantitative characters described above. The values are presented in Table 76. The table indicates that while some characters bear weak or no correlation, others are strongly correlated. The former traits vary independent of each other. In the latter, variation in one parameter is proportionately reflected in the other. The details of such correlated character combinations are discussed as under:
Table 76: Coefficients of correlation computed between the quantitative characters of S. lappa.

<table>
<thead>
<tr>
<th></th>
<th>Length of apical leaf</th>
<th>Breadth of basal leaf</th>
<th>Plant height</th>
<th>Length of basal leaf</th>
<th>No. of heads/plant</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of leaves/plant</td>
<td>0.003</td>
<td>0.013</td>
<td>0.068</td>
<td>0.028</td>
<td>0.210</td>
</tr>
<tr>
<td>No. of heads/plant</td>
<td></td>
<td>0.023</td>
<td>0.201</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td>Breadth of basal leaf</td>
<td></td>
<td></td>
<td>0.328*</td>
<td>0.403*</td>
<td>0.031</td>
</tr>
<tr>
<td>Breadth of apical leaf</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.521</td>
<td>0.102</td>
<td>0.117</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of apical leaf</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.133</td>
<td>0.200</td>
<td></td>
</tr>
<tr>
<td>Plant height</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.280</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of florets/plant</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.327</td>
</tr>
<tr>
<td>No. of seeds/plant</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.428</td>
</tr>
</tbody>
</table>

* Significant at 5% level.

i) Relationship between the plant height and leaf size:

The height of the plants seems to be strongly correlated with the size of the leaves (r = 0.328).

Therefore, the taller plants bear distinctly larger leaves. As mentioned earlier also, increase in the plant height and surface area of the leaves are quite advantageous for
the species as they help to offset the effect of shady environment in which the plants find themselves in most of the Himalayan habitats.

(ii) Relationship between the length and breadth of leaves:

The leaves of this species are invariably broader than long. This shape remains constant despite wide variation in the foliar dimensions. This is so because the length and breadth of the leaves bear a significant positive correlation \( r = 0.603 \) and \( 0.529 \).

(iii) Relationship between the number of heads and the number of florets per plant:

There is a proportionate increase in the floret production as the number of capitula per plant increases. The two parameters are significantly correlated \( r = 0.827 \) and exhibit parallel variations.

(iv) Relationship between the number of heads and the number of seeds:

As holds true of the florets, the total number of seeds a plant produces increases with increase in the capitular number per shoot \( r = 0.428 \). However, as already mentioned, the seed production is affected to some extent even by the position of capitula on a shoot.
TRANSPLANT EXPERIMENTS:

As discussed above, the quantitative characters of the three taxa depict considerable variability at intra- and interpopulational levels. In order to assess whether these differences are a phenotypic expression of the prevailing environmental conditions or stem from the genetic make up of the individuals, several plants were drawn from the natural habitats and grown under uniform conditions on the Kashmir University campus. The data obtained are presented in Tables 77-79.

The data indicate that when cultured under strictly uniform environment, the variability pattern in the quantitative characters gets considerably modified with respect to the range as well as the mean. Plants of *P.hexandrum* and *S.lappa* showed a decline in the overall stature including the height and the foliar dimensions when shifted from the shady natural habitat and cultured in a fully exposed situation on the campus (1550 m). The plants of *A.heterocephillum* obtained from high altitude Sangergloo population (3000 m) showed marked increase in their height during the very first year of being transplanted at the lower altitude. Earlier also, Shah and Yadav (1970) observed a similar change when plants of the species were tamed at lower altitude.

The mean values of the quantitative characters of the natural populations and their transplant samples exhibit statistically significant differences (Tables 80 & 81).
Table 77: Average values of the quantitative characters of 5 natural populations of *P. hexandrum* and their transplant samples.

<table>
<thead>
<tr>
<th>Population</th>
<th>Plant height</th>
<th>Total leaf area/plant</th>
<th>Floral spread</th>
<th>Fruit size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>T</td>
<td>N</td>
<td>T</td>
</tr>
<tr>
<td>Gratnar I</td>
<td>i.</td>
<td>25-47</td>
<td>20-35</td>
<td>640-1200</td>
</tr>
<tr>
<td></td>
<td>ii.</td>
<td>35.55</td>
<td>25.5</td>
<td>825.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tangmarg</td>
<td>i.</td>
<td>6-45.2</td>
<td>20.5-30.2</td>
<td>520-1003</td>
</tr>
<tr>
<td></td>
<td>ii.</td>
<td>28.53</td>
<td>21.4</td>
<td>748.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gulmarg I</td>
<td>i.</td>
<td>13-29.8</td>
<td>10.5-30.0</td>
<td>369-723</td>
</tr>
<tr>
<td></td>
<td>ii.</td>
<td>24.7</td>
<td>20.2</td>
<td>477.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gulmarg II</td>
<td>i.</td>
<td>12.4-24.6</td>
<td>15-30.5</td>
<td>338-460</td>
</tr>
<tr>
<td></td>
<td>ii.</td>
<td>20.05</td>
<td>20.6</td>
<td>320.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sanger gloo</td>
<td>i.</td>
<td>10.2-40.5</td>
<td>20.0-28.0</td>
<td>310-687</td>
</tr>
<tr>
<td></td>
<td>ii.</td>
<td>23.4</td>
<td>20.5</td>
<td>446</td>
</tr>
</tbody>
</table>

* N = Natural population   i= Range
T = Transplant sample   ii= Mean.
Table 78: Average values of the morphological traits of the plants of natural populations and the transplants in *A. heterophyllum*.

<table>
<thead>
<tr>
<th>Character</th>
<th>Natural Populations</th>
<th>Transplant sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuber length</td>
<td>3.36</td>
<td>2.84</td>
</tr>
<tr>
<td>Tuber girth</td>
<td>2.7</td>
<td>2.61</td>
</tr>
<tr>
<td>Plant height</td>
<td>53.29</td>
<td>88.2</td>
</tr>
<tr>
<td>No. of leaves/plant</td>
<td>9.05</td>
<td>8.82</td>
</tr>
<tr>
<td>No. of flowers/plant</td>
<td>28.8</td>
<td>24.5</td>
</tr>
</tbody>
</table>

Table 79: Average values of the morphological characters of the plants of *S. lappa* growing in nature and their transplants.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Natural population</th>
<th>Transplant sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height(cm)</td>
<td>164.63</td>
<td>87.2</td>
</tr>
<tr>
<td>No. of leaves/plant</td>
<td>9.83</td>
<td>6.50</td>
</tr>
<tr>
<td>Size of the basal leaf (cm)</td>
<td>33.66</td>
<td>18.75</td>
</tr>
<tr>
<td>Size of the apical leaf (cm)</td>
<td>17.5</td>
<td>18.75</td>
</tr>
<tr>
<td>No. of florets/plant (in 7 headed shoots)</td>
<td>544.0</td>
<td>5728.0</td>
</tr>
</tbody>
</table>
Table 80: t values of the morphological traits of *P. hexandrum* obtained by comparing the mean values of natural populations and their transplant samples.

<table>
<thead>
<tr>
<th>Characters</th>
<th>POPULATIONS</th>
<th>Sanger-loo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gratnar I</td>
<td>Tangmarg I</td>
</tr>
<tr>
<td>Plant height</td>
<td>3.170</td>
<td>3.120</td>
</tr>
<tr>
<td>Leaf area per plant (2 leaved)</td>
<td>2.610</td>
<td>4.080</td>
</tr>
<tr>
<td>Floral spread</td>
<td>0.582</td>
<td></td>
</tr>
<tr>
<td>Fruit length</td>
<td>1.744</td>
<td></td>
</tr>
<tr>
<td>Fruit diameter</td>
<td>2.370</td>
<td></td>
</tr>
</tbody>
</table>

* : Significant at 0.05  
** : Significant at 0.01  

Note: t values in this table have been computed using 7-headed shoots.

Table 81: t values of the morphological characters of *S. lappa*, obtained by comparing the average values of the natural population and the transplant sample.

<table>
<thead>
<tr>
<th>Plant height</th>
<th>No. of leaves</th>
<th>Length of basal leaf</th>
<th>Length of apical leaf</th>
<th>Breadth of basal leaf</th>
<th>Breadth of apical leaf</th>
<th>No. of florets/plant</th>
</tr>
</thead>
<tbody>
<tr>
<td>**</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>**</td>
</tr>
</tbody>
</table>

* : Significant at 0.01  
** : Significant at 0.05  

Note: t values in this table have been computed using 7-headed shoots.
These results are initially suggestive of the variability in the quantitative traits in natural populations being environmental in origin. This proposition is, however, only partly supported by the results of the culture experiments. Thus when cultured under uniform environment, the plants tend to retain their populational differences, though in a modified form. This explains, why the populations presently scanned show statistically significant differences in their mean values even in the transplant conditions (Table 82). Put together, both these observations suggest that the variability in the quantitative characters of the species is partly environmental and partly germinal in origin.

Table 82: t values comparing means of transplant samples of different populations of *P. hexandrum*.

<table>
<thead>
<tr>
<th>Plant height</th>
<th>Leaf area</th>
<th>Floral spread</th>
</tr>
</thead>
<tbody>
<tr>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Tangmarg</td>
<td>3.366</td>
<td>3.038</td>
</tr>
<tr>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Gulmarg I</td>
<td>3.841</td>
<td>10.522</td>
</tr>
<tr>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Gulmarg II</td>
<td>3.358</td>
<td>10.391</td>
</tr>
<tr>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Sangergloo</td>
<td>4.205</td>
<td>9.078</td>
</tr>
</tbody>
</table>

* : Significant at 0.05
** : Significant at 0.01.
At intrapopulational level also, the situation seems to be quite interesting. Inspite of the apparent similarity of the environmental factors to which a population is normally exposed, remarkable variability exists in its components. When grown under uniform environment the variability is retained but the range narrows down (Table 77). The mean values for various characters modify, and show statistically significant differences when compared with the mean values of their counterparts growing in the natural populations. These results suggest that plant to plant variations with respect to quantitative characters existing within a population exposed to apparently similar extrinsic conditions may be both environmental as well as genetic. It, however, needs to be borne in mind that the environmental variability within a population (hence essentially the same environment) appears to be rather strange. But it is not improbable because in no natural population are two plants subjected to strictly similar environment.

III. FLOWERING PHENOLOGY :

Of the numerous factors involved in the sexual selection of plants, phenology assumes a great significance. The phenological episode of a species would constitute all the events from seed germination to the death of the individual. However, the process of flowering is of nuclear importance because on it depends the reproductive
success of a species. The initiation and duration of bloom together with the number and arrangement of flowers affect the pollinator visitation patterns. Such patterns have a direct bearing on the success of the sexual process of a plant.

Many workers viz., Massey and Whitson (1977) and Henifin et al. (1981 a, b ) have laid particular emphasis on the need to study the phenological episodes of the rare and threatened taxa. These studies form the basis in the assessment criteria of such taxa and prove useful in planning out the conservation strategies as well as formulating measures for cultivating them on a large scale. In respect of presently investigated taxa these studies obtain a great significance because they are known to be rare and threatened in the Himalayas (Arora and Nayar, 1983; Gaur and Semwal, 1983; Siddique et al. 1987). The data obtained are discussed below:

Podophyllum hexandrum:

The species depicts considerable variability in its flowering phenology. The sprouting of the plants initiates during early spring at lower altitudes and nearly 6 - 8 weeks later at higher altitudes. Anthesis is fairly asynchronous from plant to plant and population to population and proceeds from March through May. This asynchrony prevails in the subsequent developmental stages.
Thus, in the populations whose components anthese first, the petal shedding, fruit development and senescence also begin early and those in which anthesis commences late, the subsequent phases are also postponed. Plants growing at comparatively lower altitudes show signs of senescence much earlier than those at higher altitudes. Occasionally, some plants may resprout during August – September. Secondary sprouting has also been noticed in this species by Krishnamurthy et al. (1965).

*Aconitum heterophyllum*:

As holds true of *P. hexandrum*, the species displays remarkable interpopulational differences in various phenological events. The plants begin to sprout in March. The individuals inhabiting relatively low altitudes (2450 – 2550 m) tend to make their appearance 30 – 40 days earlier than those located towards higher reaches (3000 m). Vegetative growth continues for nearly two months whence the individuals switch over to the sexual phase. This shift from vegetative to the sexual phase does not occur simultaneously but is staggered over different time periods in these populations.

Neither the individuals within a population nor all the flowers of an individual bloom simultaneously. Flower opening starts in late June and proceeds upto
ending August in different populations. Within a plant, the floral bud opens acropetally in a regular sequence. This phenomenon is characteristic of many other angiosperm taxa and has a great bearing on the nature of the breeding system a species operates. Faegri and Vander Pijl (1971), Proctor and Yeo (1972) and Wyatt (1982) opine that while on the one hand it helps to limit the number of self-pollinations within an inflorescence, it enhances the outcrossing rates on the other.

**Saussurea lappa**:

Plants of the species make their appearance above the ground surface during April and the process of sprouting is staggered over a period of nearly 21 days. Following an eight week's active vegetative period, the plants switch over to the sexual phase and produce floral buds. As holds true of *A. heterophyllum*, the opening of the florets depicts a high degree of asynchrony from floret to floret in a capitulum, capitulum to capitulum
in a plant and plant to plant in a population. This asynchrony provides a means to extend the duration of flowering in these species. The resultant decrease in the temporal overlap of flowering within and between individuals of a population enhances the pollination efficiency (Wyatt, 1982), thereby increasing the probability of high fruit set. Some degree of overlapping, however, exists at each level. In a capitulum the anthesis starts from periphery and proceeds centripetally while as within a shoot, the anthesis initiates from the apical capitula and proceeds basipetally. It takes about 4 - 8 days for all the florets of a capitulum and about 13 - 22 days for all the capitula of a plant to anthesis. The asynchronous anthesis as opined by Wyatt (1982) is quite advantageous for a species as it boosts its outcrossing rates.

Predation:

Not all the plants which produce sexual buds are able to develop seeds. Several capitula are heavily predated by certain insect larvae. The field observations suggest that the humid environment favours the larval infestation. In drier habitats, however, the incidence of larval predation is fairly low.

The insect larvae feed on the young developing ovules, thereby rendering such florets seedless. Occasionally, the larvae bore a hole at the top of the seed. It
is quite probable that in such cases the larvae after partially consuming the ovules, bore an exit hole and leave to pupate. Earlier also, Estes and Thorp (1975) reported that capitula of *Pyrrhopappus carolinianus* - a confamilial of *S. lappa* are utilised by noctuid moths (*Schinia mitis*) as mating and oviposition sites, thereby destroying these heads to varying degrees. That the larvae actually feed on the developing seeds has aptly been demonstrated in several plant species, viz. *Polemonium foliosissimum* and *Ipomopsis aggregata* by Zimmerman (1980, 1982b) and Zimmerman et al. (1984). Insects belonging to the genus *Hylemya* are believed to oviposit on the latter species.

From time to time numerous workers (Clausen and Hiesey, 1958; Mc Millan and Pagel, 1958; Paterniani, 1969; Jones, 1971; Abott, 1976; Murfet, 1977; Mc Intyre and Best, 1978; Primack, 1980; Gross and Werner, 1983; Schmitt, 1983; Zimmerman and Gross, 1984) have demonstrated that the flowering time in angiosperms is genetically controlled. *P. hexandrum* is exclusively a spring flowering herb while *A.heterophyllum* and *S. lappa* are summer-flowering species. In Kashmir Himalayas too, where these species grow in ecologically diverse habitats ranging in altitude from 2100 - 4000 m, this specific flowering behaviour is retained over the entire geographical range which clearly suggests that the flowering time even in these species is under genetic control. These taxa,
however, exhibit temporal differences between various populations in the initiation and duration of different phenophases. These differences seem to be largely ecological in nature rather than genetic.

That the environment registers some influence on the commencement of various phenophases in these species is amply demonstrated by the transplant experiments in which plants drawn from different natural populations (located at varying altitudes) were grown under uniform environment at an altitude of 1550 m. Notwithstanding their source, the transplants from all the populations passed through various phenophases almost simultaneously quite unlike their natural counterparts which suggests that the physical environment definitely affects the flowering phenologies of these taxa. Earlier, Jackson (1966) and Shah and Yadav (1970) also collected evidences indicating the crucial role the environment can play in this regard.

IV. BREEDING SYSTEM:

Of the numerous factors responsible for speciation, breeding system is one upon which depends not only the reshuffling of the genetic material through recombination but also the reproductive potential of a species. The breeding system of an individual would constitute the
mechanism of gamete differentiation, pollen transfer, fertilization and the modes of propagation. The nature of the breeding system is largely determined by the temporal and spatial distribution of the sex organs. While homogamous condition favours inbreeding, devices such as dichogamy, hercogamy, self-incompatibility and male sterility favour outbreeding.

The three taxa presently investigated are hermaphrodite. The following aspects have been analysed in these taxa:

(i) Pollen emission and stigma receptivity;
(ii) Pollen ovule ratio;
(iii) Pollination system;
(iv) Breeding behaviour;
(v) Modes of propagation.

**Podophyllum hexandrum**

**Pollen emission and stigma receptivity:**

The anthers of a flower dehisce continually from the day of anthesis or two days latter. The dehiscence initiates on different dates in various populations. This temporal difference in the pollen emission at inter-populational level most probably stems from the differences in the temperatures that prevail at different sites.
during flowering of the species. At comparatively lower altitudes, the temperature rises relatively earlier in the season while towards higher reaches it happens so by late April or early May. Thus, while anther dehiscence initiates much earlier in low altitude populations, the process is postponed by over two months at high altitudes.

The receptivity of the stigma coincides with pollen emission and increases up to 48 hrs. after anthesis. The simultaneous availability of mature pollen and receptive stigma in one and the same flower provide ample opportunities for self-pollination in the species.

(ii) Pollen - ovule ratio:

The pollen-ovule ratio is believed to be an integral part of a plant's breeding system (Cruden, 1977). This ratio has been found to increase from autogamous to allogamous taxa (Cruden, 1976, 1977; Schoen, 1977; Miller, 1978; Cruden and Jensen, 1979; Spira, 1980; Short, 1981; Wyatt, 1984; Preston, 1986) and therefore, provides an index of the nature of the breeding system operative in a species. Some species, however, display lack of such a correlation (Kawano and Masuda, 1980; Lord, 1980; Arnold, 1982; Pellmyr, 1985). Depending upon several factors viz. the type of pollen vector (Hammer, 1978; Tomlinson et al. 1979), the mechanism of pollination (Cruden, 1977; Cruden and Jensen, 1979;
Schlising et al. 1980; Koptur, 1984), the developmental changes within a species (Lord, 1980) and the modes of asexual reproduction (Short, 1981), the pollen-ovule ratio in such species deviates from that expected of their breeding systems.

Despite these occasional exceptions it seems doubtless that pollen-ovule ratio does reflect a plant's breeding option (Cruden, 1977; Short, 1981; Preston, 1986). The general trend is that there is a decrease in the pollen-ovule ratio from xenogamy to autogamy as has been aptly demonstrated in several genera including Leavenworthia (Lloyd, 1965); Eupatorium and Senecio (Cruden, 1977). The pollen-ovule ratio registers a similar decrease from chasmogamous to cleistogamous condition as holds true of Lamium amplexicaule (Lord, 1980). P. hexandrum produces single flowered shoots. Thus pollen-ovule ratio per flower is equivalent to the pollen-ovule ratio per shoot. Both the pollen and ovule production in the species depict considerable differences from plant to plant and population to population, being highest (pollen = 2,01, 058.29 and ovules = 85.28 per plant) in Gratnar I and lowest (almost half of this) in the Gulmarg II population. This drastic reduction in the pollen and ovule yield of the latter population seems to be attributable to the extremely reduced vigour of these plants. The data obtained (Table 17) reveal that in all the populations presently scanned the plants
producing higher number of pollen grains bear correspondingly larger number of ovules and likewise those yielding little pollen bear fewer ovules. Obviously, the two parameters exhibit a positive correlation \( r = 0.521 \). The pollen-ovule ratio in the species ranges between \( 2599.51 \pm 265.7 - 4129.14 \pm 186.37 \) in various populations. The interpopulational differences (excluding Gulmarg II population) noticeable in this regard are statistically not significant (Table 83).

Table 83: \( t \) values comparing the pollen-ovule ratio of different Kashmir Himalayan populations of *P. hexandrum*.

<table>
<thead>
<tr>
<th>Populations</th>
<th>Gulmarg II</th>
<th>Ahrbal</th>
<th>Tangmarg</th>
<th>Naranag</th>
<th>Gratnar</th>
<th>Gulmarg I</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sangergloo</td>
<td>4.11</td>
<td>0.86</td>
<td>0.05</td>
<td>0.52</td>
<td>0.70</td>
<td>0.37</td>
</tr>
<tr>
<td>Gulmarg II</td>
<td>*</td>
<td>3.27</td>
<td>3.02</td>
<td>4.68</td>
<td>4.10</td>
<td>2.73</td>
</tr>
<tr>
<td>Ahrbal</td>
<td>*</td>
<td>*</td>
<td></td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Tangmarg</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Naranag</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Gratnar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*: Significant at 0.05.

The higher pollen-ovule ratio of the species indicates its outcrossing nature. It, however, needs to be mentioned here that the onset of anther dehiscence and receptivity of the stigma in one and the same flower is more or less
simultaneous which creates conditions quite congenial for selfing. Synchrony of the male and female phases on the one hand and higher pollen-ovule ratio on the other create a paradoxical situation. While the former is an inbreeding device, the latter is a pointer towards the outbreeding nature of the species.

Coexistence of higher pollen-ovule ratio and synchronous development of male and female phases in the same species suggests that the species practises both the sexual options, inbreeding as well as outbreeding.

(iii) **Pollination system**:

A large number of species belonging to the families Podophyllaceae, Ranunculaceae and Asteraceae practice entomophilous xenogamy (Mogford, 1974; Macior, 1975; Estes and Thorp, 1975; Bernhardt, 1976; Sawanson and Sohmer, 1976a; Miller, 1978; Waddington, 1981; Waser and Price, 1981; Lawrence, 1985) although many reproduce autogamously as well.

In *P. hexandrum* the high pollen-ovule ratio indicates the outbreeding nature of the species. During the present study, however, no insect visitors were observed on its flowers. The absence of pollinators in the natural habitats of the species seems to be
attributable to: i) the severe climatic conditions, frequent downpours and extremely low temperatures which curb the insect visitation in the entire area ii) non-showy flowers and iii) sporadic representation of the plants. As an alternative, one could conceive of anemophily as a second option. Aerial transport, however, does not seem to be possible in the species because the pollen are shed in clumps and, therefore, are quite heavy. Moreover, the frequent rains the species is invariably faced with at the time of pollen emission wash off the pollen tetrads and do not allow their aerial transport. These circumstances elude the precise mode of the pollen flow from anthers to the stigmas in the species. In an attempt to unravel the exact nature of the breeding system the species operates, floral morphology was closely screened and three types of flowers designated "A", "B" and "C" were identified. Of these the latter two are characterised by differences in the position of anthers in relation to the stigma. This positional isolation hinders any contact between the two sex organs. These flowers seem to heavily depend upon some external agent for pollination. Presence of such flowers gives ample credence to the prediction made on grounds of pollen-ovule ratio that the species may be outcrossing in nature. However, as discussed above, the inclement weather conditions, non-showy flowers and sporadic representation of the plants
do not seem to allow outcrossing in the species. As a result, the chances of the flowers of types "B" and "C" getting pollinated by insects or through air are quite bleak. Lack of pollination leads to the abscission of these flowers. Premature floral drop is known in many other angiosperms and is attributed to the failure of fertilisation (Howard et al., 1919; Shaw et al., 1933; Gupta and Maty, 1987). Under such circumstances the only option for the realization of the sexual reproduction in the species is the exclusive reliance on a mechanical syndrome to affect the transfer of pollen to the stigma of the same flower. This is made possible by producing type "A" flowers which provide opportunities for selfing. In these flowers, the anthers and the stigmatic surface are positioned at the same level. Usually their petals close (Fig. 40) thereby exerting a pressure sufficient to bring the anthers in contact with the stigma. This phenomenon seems to represent "ecological cleistogamy" (Sensu Percival, 1965) and appears to be induced by the excessive atmospheric humidity which prevails underneath the forest canopy especially during the blooming season of the species. In such a situation, shedding of pollen in clumps seems to be quite advantageous and serves a dual purposes. While on the one hand it ensures a large number of pollen reaching the stigmatic surface in one possible contact between the sex organs, thereby minimizing the pollen wastage, it possibly also creates conditions for efficient pollen germination, because the pollen grains are
known to germinate more effectively in groups rather than in singles both in vivo and in vitro (see Schemske and Fenester, 1983).

(iv) Breeding behaviour:

Knowledge about the breeding tactics adopted by a taxon is of paramount importance in the successful operation of the hybridisation programmes aimed at evolving genetically superior forms. The breeding behaviour of the species was analysed from this standpoint and the details are discussed below.

The bagging experiments (Fig. 126) reveal that the unemasculated flowers when left open set enough seed. This, however, provides no clue regarding the precise mode of the formation of the seeds, whether by outcrossing or selfing. As discussed earlier the higher pollen-ovule ratio and the simultaneous maturation of the male and female phases suggest that the species enjoys both the options—outbreeding as well as inbreeding. The experiments on controlled crossing confirm this inference. Thus, the plants whose flowers were emasculated and hand pollinated with pollen from a different source as well as those whose flowers were forced to self pollinate set appreciable quantities of seed. It is, however, intriguing to note that despite being a potential outbreeder, the plants did not set any seed from the flowers which were
Fig. 126: Breeding experiments conducted in *P. hexandrum*.
Seeds Produced

No Seeds

Pollinate and open AND open AND allow flowers to open

Mnasculated

Brogened

Self pollinate and open AND allow flowers to open

Unmasculated

Podophyllum

Rhizome

Underground
emasculated, left open and allowed to open pollinate. Failure of seed set in such flowers is primarily on account of the non-availability of the pollinators. In order to compensate for the lack of natural pollen vectors, the species seems to have developed some inbreeding variants (producing type "A" flowers) which as discussed earlier, are beset with ample opportunities for selfing. Earlier also, Hagerup (1951) demonstrated that in many angiosperm taxa, selection favours inbreeding in response to the non-availability of pollinators.

The bagging experiments under discussion, however, rule out the apomictic behaviour of the species. Swanson and Sohmer (1976 a) also noticed lack of apomictic seed production in *P. peltatum* - a close congener of *P. hexandrum*.

In order to ascertain the extent of cross compatibility at the intra- and interpopulational levels, several crosses were performed. These crosses were successful and produced $39.7 \pm 4.22 - 49.51 \pm 4.31$ seeds per fruit. The success of these crosses establishes the cross compatible nature of the species. Seed yield was, however, low (i.e. $28.68 \pm 3.8$ seeds/fruit) in the cross made between plants of Gulmarg I and Gulmarg II populations. This may partly be attributed to the comparatively higher pollen sterility (22.22 %) of the
plants of the latter population which acted as pollen parents. While working with \textit{P. peltatum}, Swanson and Sohmer (1976a) also arrived at a similar conclusion that the low seed set in some crosses are due to higher pollen sterility.

(v) **Modes of propagation:**

Of the two well known systems of reproduction, asexual and sexual; one or both may be operative in a taxon. Together, the occurrence of these systems in one and the same species gives it an evolutionary edge over those operating only one system. Since such species have more than one reproductive option, they are able to adjust with ease to any changes in their environments which ensures their sustained survival. The asexual system is genetically invariant while the sexual system freely allows a high degree of genetic variability. Therefore, while the latter system generates variability for natural selection to operate, the former fixes this variability to make sure its faithful reproduction generation after generation (Mather, 1966). This holds true of the presently investigated taxa as well since they operate both the reproductive systems asexual as well as sexual. Such a breeding system fits into the type "C" of Heselop - Harrison (1953).

\textit{P. hexandrum} heavily leans on the vegetative
mode of propagation which is accomplished through the production of winterbuds on the underground rhizome. In this respect it closely resembles its congener *P. peltatum* (Holm, 1899; Swanson and Sohmer, 1976a; Sohn and Policansky, 1977). The species can thus be cultivated from rhizome cuttings. The youngest "top" portions of the rhizome with leafy buds have shown encouraging results (Krishnamurthy et al., 1965).

Sexual reproduction through seeds seems to be of limited value in this species. The fruits are indehiscent; thus the seeds are not scattered over long distances. Sometimes, the long distance transport is affected by the birds. The seeds remain dormant for nearly two growing seasons as has also been reported by Chatterjee (1952). Krishnamurthy et al. (1965), however, found that the seeds of this species grow immediately after overwintering although the percentage germination is quite low (45%). Seedlings are difficult to trace in the native haunts of the plant. It may be argued that since in most of the cases, seeds are not scattered, hence as they germinate the seedlings arise in clumps. This results in precocious and undesired competition among the juvenile seedlings in much the same way as happens in *P. peltatum* (Gleason and Cronquist, 1964; Swanson and Sohmer, 1976b). The natural consequence is that most of the seedlings
collapse leaving behind just one or two descendents. Moreover, the seedlings fall prey to heavy biotic interference in the forests.

**Aconitum heterophyllum** :

(i) **Pollen emission and stigma receptivity** :

The multiflowered inflorescences of the species bear protandrous hermaphrodite flowers. The anthers of an individual flower shed their pollen within 4 - 5 days after anthesis. During this process, the non-receptive stigmas are concealed by the stamens. Nearly two days after the dehiscence is over, the stigmatic surfaces become receptive and are exposed to receive "foreign" pollen. Such a system of pollen presentation and stigma receptivity favours outcrossing and prevents selfing within a flower. Similar phenomena have been observed in other aconites viz. *Aconitum septentrionale* and *A. columbianum* (Løken, 1949, 1950; Brink, 1980).

The anthesis and the anther dehiscence proceed from bottom upwards in a plant. Thus, within an inflorescence, the flowers towards the bottom act as functionally female (pollen recipients) while those towards the apices act as functionally male (pollen donors). There is a complete isolation of the male and female phases at the level of an individual flower which rules out any possibility of selfing. On the other hand the two phases overlap.
appreciably in flowers occupying different positions within an inflorescence. This system makes possible the transfer of pollen from one flower to another within an individual (geitonogamy) and also promotes the chances of plant to plant pollen flow within a population (xenogamy). These features are characteristic of several other members of Ranunculaceae viz., Aconitum spp. (Løken, 1949; Heinrich, 1979) and Delphinium spp. (Epling and Lewis, 1952; Benham, 1969 and Waddington, 1981).

(ii) Pollen - ovule ratio:

The species produces highly variable number of male and female gametes. In an individual plant, however, the number of pollen and ovules produced by flowers borne at different positions within an inflorescence (basal-apical) remains almost the same.

As holds true of P. hexandrum, the pollen production in this species too bears a significant positive correlation ($r = 0.702$) with the number of ovules a plant produces. The pollen - ovule ratio fluctuates between $10,830.54 \pm 749.94$ and $12,811.87 \pm 801.0$ in the populations presently studied. The differences in the pollen - ovule ratio between various natural populations are statistically non-significant. The average pollen-ovule ratio for the species works to $11,498.34 \pm 275.19$. Being somewhat nearer to the ratios typical for
several xenogamous taxa (Cruden, 1977; Koul, 1985). This ratio suggests outbreeding nature of the species.

(iii) **Pollination system:**

It is now well known that the genus *Aconitum* is primarily pollinated by bumblebees (Aurivillius, 1887; Løken, 1949, 1950; Pyke, 1974; Heinrich, 1979; Brink, 1980). The floral form and the location of the nectaries (which are concealed in the hood) are so highly specialized for these insects that it has been nicknamed "bumblebee flower" (Kronfeld, 1890; Heinrich, 1977). Leppik (1964), therefore, theorized that the ancestors of the present day bumblebees were largely responsible for the development of *Aconitum* flowers.

Flowers of the species under discussion offer two energy rewards to the visiting insects—the pollen and the nectar. Such plants have an advantage over the ones producing only pollen (Zimmerman, 1982a). The flowers are foraged by at least three species of *Bombus* and a solitary species of *Bremus*. The former are the regular visitors while the latter makes infrequent visits and seems to be exclusively a pollen feeder. It prefers to visit only the functionally male flowers with abundant pollen and plays no role in the pollination. The species may thus be disregarded as a potential pollinator. Løken (1950)
believes that bees which collect only the *Aconitum* pollen have no reason to visit the functionally female flowers and probably are not the pollinators. Compared to *Bombus* spp. the frequency of visitations of *Bremus* sp. is fairly low.

Of the three species of *Bombus*, Acc. B 20 bites holes into the hood to collect the nectar without touching the essential organs (Fig. 70) and, therefore, has no role in the pollination. Such "nectar thieves" have been reported on several other aconites viz. *Aconitum septentrionale* (Løken, 1949, 1950) and *A. columbianum* (Brink, 1980). The remaining two species namely Acc. B 18 and Acc. B 19 are by far the only consistent visitors to the flowers. Primarily they forage on the flowers for nectar and in the process their body parts are heavily loaded with pollen.

A bee starts foraging from lower functionally female flowers, progressively moves upwards often neglecting the topmost flower(s) in an inflorescence and then moves to the lower flowers on the next plant. Thus pollen are transported from an upper functionally male flower of one plant to a lower functionally female flower of the other. Pyke (1974) attributes the neglect of the uppermost flowers to the decreased presentation of the nectar by these flowers. The author found that the old basal flowers
usually contain more nectar compared to the upper younger ones. The bee prefers flowers with more nectar and thus starts foraging from bottom upwards in an inflorescence. The decreasing nectar production up a raceme with an upward foraging behaviour of bees is believed to enhance their foraging efficiency (Pyke, 1974) and maximizes the degree of xenogamy. This characteristic behaviour of the bumblebees has been reported on several other species with protandrous, acropetally maturing flowers. These include: *Aconitum septentrionale* (Løken, 1949); *A. napellus* (Heinrich, 1979); *Delphinium* spp. (Epling and Lewis, 1952; Benham, 1969; Cruden and Hermann - Parker, 1977; Waddington, 1981); *Epilobium angustifolium* (Benham, 1969; Proctor and Yeo, 1972) and *Digitalis purpurea* (Percival, 1965; Percival and Morgan, 1965; Faegri and Vander Pijl; 1971). In *A. napellus*, however, Heinrich (1979) found that the bumblebees visit successively upper flowers in the inflorescence whether or not the nectar quantities are greater in the lower ones. He suggested that this systematic foraging behaviour has an adaptive advantage for the bees since it reduces revisitation of flowers in one and the same raceme. This contention is also supported by Wyatt (1982).

Foraging of the bumblebees on *A. heterophyllum* is greatly affected by the prevailing environmental conditions. Higher temperatures and heavy showers curb their movements.
to a measurable extent while mild rains or clouds have no apparent effect on their activity. Similar responses have been recorded for Bombus spp. and many other hymenopterans in a large number of flowering taxa (see Løken, 1949; Kouli, 1985).

(iv) Breeding behaviour:

In order to understand the breeding behaviour operative in this species, several bagging experiments (Fig. 127) were conducted. The experiments reveal that the emasculated flowers when allowed to open pollinate yield almost the same quantity of the seed as do the normal unmolested ones, allowed to open pollinate (42.0 ± 3.8 and 46.8 ± 4.2 per fruit respectively). This clearly suggests cross-compatible nature of the species. The conclusion is amply supported by the fact that the crosses involving two distinct plants were successful and produced an average of 28.5 ± 3.0 seeds per fruit which represents an appreciable seed set. Being protandrous like many other aconites (Løken, 1949, 1950; Brink, 1980) A. heterophyllum is exclusively cross-pollinated and normally does not self-pollinate. The experiments presently conducted, however, reveal that the species is potentially self-compatible. Thus, when stigmas of a flower where impregnated with pollen from a different flower of the same plant (geitono-gamous pollination) the seed set was fairly high.
Fig. 127: Breeding experiments conducted in *A. heterophyllum*. 
NO SEED

SEED PRODUCED

Pollination

Bagged flowers

Selfed not possible due

Emasculated

Pollen from one plant

Pollen of one plant

Same plant

Open plant

Open and left open

Flowers tagged

Unemasculated

Acornum

Underground tubers
Strict selfing within an individual flower is out of question owing to strong protandry.

From the above account it becomes apparent that the species can reproduce both geitonogamously as well as xenogamously. It may, however, be borne in mind that the pattern of pollen presentation and stigma receptivity together with the foraging behaviour of the bumblebees within an inflorescence (bottom – upwards) sufficiently lower the chances of geitonogamy. The species, therefore, seems to heavily lean upon the entomophilous xenogamy in natural populations. A similar breeding system is at work in some other species of the genus viz., *A. columbianum* (Macior, 1974; Brink, 1980).

(v) **Modes of Propagation:**

Reproduction in this taxon is accomplished vegetatively through underground tubers and sexually through seeds. A plant usually produces a single daughter tuber. After overwintering, this collateral tuber gives rise to a single shoot in the next growing season. Asexual reproduction, therefore, is restricted only to the replacement of an individual plant and year to year maintenance of populations. The same behaviour is exhibited by many other aconites (Brink, 1980, 1982) which produce bulbils as an additional means of vegetative propagation. Bulbifery, however, has not been observed in *A. heterophyllum* during the present investigations.
The sexual reproduction through seeds is the predominant mode of propagation in the species. Depending upon the number of flowers a plant bears as also the pollinator efficiency, the total seed yield varies from 
\[374.4 \pm 33.0 - 799.46 \pm 41.14\] per plant.

In natural populations the sexual system of the species is faced with numerous threats. Firstly, the plants being extensively grazed lose most of their flowering tops. The few that escape, actually rescue the species. Secondly, the handful of seeds that are produced have to overcome prolonged dormancy. Thirdly, the new recruits that arise are faced with stiff competition for nutrients and space with the plants already established in their neighbourhood. In the process, many seedlings are weeded out leaving behind only a few that develop into fullfledged plants. This is one of the major reasons why the species has a fairly sporadic representation in its natural habitats in Kashmir Himalayas.

*Saussurea lappa* :

**Pollen emission and stigma receptivity** :

The capitula of this species bear hermaphrodite, weakly protandrous florets. In a floret, the anthers dehie while the stigma is still concealed within the anther collar. As the stigma grows, it pushes through the pollen mass, most of which is brushed by the sweeping hair
of the style. This pollen can be seen as white granular mass on the tip of the anther collar (Fig. 99). Within an hour or so, the stigmatic branches diverge and carry the pollen on the receptive surfaces which initially suggests selfing in a floret. Such a unique sequence of anther dehiscence and stylar extension characterises many other Asteraceae (Lawrence, 1985).

The inflorescence is determinate with apical capitula maturing first. Anthesis within a capitulum commences from the periphery and progresses centripetally. This is also true of *Pyrohopappus carolinianus* (Estes and Thorp, 1975) and *Senecio* spp. (Lawrence, 1985). The dehiscence of anthers in a capitulum and within a plant is fairly asynchronous. This is the reason why pollen are available for a long period of 7 - 11 days in a capitulum and 16 - 25 days in a plant.

Stigma receptivity exhibits a similar trend. In a capitulum, the marginal florets may, therefore, act as functionally female while those towards the centre as functionally male. Thus, the pollen in the species are always carried from the central florets to the marginal florets of the same or different capitula as depicted in Fig. 106. Although this creates conditions conducive for geitonogamy but within a plant, the pollen flow from apical to the basal florets is generally not possible because either the basal capitula fail to open or anthese
much latter than the apical ones (Fig. 106). Moreover, the basal capitula are often neglected by the insect visitors which preferably remain confined to the apical ones. Hence the pollen transfer in the reverse direction (basal to apical capitula) also does not occur. Instead it is restricted only to the capitula clustered at the top of the shoots.

The opening of the capitula borne on different shoots arising from a single rhizome overlaps to a great extent. This synchronization favours the inter-stalk pollen exchange which has also been reported in many other perennial angiosperm taxa (Ponomarev, 1960; Lindsey, 1982; Koul, 1985).

(ii) Pollen-ovule ratio:

The plants bear varying numbers of capitula ranging between 3 - 10. The data obtained reveal that the pollen and ovule production increases progressively with increase in the number of capitula per shoot. In terms of pollen production, therefore, the plants bearing 4 and 8 capitula exhibit significant differences from each other (t = 6.26, p = 0.05). A similar trend exists in the ovule production which is more than double in 8-headed shoots compared to the 4-headed ones (t = 4.28, p = 0.05). Even within an individual plant, the pollen and ovule production of the apical and basal capitula is not uniform (Table 61). These differences are, however,
The pollen-ovule ratio in the species is almost uniform from capitulum to capitulum, and plant to plant. The differences that are exhibited at the interpopulational level are also marginal and statistically non-significant.

In order to establish whether the pollen ovule ratio is determined genetically or environmentally, transplant experiments were conducted in which plants inhabiting an altitude of 2500 m were grown at an altitude of only 1550 m in a totally different habitat. They behaved in much the same way as their natural counterparts (Table 84). This indicates that the gamete production in the species is least affected by changes in the environment; the pollen-ovule ratio, therefore, seems to be under genetic control.

Table 84: Comparison of the pollen-ovule ratio of natural and transplant population in 6-headed shoots of *S. lappa.*

<table>
<thead>
<tr>
<th>Character</th>
<th>Natural population</th>
<th>Transplant population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pollen production per individual</td>
<td>5946680.1 ±</td>
<td>5711640.9 ±</td>
</tr>
<tr>
<td></td>
<td>139533.32</td>
<td>17915.70</td>
</tr>
<tr>
<td>Ovule production per individual</td>
<td>432.12 ± 3.2</td>
<td>431.50 ± 9.15</td>
</tr>
<tr>
<td>Pollen-ovule ratio</td>
<td>13761.87 ± 188.98</td>
<td>13245.0 ± 162.81</td>
</tr>
</tbody>
</table>
The higher pollen-ovule ratio (Table 60) suggests outbreeding nature of the species. The same inference has been drawn even on grounds of the pollen presentation and stigma receptivity patterns discussed earlier.

It may be mentioned here that the pollen-ovule ratio in many of the outbreeding species may be lower or higher than that estimated for *S. lappa*. While the lower ratios (1500 - 7000) characterise some allogamous species of the tribe Inulinae (Asteraceae) and genus *Senecio* (Short, 1981; Lawrence, 1985) the higher ones have been reported in certain unrelated taxa such as *Amorpha canescens* (P/0:16807) and *Salvia cardinalis* (P/0:19525) (see Cruden, 1977).

(iii) Pollination system:

There is a fairly high degree of asynchrony in anthesis of florets within a capitulum and at the level of an entire plant. Asynchronous anthesis is known to promote outcrossing rates (Wyatt, 1982). The fact that in a floret the stigma pushes through the anther collar after dehiscence and gets loaded with its own pollen suggests selfing within a floret. But in strong contrast to some compositae (Lawrence, 1985) and like many others (Lewis, 1966; Lawrence, 1985), the pollen of a floret in this species are unable to germinate on their own stigmas as revealed by the bagging experiments conducted during
the present study (to be discussed ahead). This speaks of self-incompatible nature of the species.

Being protandrous and self-incompatible, the species is exclusively cross-pollinated and leans heavily on external pollinating agents. As holds true of composites in general, the florets in the species are aggregated in compact capitula. Several workers contend that heads of composites represent single flowers (Wernham, 1912; Good, 1931, 1956; Leppik, 1960). Burt (1961), however, pointed out that, this is true only in terms of pollinator attraction and that presentation of many single ovuled flowers (such as those of *S. lappa*) for pollination over a greater period of time results in much higher rates of outcrossing than in many ovuled single flowers.

Two species of Hymenoptera (*Bombus* spp.) and a single Dipteran (*Syrphus* sp.) visit the heads in search of food in the form of pollen. However, only the former carry *Saussurea* pollen and may thus be the probable pollinators of the species.

Usually the lowest "heads" on the stem are neglected by the insects and they fail to produce seeds. Abortion of such capitula may be attributed to failure of fertilization (see Howard *et al.*, 1919; Shaw *et al.* 1933) or resource limitations (see Hardin, 1956; Mooney and Bartholomew, 1974; Benseler, 1975; Stephenson, 1981).
However, some plants have developed a compensatory mechanism by bringing the lower capitula which are normally neglected by insect visitors in level with the upper ones thus exposing even these to the pollinators (Fig. 109). This ensures pollination and seed production in maximum number of capitula within a plant.

(iv) Breeding behaviour:

The breeding experiments (Fig. 128) firstly rule out the apomictic behaviour of the species (the florets not allowed to pollinate aborted). Even the capitula allowed to undergo selfing failed to set seed which confirms the self-incompatible nature of the taxon. Self-incompatibility is well known in several other genera of Asteraceae (Brewbaker and Majumdar, 1961; Lawrence, 1985). Perusal of literature reveals that most of the self-incompatible species are perennial while majority of the self-compatible ones are annuals. Perennial habit and self-incompatible nature go hand in hand even in the species under discussion. Stebbins (1958) observed this trend in tribe cichorieae (Lactucaeae) of the family Asteraceae also.

Being self-incompatible the only sexual option available to the species is xenogamy. This is the reason why the open pollinated plants produce large number of seeds. That the species is truly outbreeding in nature is also suggested by the higher pollen-ovule ratio and the pollination system.
Fig. 128: Breeding experiments conducted in *S. lappa*. 
Seed produced

Unemasculated capitula tagged and left open

Unemasculated capitula bagged and allowed to pollinate

No seed

Stigma of florets excised prior to pollination and the capitula left open

Såsurea

Underground rhizome
The species propagates sexually through seeds and vegetatively through the buds borne on the underground rhizome.

After maturation, the achenes are blown by wind to rather short distances only because the species usually inhabits the gorges where the breast walls of the mountains restrict their long distance transport.

The efficient dispersal of the achenes is further hindered by their heaviness. Seeds do not exhibit dormancy and are capable of immediate germination as they land on a suitable substrate. In natural populations, however, the seedlings are preyed upon by the vagaries of weather. The sub-zero temperatures at high altitudes during October - November kill the baby plants while they are still at the cotyledonary stage of development. Only the seeds that escape immediate germination till the following spring actually contribute to the new recruitments. Immediate germination may be postponed in two ways: (i) some seeds remain within the capitula on the dead shoots and are dispersed belatedly and (ii) the seed production may immediately be followed by sufficient lowering of temperatures which prevents them from germination till the favourable season returns.

As the seeds germinate in the late spring, they encounter stiff competition with the early sprouters which
have already established by the time *Saussurea* seedlings make their appearance. Hence, the sexual system is of a limited value in the propagation of the species which, therefore, has to rely mainly on the vegetative mode.

The above discussion indicates that all the three taxa investigated now have two reproductive options, asexual and sexual. The homogamous condition in *P. hexandrum* allows for selfing while the other two taxa are either strongly dichogamous or weakly so. The "temporal dioecism" prevalent in *A. heterophyllum* is a barrier for selfing within an individual flower. However, ample opportunities are provided for geitonogamy because of some degree of overlap of male and female phases within a plant. At the same time, the asynchronous development of these phases in different individuals of a population provides greater chances for gene flow between them. *S. lappa* is weakly protandrous. The species provides enough chance for pollen flow between capitula within a plant, different individuals arising from the same rootstock and also between different individuals in a population.

All the three taxa depict a high degree of pollen strainability. The pollen-ovule ratio indicates that all these are readily referable to a generalised outbreeding class. The enormous quantities of pollen produced may serve to ensure effective pollination in a situation where lot of pollen is likely to go waste through insect
vectors and also washed away during the incessant rains which is a regular feature of the habitats endured by these taxa.

Regarding the pollination mechanisms at work in them, the present investigations clearly reveal that the success of their sexual system is dependent on entomophilous pollination. The transfer of pollen from the seat of its formation to the site of its action is mediated through a large number of insects. Species of Bombus, however, seem to be the primary pollinators. In the absence of insect vectors, *P. hexandrum* can reproduce autogamously.

The breeding behaviour suggested by pollen-ovule ratio of these species is confirmed by the bagging experiments. *P. hexandrum* through a potential outbreeder seems to have opted for inbreeding probably due to the lack of natural cross pollination. *A. heterophyllum* although normally cross-pollinated is self-compatible too. *S. lappa*, is, however, exclusively self-incompatible.

V. REPRODUCTIVE EFFORT AND RESOURCE PARTITIONING IN THE SEX ORGANS:

The energy allocation pattern of a species is programmed in such a way as to achieve maximum evolutionary fitness. This partitioning of the resources may vary according to the habitat and community characteristics of
a taxon. As an adaptive tactics, plants allocate maximum proportion of biomass towards reproduction in the highly disturbed habitats (or less mature communities) than in the less disturbed habitats or more mature communities. The differences in the reproductive allocation may either be controlled genetically or may be environmentally induced. The environmental factors include plant density, soil fertility, habitat characteristics, stability of the plant communities and altitude etc. (Clausen et al., 1940, 1948; Mooney, 1963; Billings and Mooney, 1968; Johnson and Cook, 1968; Ward, 1969, Rochow, 1970; Bliss, 1971; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Ogden, 1974; Hickman, 1975; Abrahamson and Hershey, 1977; Abrahamson, 1979; Jolls, 1980; Kawano and Masuda, 1980). Perusal of literature reveals that analysis of the energy allocation patterns can provide invaluable information regarding the reproductive status of a species. Therefore, in case of rare and threatened taxa to which the presently investigated species also belong, studies on resource allocation patterns in relation to the breeding systems assume a significance of their own. The present investigations represent the first attempt in this direction and reveal that the partitioning of resources in the species is correlated with the habitat characteristics and altitudinal gradient as discussed below:

(a) *Podophyllum hexandrum*:

The dry biomass accumulation to the shoots of
this species fluctuates between 5.39 ± 0.49 and 10.18 ± 1.13 gm/individual in the presently studied populations.

The partitioning of resources is biased more towards the leaf tissues than the stem. The increased allocation towards leaves is believed to be an adaptive response to shading (Abrahamson and Gadgil, 1973) in a situation where plants of dissimilar growth forms compete with each other for light. *P. hexandrum* inhabits forest undergrowth and encounters tough competition for light with associated shrubs especially *Viburnum foetens* and also from the surrounding trees which seldom allow sufficient light to reach the forest floor. This is true of all the populations except Sangergloo. Even plants of this population are partially shaded as they are interspersed among stands of *Betula utilis*. In such a situation the increased allocation to leaves may help the plant to increase its photosynthetic efficiency in light limited conditions.

The reproductive effort (RE) ranges between 35.46 ± 2.41 - 40.89 ± 2.28% in these populations. Obviously, although the total biomass allocation to the aerial shoots exhibits a two fold increase but this is not associated with a corresponding variability in the RE. Similar observations have also been recorded in *Senecio vulgaris* which does not show any significant changes in the RE over even a seven fold increase in the biomass of plants (Harper and Ogden, 1970).
The RE tends to increase with increase in the altitude of the populations. It is lower in populations growing below 2600 m and higher in those located above this altitude (Table 21). The present observational support to the findings of Kawano and Masuda (1980) that RE increase with increase in altitude. The increased RE towards higher altitudes may be due to the fact that at these sites, plants experience severe environments and in such harsh conditions may ensure their reproductive success by allocating more energy towards reproduction (Mac Arthur and Wilson, 1967).

(b) *Aconitum heterophyllum*:

The total biomass accumulation per individual in this taxon is lesser than that of *P. hexandrum*. In general, the plants allocate maximum proportion of biomass towards the stem tissues (Table 45). Increased investment in the stem is a response to shading when plants of similar growth form compete with each other in the absence of any overhead canopy (Abrahamson and Gadgil, 1973). In Kashmir Himalayas, *A. heterophyllum* usually grows in the open alpine meadowlands which are bereft of any trees. Even the shrubs are scant. The species, therefore, has to compete for light with associated herbs like *Morina coulteriana*, *Salvia hians*, *Nepeta* spp., *Senecio chrysanthemoides* and several grasses. Even in the temperate zone the species inhabits mostly the forest openings where only the herbs are the potential competitors.
for light and other resources. That increased allocation towards the stem as reported in several other species viz., *Aster nemoralis* (Brouillet and Simon, 1979) and *Polygonum* spp. (Hickman, 1977) is a result of competition with neighbouring herbs corroborate our findings in *A. heterophyllum*.

The sexual reproductive effort of the species lies well within the range reported to be typical of herbaceous perennials (5 - 25%, Harper *et al.*, 1970) and decreases with increase in altitude (except Sangergloo population whose plants bear numerous lateral inflorescences, hence higher floral density). Such a trend has also been observed in Kullu valley of Himachal Pradesh (author's unpublished data) where the species registers a remarkable decrease in the flower production from lower (2600 m) to higher altitudes (3100 m Rohtang Pass). That this holds true of many other angiosperm taxa has aptly been demonstrated by numerous workers (Billings and Mooney, 1968; Johnson and Cook, 1968; Bliss, 1971; Hickman, 1975) who report a drop in the floral density and biomass allocation to sexual tissues with increase in altitude.

The vegetative reproductive effort (VRE) in this taxon ranges between 12.1 - 59.5% and the sexual reproductive effort (SRE) between 10.8 - 17.6%. These parameters are known to vary from population to population in many
other angiosperms viz. *Solidago canadensis, Tussilago farfara* etc. (Bradbury and Hofstra, 1976; Ogden, 1974). In vegetatively reproducing species, SRE tends to remain constant while VRE varies (Ogden, 1974; Abrahamson, 1975; Holler and Abrahamson, 1977). Contrary observations have, however, been made by McNamara and Quinn (1977) in *Amphicarpum purshii*, Zeide (1978) in *Gymnarrhena micrantha* and Pitelka et al. (1980) in *Aster acuminatus*.

In all the populations of *A. heterophyllum*, presently scanned, the VRE is more than SRE. Low SRE and high VRE characterise a number of other herbaceous taxa (see Anderson and Louks, 1973; Whigham, 1974; Kawano and Nagai, 1975; Webber and May, 1977; Muller, 1978; Silva, 1978; Pitelka et al., 1980; Spira and Pollak, 1986).

(c) *Saussurea lappa*:

Plants of *S. lappa* outnumber those of *Podophyllum* as well as *Aconitum* in terms of dry matter accumulation in the above ground organs. The total above ground dry biomass accumulation ranges between 24.68 - 70.92 gm/shoot.

The biomass is not partitioned evenly among the different organs of the plant, maximum amount being found in the organs of support (i.e. stem) followed by the leaves and lastly the flowering heads.
The increased commitment of energy towards stem in this species is characteristic of several other plants growing in shady environments of the forest (Abrahamson and Gadgil, 1973; Abrahamson, 1979). *S. lappa* grows in densely forested areas where light is one of the major limiting resources and thus plants have adopted accordingly.

The RE fluctuates between 20.22 ± 0.80 and 27.52 ± 0.75 and displays a progressive increase from low humid environments to higher altitudes which represent comparatively drier habitats. Increase in RE with increase in altitude has been reported in numerous angiosperm taxa (see Mac Arthur and Wilson, 1967; Kawano and Masuda, 1980). Some workers have demonstrated that increase in RE is associated with decrease in the humidity in several members of Asteraceae like *Solidago* spp. (Abrahamson and Gadgil, 1973). Many workers (Werner, 1976; Werner and Platt, 1976), however, found that although increase in the proportion of resources allocated to stem and leaf tissues is a positive function of soil moisture, it is not necessarily associated with a distinct pattern of reproductive effort.

Resource Partitioning in the Sex organs:

Energy allocation to male and female components of the sexual function has been the focal point of many
recent studies (Williams, 1975; Smith and Evenson, 1978; Lloyd, 1979; Vernet and Harper, 1980; Charlesworth and Charlesworth, 1981; Doust and Cavers, 1982). This work has brought to light a positive correlation between male - female investment and the breeding system in plants. Inbreeding species allocate more resources towards the female than the male sex organs. Reverse is, however, true of outbreeders.

In *P. hexandrum*, the biomass of the male and female tissues prior to fertilization is nearly the same (male = 30.89% and female = 31.13%) with a slight tilt towards the female component. This is suggestive of the inbreeding nature of the species with equal opportunities for outbreeding - a fact already established on grounds of floral morphology and the results of the breeding experiments conducted during the present investigations. Doust and Cavers (1982) however, reported higher biomass accumulation in the male than the female tissues in *P. peltatum* which is known to be an exclusive outbreeder.

*A. heterophyllum* registers a higher commitment of energy towards the male than the female tissues, the resource allocation pattern to the male and the female function being in the ratio of 3:1 (Table 46). This is a pointer to the outbreeding nature of the species. The breeding experiments conducted during the present study
and the pollination system operative in it confirm this contention. The increased allocation of resources towards androecium has been reported for many other outbreeding taxa (Doust and Cavers, 1982). Despite the higher pre-fertilization allocation strategy towards the male component in an outbreeder, it has been argued (Doust and Cavers, 1982) that outbreeders have to pay more maternal than the paternal cost in the fulfilment of reproduction because of the post fertilization nursing of the developing embryos.

VI KARYOLOGY AND POLLEN MOTHER CELL MEIOSIS:

Podophyllum hexandrum:

The genus Podophyllum comprises ten species and is dibasic with \( x = 6 \) and 8. The cytological investigations made so far on these species are woefully inadequate and restricted only to the chromosome count (Mottier, 1897; Overton, 1905; Litardiere, 1921; Kaufmann, 1926; Langlet, 1928; Miyaji, 1930; Darlington, 1936; Delay, 1947; Newman, 1959). The sole detailed studies that have become available so far (Newman, 1959; 1966, 1967; Muhling and Wilson, 1961) pertain to the karyology and pollen mother cell meiosis of a single species, \( P. \text{ peltatum} \).

As revealed during the present investigation,
*P. hexandrum* is diploid having \(2n = 2x = 12\). This count is quite in conformity with the earlier counts (see Fedorov, 1969; Siddique *et al.*, 1990). The complement comprises meta-, submeta-, and acrocentric chromosomes in the ratio of 1 : 3 : 2. The ratio between the longest and the shortest chromosomes works to 1.87. In respect of the degree of asymmetry, the complement fits into type "3A" of Stebbins (1971). This goes hand in hand with the primitive evolutionary status of the taxon. The nucleolar chromosomes of the species seem to vary in number from cell to cell. Their actual count was, however, authenticated on grounds of their activity estimated in terms of nucleolar organization. These studies reveal the occurrence of 1 - 4 nucleoli per cell. This number is strictly in line with 4 NORs per complement in the species. Such a positive correlation between the number of nucleolar chromosomes per complement and the number of nucleoli per nucleus is also known to exist in many other angiosperm taxa (Koul and Wafai, 1980; Langer and Koul, 1982; Sharma *et al.*, 1986; Koul *et al.*, 1988).

The pollen mother cell meiosis proceeds normally with a few occasional abnormalities such as the precocious separation of one or two bivalents and formation of 1 - 4 chromosome fragments. These anomalies, however, do not seem to affect the meiotic system. The species thus produces up to 95% of healthy and stainable pollen.
Aconitum heterophyllum:

Aconitum is a fairly large genus of the family Ranunculaceae and comprises nearly 300 species. Of these only 47 (which constitute mere 15.66% of the entire genus) are known cytologically. The studies conducted so far have remained confined mainly to the chromosome count and reveal that the genus is monobasic having \( z = 8 \) and exhibits a high degree of polyploidy (\( > 15\% \)) as shown in Table 85.

| 2n = 2x  = 16 | 23 |
| 2n = 3x  = 24 | 2  |
| 2n = 4x  = 32 | 16 |
| 2n = 6x  = 48 | 5  |
| 2n = 8x  = 64 | 1  |

Perusal of literature reveals that polyploidy is particularly widespread in the section Eu - Aconitum to which the species under discussion also belongs. The preponderance of polyploidy speaks of the pivotal role polyploidy has in the evolution of the genus (Schafer and La Cour, 1934).
The present investigations reveal that *A. heterophyllum* is diploid having $2n = 2x = 16$. This confirms the earlier counts of Schafer and La Cour (1934); Mehra and Sobti (1955); Mehra and Remanandan (1972) and Virjee *et al.*, (1983, 1984). The chromosome complement comprises meta-, submeta- and acrocentric chromosomes in the ratio of $1 : 3 : 4$. Earlier also, Schafer and La Cour (1934) while describing the somatic chromosomes of a large number of aconites, analysed the karyomorphology of the species and found these three types of chromosomes in the ratio of $1 : 1 : 6$. The details are summarized in Table 86 (see also Fig. 129).

Table 86: Karyology of *A. heterophyllum* as described by Schafer and La Cour (1934) compared with the present observations.

<table>
<thead>
<tr>
<th>Sr. No.</th>
<th>Features of the karyotype</th>
<th>Schafer &amp; La Cour (1934)</th>
<th>Present observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Diploid chromosome number.</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>2.</td>
<td>No. of metacentric chromosomes</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>3.</td>
<td>No. of submetacentric chromosomes</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>4.</td>
<td>No. of acro-centric chromosomes</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>5.</td>
<td>$m : sm : ac.$ chromosomes.</td>
<td>$1 : 1 : 6$</td>
<td>$1 : 3 &lt; : 4$</td>
</tr>
</tbody>
</table>

Comparison between the earlier and the present observations on the karyomorphology of the species drawn
Fig. 129: Somatic chromosome complement and karyodiagram of *A. heterophyllum* as drawn by Schafer and La Cour (1934).
in the table above glaringly brings out a considerable disagreement between the two. It needs to be pointed out here that the studies made by Schafer and La Cour (l.c.) are based on sectioned material. This method is inadequate for karyological analysis and, therefore, casts doubt on the validity of these observations. If the details made available by these studies are factual, the disparity between the earlier and the present observations should speak of chromosome polymorphism in the species. Once established, it could be implicated as a potent evolutionary factor in the species which is a stable diploid and does not exist in polyploid form.

The length of the longest and the shortest chromosomes is in the ratio of 2.55. On grounds of the degree of asymmetry, the karyotype fits into type 38 of Stebbins (1971).

The pollen mother cell meiosis of the species proceeds normally with perfect homologous pairing and regular anaphasic segregation. Thus, the gamete differentiation is normal and large quantities of functional pollen are produced. Mehra and Ramanand (1972), however, observed anomalies such as extended heterochromatic arms and late disjunction of some chromosomes in the species. These anomalies do not impair the process of meiosis. The species, therefore, produces fairly large quantities of healthy and stainable pollen (98-99%
Saussurea lappa:

The genus *Saussurea* is based on nearly 400 species. Surprisingly, only 24 which constitutes mere 8.5% of the entire genus, are known cytologically (see Fedorov, 1969; Virjee et al. 1983, 1984, 1985). These studies reveal that the genus is tribasic having $x = 13, 16$ and 18. Of the 34 species, 29 are diploid and 5 polyploid (Table 87).

Table 87: No. of the species of the genus *Saussurea* showing various ploidy levels. (Data summarized from Fedorov, 1969; Virjee et al. 1983, 1984, 1985).

<table>
<thead>
<tr>
<th>Chromosome number</th>
<th>x</th>
<th>Ploidy level</th>
<th>No. of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
<td>13</td>
<td>diploid</td>
<td>24</td>
</tr>
<tr>
<td>32</td>
<td>16</td>
<td>diploid</td>
<td>3</td>
</tr>
<tr>
<td>36</td>
<td>18</td>
<td>diploid</td>
<td>2</td>
</tr>
<tr>
<td>39</td>
<td>13</td>
<td>triploid</td>
<td>1</td>
</tr>
<tr>
<td>48</td>
<td>16</td>
<td>triploid</td>
<td>2</td>
</tr>
<tr>
<td>52</td>
<td>13</td>
<td>tetraploid</td>
<td>2</td>
</tr>
</tbody>
</table>

*S. lappa* - the species under discussion is exclusively diploid. So far, the species was known to be monobasic having $x = 13$ (see Fedorov, 1969; Virjee et al., 1985). The present investigations have, however, brought to light yet another base number $x = 18$ in the species which, therefore, turns out to be dibasic rather
than monobasic. The plants presently worked out are diploid having $2n = 2x = 36$. Evidently, therefore, the species exists in two diploid cytotypes, one having $2n = 2x = 26$ and the other $2n = 2x = 36$. This speaks of a remarkable numerical chromosome polymorphism at work in the species which in absence of polyploidy could serve as a potent factor in its evolutionary diversification.

The present analysis of the karyomorphology of the species represents the first ever made in this direction. The somatic complement comprises only two types of chromosomes namely submetacentric and acrocentric in the ratio of $1:2$. The chromosomes of the species are very small and the ratio between the length of the longest and the shortest chromosomes of the complement equals 3.16. On grounds of the degree of asymmetry, the karyotype fits into the type 2B of Stebbins (1971).

The pairing behaviour of the chromosomes is fairly normal though anomalies such as clumping of few or more bivalents occur occasionally. The anaphasic disjunction is regular. As such the gamete differentiation proceeds without error and the species produces enormous quantities of viable pollen.

The success of the sexual breeding system of a species depends upon the mode of gamete differentiation
it follows. In the three taxa investigated now, the differentiation of male cells is quite regular. The pmc meiosis is characterised by perfect synapsis between the chromosomes and regular anaphasic disjunction. The sporogenesis follows a normal course and 90% pollen are healthy and intensely stainable. Normal meiotic behaviour and sporogenesis impose genetic stability upon these species and ensure fertility and high seed set.

VII. PRESENT STATUS OF THE TAXA UNDER DISCUSSION AND FUTURE STRATEGY:

The present investigations reveal that *Podophyllum hexandrum*, *Aconitum heterophyllum* and *Saussurea lappa* are fairly stable diploid taxa with normal gamete differentiation, efficient pollination and profuse seed production. The sexual reproduction is assisted by asexual system in their maintenance and propagation. Such an efficient breeding system superimposed upon the stable diploid nature ensures their wider multiplication and conservation in nature. Why then are these taxa sporadically represented in the Himalayas and known to be rare and threatened? The answer lies in a number of intrinsic and extrinsic factors that seem to impair their expansion and large scale multiplication in the natural habitats. These include: premature floral drop, fruit predation, inadequate seed dispersal, prolonged seed dormancy, slow germination, high seedling mortality, stiff competition of the seedlings with the already established plants for nutrients etc. Besides these, an array of other
ecological / biotic factors pose a serious threat to their very existence at least in this part of the Himalayas. Of these, the important ones are discussed below (see also Figs. 130 - 132).

(i) **Restricted distribution**:

As shown earlier, the three taxa are restricted only to the narrow geographical regions of the north west Himalayas. Obviously, they obtain a critically low worldwide representation. Any threat to their survival in this area can be catastrophic and the species may vanish from the biological world itself!

(ii) **Habitat specificity and destruction**:

Habitat structure is an important determinant of the proliferation of a taxon. In Kashmir Himalayas the species under discussion have a limited ecological amplitude and are confined to the montane habitats only where they are restricted to certain microsites which experience most severe climatic hazards all the year round. Obviously, these species have stringent ecological requirements and remarkable endurance for such critical habitats. Any alteration and imbalance in these habitats can prove fatal and lead to the total loss of this valuable germplasm. Hodgson (1986) has aptly pointed out that, "the degree of habitat destruction is an important determinant of species distribution and abundance". Many high altitude
Fig. 130: Reproductive strategy and survival chance of *P. hexandrum*. 
Fig. 131: Fate of reproduction and causes of decline in A. heterophyllum.
ACONITUM

TUBERS

EXTRACTION

DECLINE

SEEDS

SEEDLINGS

SEEDLINGS

COMPETITION

GRAZING

FEW SURVIVE

EXTENSIVE

DEATH

LOW SEED SET

SEEDLINGS

REduced ALlocation TO DAUGHTER TUBERS

WEAK PLANTS

FEW SURVIVE
Fig. 132: Reproductive strategy and survival rate of S. lappa.
SAUSSUREA

RHIZOME
- EXTRATION
- DECLINE

SEEDS
- RESTRICTED DISPERSAL
- SEEDLINGS
  - MORTALITY
  - FEW SURVIVE

Grazing

EXTENSIVE
- NO SEED
- DEATH OF SHOOTS

MODERATE
- REDUCED ALLOCATION TO RHIZOME
- LOW SEED SET
  - WEAK RHIZOME
  - WEAK PLANTS
  - FEW SURVIVE
habitats in the Kashmir Himalayas have been heavily deforested and artificialised for numerous "developmental" purposes including the expansion of agriculture. Disturbances like these lead to creation of new habitats which are usually unfit for most of the earlier occupants. Often these habitats are colonized by weedy species which throw the earlier occupants into stiff competition when they start rejuvenating on these newly created habitats.

Tourism development is well known for the share it has in creating ecological disturbances (see Gaekward, 1984). Kashmir Himalayas represent a renowned tourist resort and a strategic border area. Therefore, a reticulum of roads has been extended through the heart of the forests into the alpine regions which represent the home of the taxa under reference, (Fig. 133). This exposes the natural abode of these taxa to direct biotic and abiotic interference. For example, the habitat of Saussurea lappa has fallen prey to ruthless destruction all along the Tragbal - Gurez and the Duksum- Simthan state highways in the northwest and southeast of Kashmir valley. These sites represented a rich repository of the species only five years back but at present it is extremely difficult to locate even a single plant from these areas. It is lamenting to note that the species is unable to reestablish itself on the newly created habitats and is thus rarely seen in these belts now. Likewise, the construction of
Fig. 133: Extension of roads deep into the heart of forests results in landslides and loss of valuable germplasm.

Fig. 134: The huge chair car project under construction in the Gulmarg forest area.
tourist hutments, hotels and other projects within the forests has led to the depletion of natural populations of these plants. For example Gulmarg I population which was full of P. hexandrum during 1986 - 1987 is now bereft of any individual of this species. This is because of the construction of a huge monocable chair car lift extending from Gulmarg to the alpine zone of Apherwat (Fig. 134).

Soil erosion - one of the after effects of such "developmental" processes is of a grave ecological consequence as it drastically alters the vegetal cover and habitat of a particular area. Dewan (1986) reported that India looses 6000 million tonnes of soil every year which causes a loss of approximately 8.4 million tonnes of soil nutrients. This ailment has also engulfed a large part of Kashmir Himalayas where the erosion occurs mainly due to the massive deforestation. According to an estimate, the total forest area of the J & K state was 10% of its geographical area during 1972 - 1975. By 1980 - 1982, this figure reduced to 6.5% only.

(iii) Non-judicious exploitation:

One of the most important factors responsible for the rarity of the taxa under reference is their unplanned and indiscriminate extraction for the drug based industry as well as the traditional medicare without regard to their rate of multiplication and survival. Seemingly
this is the reason why these taxa have been declared as rare and threatened in the entire Himalayan region (Arora and Nayar, 1983; Gaur and Semwal, 1983; Shah, 1983; Siddique et al., 1987). The three taxa constitute valuable "root drugs". Stress on the underground parts (rhizomes/tubers) which represent the asexual reproductive propagules is thus quite natural. The official as well as the unauthorized extraction of this raw-material by the non-governmental agencies especially for immediate monetary gains is one of the potent threats to these species. It is worrying to note that no serious efforts have ever been initiated to propagate any one of these taxa on a commercial scale so as to cater adequately to their growing demands vis-a-vis save them from extinction.

(iv) Grazing:

Grazing and trampling have often been identified as potent threats to endangered species (Cook and Dixon, 1987). These factors, "reduce the size of the adults, often reduce seed production and may even kill the adults" (Widen, 1987). Grazing is a menace in Kashmir Himalayas also where the percentage of forest growing cattle in relation to the total bovine population has been estimated to be 113.5% (Javied, 1982). While on the one hand the taxa under discussion face rarity and need protection, the onslaught of continued and indiscriminate grazing on the
other pose a serious threat to their very existence. Grazing and trampling rob them off their sexual propagules to an alarming extent, with the result that their rate of multiplication and survival are drastically reduced. As such these species are forced to bank upon vegetative means for propagation and year to year maintenance. Even the vegetative propagules can not guarantee their long term survival so long as they remain under a constant extraction pressure and continue to provide the raw material for the pharmaceutical industry.

Future Strategy:

Kashmir Himalayas represent the cradle of more than 200 medicinally important plant species which not only provide relief to the ailing but also livelihood to many and earn considerable revenue to the state. Sufficient indications are now becoming available that this rich germplasm is getting sacrificed at the altar of yield based extraction for the drug industry and several biotic and abiotic processes. The natural outcome of these processes is the impoverishment of the medicinal plant wealth of the area. The situation is worse confounded in species that are faced with highly specialised ecological requirements and thus have limited geographical arenas at their disposal or are endemic in nature. Any kind of habitat destruction can be catastrophic in respect of such species. Collectively all these factors
have brought a sizable number of medicinally important taxa particularly the ones presently investigated, to the brink of extinction and these are now only sparsely represented even in their specific ecological niches.

This is high time to plan conservation strategies lest these species are lost for all times. Legislative protection should be ensured for such species. Although this has been done for A. heterophyllum and S. lappa, yet the illegitimate extraction is going on and these herbs are fast dwindling. Steps should be taken to effectively stop such "malpractices" which can best be achieved by mobilisation of mass media.

Further, in order to restore the growth and multiplication of these taxa and ensure sustained supply of the raw material to the drug industry the vulnerable habitats must be immediately conserved on priority basis.

Also it is need of the hour to raise germplasm banks of these vanishing species. To achieve this noble goal, well protected areas in as natural a setting as possible must be made available. In Kashmir Himalayas, we already have five sanctuaries and nineteen biosphere reserves spread over an area of about 269.36 and 354.07 sq. kms respectively. These could be best utilised for the purpose. To make sure the success of the gene pool
reserves, purposeful action plans, adequately funded by the governmental / non-governmental agencies, need to be launched for each of these species. This will not only make their commercial cultivation a reality but also save them from extinction. The genetic improvement and rapid multiplication may be achieved through extensive breeding programmes and tissue culture technology.