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ACKNOWLEDGEMENTS. We thank J. C. Cahill and M. A. Watson for suggestions that greatly improved the manuscript.

Gamete selection and patterns of ovule and seed abortion

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Plants often produce many more ovules than can be matured into seeds. In many plants patterns of ovule and seed abortion within developing fruits are nonrandom. One common pattern involves a higher probability of seed set towards the stylar than towards the basal end of the fruit. Evidence is presented to support the argument that pollen competition and gamete selection play an important role in generating such a pattern.

ABORTION of ovules within an ovary is a common occurrence in flowering plants. Plants often produce a certain percentage of ovules that do not mature into seeds¹⁻⁶. The phenomenon of ovule abortion is important because of its effects on plant fitness and its role in the evolution of other reproductive traits^{7,8}.

Ovule abortion within developing fruits is not random^{2,3,9}. Four patterns of ovule abortion or seed set have been described among species. In the most commonly observed pattern, a greater percentage of ovule abortion occurs at the base of the fruit. This pattern of ovule abortion coincides with a reverse pattern of seed set and has been described in thirteen of the fourteen species of legumes examined by Bawa and Buckley³. In twelve of these thirteen species, ovules closest to the stylar end of the fruit were more likely to fully develop into seeds. The second pattern involves more abortions in the stylar end than in the middle or basal ends of the fruit. Marshall and Ellstrand¹⁰ observed this pattern in fruits and suggested that basal and middle seeds were being filled at the expense of seeds located in the stylar region. A similar seed set

pattern was observed for five tropical legumes by Wyatt¹¹. The third abortion pattern has been noted in the fruits of *Medicago sativa*, also a legume⁹. In this species, ovules at the even numbered positions share a higher probability of seed set than the ovules at odd numbered positions. The fourth type of pattern involves high abortion rates at both ends of the fruit¹². All of these ovule abortion patterns indicate that ovules in certain positions in the ovary are more likely to abort than others.

The factors involved in ovule abortion are often difficult to analyse because the effects of seed abortion are not easily separated from ovule abortion¹³. Bawa and Webb² defined seed abortion as the mortality of immature seeds between fertilization and seed maturation. Ovule abortion refers to ovule mortality prior to and following fertilization. These two terms are often used interchangeably and, as noted by Mikesell¹⁴, the term ovule abortion may be used to describe early aborted seeds. Not all authors distinguish between seed and ovule abortion because of the difficulties in determining the stage of development during abortion.

One plausible explanation for nonrandom patterns of ovule abortion is pollen competition and gamete selection. According to this explanation pollen tubes with the fastest growth rate are the first to enter ovary, and if the tubes enter the ovary from the stylar end, the stylar ovules will be fertilized first, the ovules in the middle of the ovary next, and the basal ovules last. The pollen competition hypothesis assumes that gametes from the fastest growing pollen tubes sire seeds that are

more viable than seeds produced from gametes with pollen tubes that have a slow rate of growth¹⁴⁻¹⁸. Thus, the stylar ovules apart from being the first to be fertilized, are also likely to receive superior gametes. As a result, such ovules should have a higher probability of success in maturing seeds than the basal ovules.

Although pollen competition hypothesis is intuitively appealing, patterns of seed development have not been often correlated with the sequence of ovule fertilization within the ovary. Here we report results of a study designed (i) to examine patterns of pollen tube growth and ovule fertilization and (ii) to compare the sequence of ovule fertilization with the position of seed abortion in *Sophora japonica* (Leguminosae). We discuss our results in relation to similar studies on other legumes¹⁹⁻²¹.

Ovule and seed abortion in *Sophora japonica*

Methods

S. japonica is a deciduous tree, which flowers in late July/early August. Originally from eastern Asia, *Sophora* was introduced to North America²² in the mid 1700s and is now planted as an ornamental. Four trees were sampled in this study; two of which were located in the Arnold Arboretum, Boston and two were situated along beach front property in Boston Harbor.

In order to study pollen-pistil interactions, approximately one hundred and fifty flowers (1-2 days old) were collected in July and August 1988, from proximal, medial and distal positions on branches. Each flower was dissected by removing all floral parts from around the pistil. Tissues were cleared for one hour in 4 N sodium hydroxide solution at 60°C. Following clearing, pistils were washed in distilled water. Pollen tubes were observed on the stigmatic surface, the style, through the transfusion tissue and in the micropyle of the ovules using Martin's technique²³. In order to determine the sequence of fertilization, the position of fertilized ovules in the ovary was recorded. An ovule with a pollen tube in the micropyle was considered to be fertilized. Ovules with pollen tubes located in close proximity to the micropyle were scored separately. The sequence of ovules in the ovary was scored by numbering first the ovules closest to the stylar end and continuing toward the peduncular end. Seventy-eight pistils were examined for pollen tube growth.

The percentage of ovule fertilization for each position was determined by dividing the number of fertilized ovules by the total number of ovules at that position for all the sampled flowers. Only fertilized ovules (ovules with a pollen tube in direct contact with the micropyle) were included. The frequency of ovule fertilization was then plotted for each ovule position

from the style to the basal region. Fertilization percentages of different ovule portions were compared.

One hundred and fifty fruits (fifty each from three stages of development) were collected in late August/early September and fixed using glacial acetic acid and ethyl alcohol (3:1) solution. The stages of development included early fruits (1.64±0.11 mm) with floral parts still attached, partially developed fruits (3.02±0.71 mm) which had lost all floral parts; and mature fruits in which some seeds were fully developed (6.54±2.33 mm). After each fruit was dissected longitudinally to maintain the original ovule sequence, the number and position of developing ovules were scored for each fruit. Ovule/seed positions were assigned as described previously.

The number of ovules per fruit in *S. japonica* ranged from seven to fifteen. In order to compare seed and ovule abortion rates among fruits having different ovule numbers, the number of ovules in each fruit was standardized according to the transformation formula described by Hossaert and Valero¹⁹: $P=11(E)/N$, where P =New ovule position, F =Former ovule position, N =Total number of ovules in ovary X .

All data on *Sophora* were converted to an average pod size of 11, the mean number of ovules per fruit. This transformation formula standardizes all ovule positions and allows a more accurate comparison between ovaries of unequal ovule number.

The percentage of seed development for each position in the pod was calculated by dividing the number of ovules at the developmental stage by the total number of ovules in that position. The frequency of ovule abortion was calculated for each position in the fruit for both middle and late fruits. The distribution of fully developed seeds for each ovule position was also examined in middle and late fruits.

In order to further examine positional trends in fertilization and ovule abortion, the data were reorganized into four classes with ovule positions assigned to each class (class I=positions 1, 2, 3; class II=4, 5, 6; class III=positions 7, 8, 9 and class IV=positions 10, 11). Frequency distributions for unfertilized ovules and mature seeds were recalculated using the new classification of ovule positions.

Results

Pollen tube growth. Seventy-eight fruits, approximately 50 per cent of the sample, were scored for pollen tubes. The remaining fruits could not be scored because of poor preparation of material, lack of pollen, lack of pollen tube growth, or because pollen tubes had not yet reached the ovary. Fewer than 25 per cent of the unscored fruits actually lacked pollen tubes. Fruits which lacked pollen tubes were typically early flowers in which pollen deposited on the stigma had not

germinated. The path of pollen tube growth was first observed at the stigma, where numerous pollen grains were aggregated. As pollen tubes travelled through the style, they decreased in number. Those that approached the micropyle, could be scored easily. The number of pollen tubes in contact with ovules varied among the flowers (Figure 1). Most fruits had a range of 1–12 and average of 5.2 pollen tubes in contact with ovules. Five per cent of the ovules had only one pollen tube in contact with the ovule. All of these single pollen tubes contacted only the first ovule. In most of the fruits examined, pollen tubes had progressed to the midpoint of the ovary. Each fertilized ovule had only one pollen tube in the micropyle. In some instances, an additional pollen tube was located in close proximity to a fertilized ovule.

The fertilized ovules displayed a nonrandom distribution (Figure 2). The frequency of ovules contacted by pollen tubes decreased from the stylar end toward the basal region. Ovules in the first position had a higher fertilization rate (80%) compared to ovules in position 11 which had the lowest rate of fertilization (12%). This distribution pattern was also observed when the original data were reclassified.

Figure 3 summarizes the distribution of unfertilized ovules (ovules not contacted by pollen tubes) in each of the four position classes. The frequency of unfertilized ovules was highest in class IV, the last quarter, and was lowest for ovules located in the first quarter of the fruit. These distribution patterns indicate

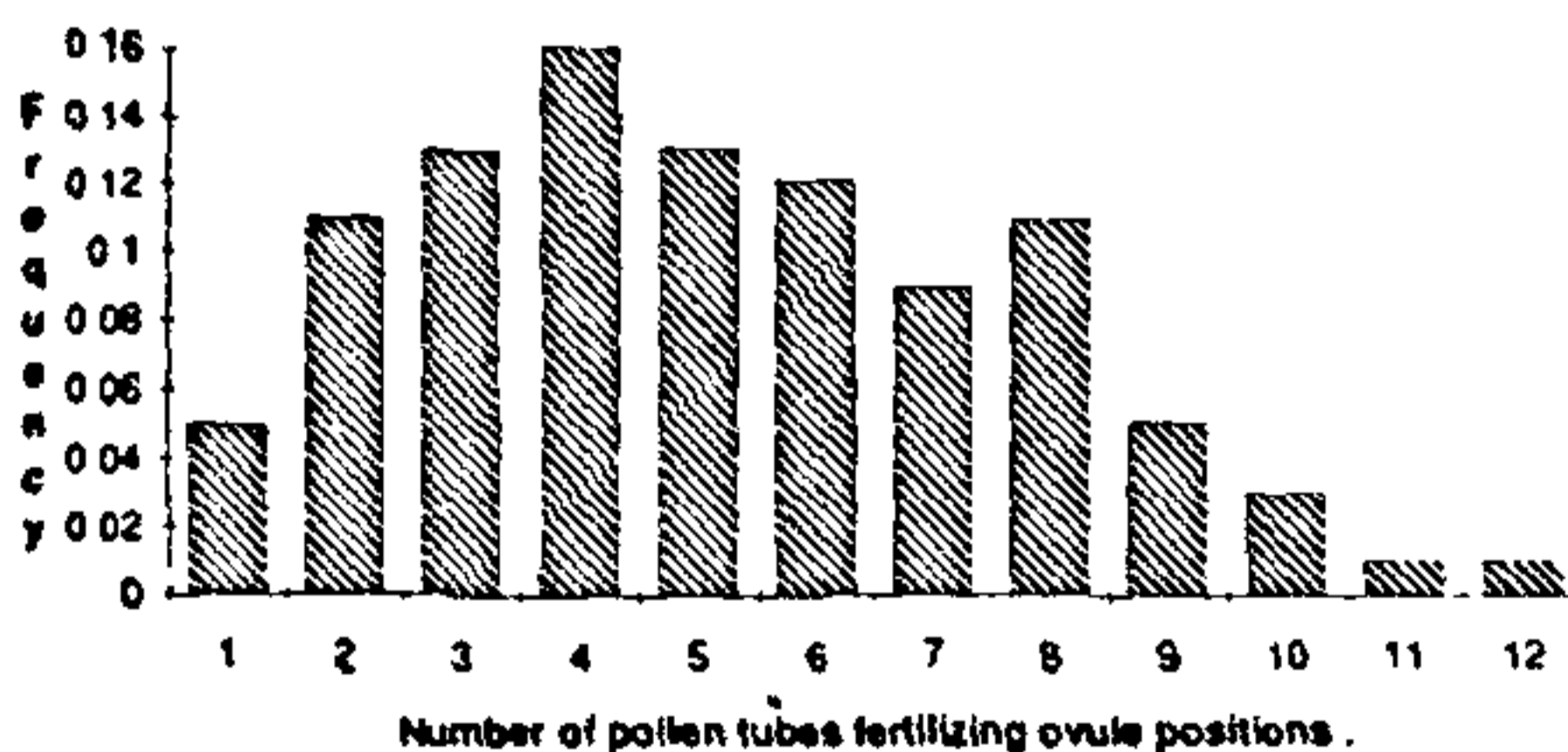


Figure 1. Frequency of flowers with specified number of pollen tubes.

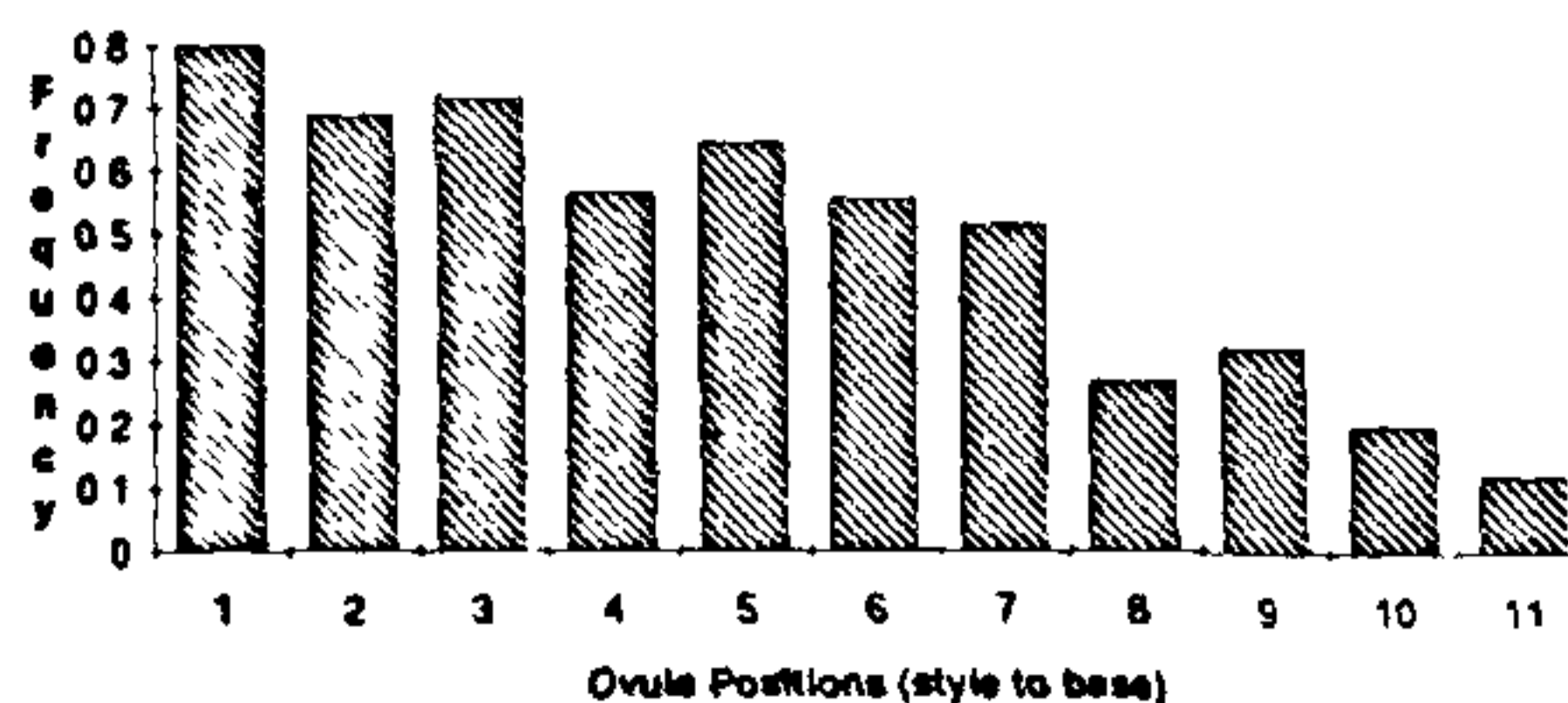


Figure 2. Frequency distribution of pollen tubes at different ovule positions.



Figure 3. Frequency of ovules not contacted by pollen tubes (ovule positions reclassified into four segments).

that pollen tubes fertilize ovules located at the stylar end first. In a few fruits, pollen tubes appeared to bypass one or two ovules. These apparently unfertilized ovules may have been contacted by pollen tubes which did not fluoresce.

Ovule abortion. Although ovule abortion was not detected in any early fruit, both mid-developed and late-developed fruits contained aborted ovules. The overall number of ovules in all fruits ranged from 7 to 15 with a mean of 11. The majority of fruits (83%) had 10–13 ovules. In both mid-developed fruits and late-developed fruits, the distribution of aborted ovules was not random. Mid-developed fruits showed an increase in frequency of ovule abortion from stylar to basal end. The frequency of ovule abortion for ovules in position 1 was 69% compared to 94% in position 11. Positions 9, 10 and 11 had the highest ovule abortion rates 85%, 81% and 94% respectively. Even though the first quarter of the ovary had low abortion frequency, ovule position one had a higher frequency rate than positions three and six.

Although the trend of increasing ovule abortion rate toward the basal region was apparent in the mid-developed fruits, data from the late developed fruits (Figure 4) illustrate this positional effect more clearly. Figure 4 also demonstrates an increase in the number of aborted ovules in position one (84%), compared to

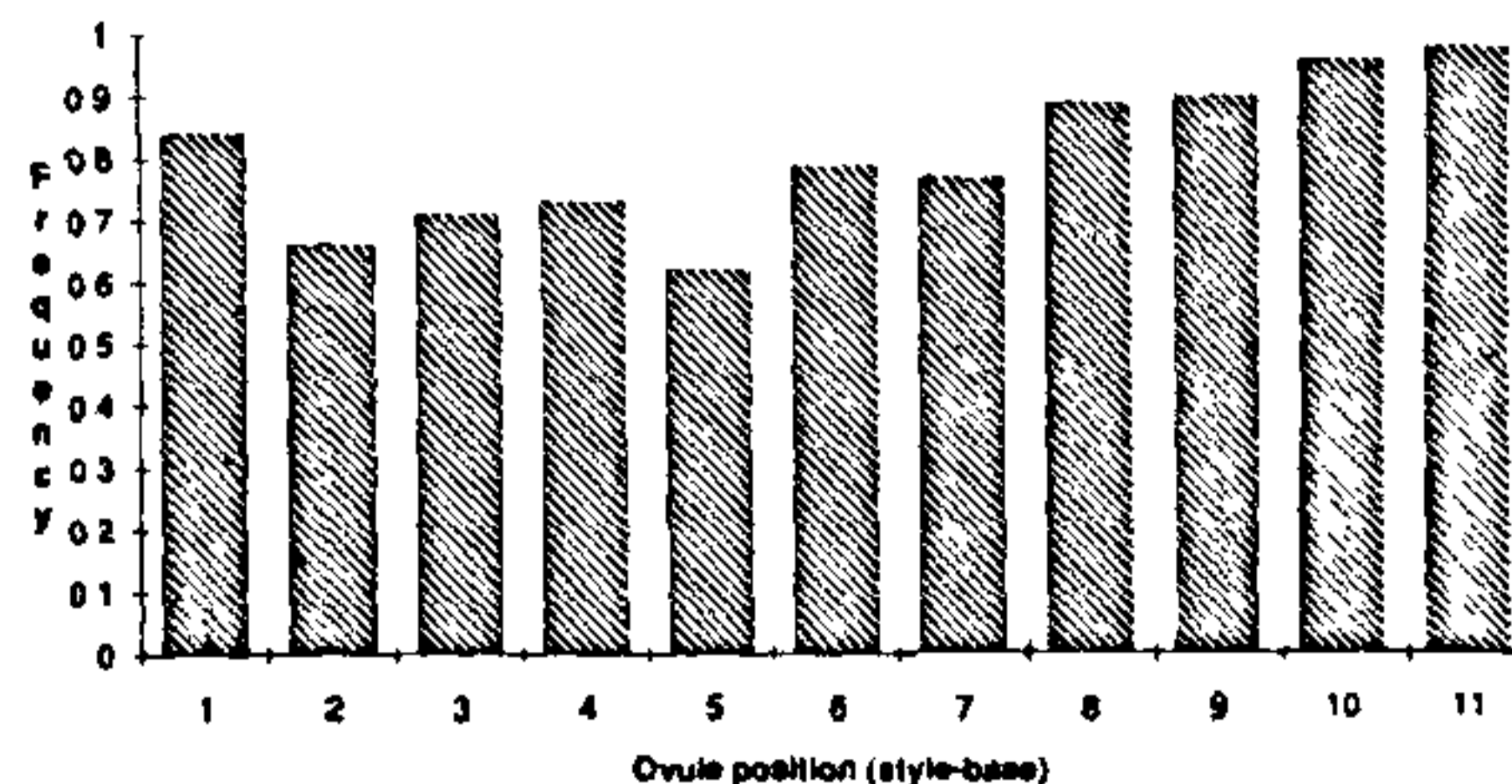


Figure 4. Ovule abortion rates at different ovule positions within late developed fruits.

position 2 (66%) and position 3 (71%). In general, there is an increase in the number of aborted ovules as the position of the ovule increases. Positions 9–12 had the highest ovule abortion rates. It was easier to distinguish between ovules and seeds in late fruits compared to mid-developed fruits because of the greater variation in seed size and shape.

Seed development. Although ovaries contain between 7 and 15 ovules, only an average of 2.3 ovules develop to maturity in late fruits. The number of seeds per fruit ranges from 1 to 6 with 86% of the fruits containing between 1 and 3 seeds (Figure 5). Nonrandom patterns of mature seed development were present in both middle and late fruits. In the mid-developed fruits, there was a general decrease in the number of mature seeds present as the ovule position increased. Two exceptions to this trend were the ovules located in positions 3 and 6. Ovules in both of these positions had higher seed development rates than ovules in the first position. There was also a general decrease in the number of mature seeds toward the lower half of the ovary in late fruits (Figure 6). However, fewer mature seeds were present in the first ovule position compared to ovule positions 2–6. This pattern was also apparent when ovule position data were regrouped into four major classes (Figure 7). The frequency of mature seeds was highest for ovules in class II and then steadily decreased for classes III and IV. The high number of seed

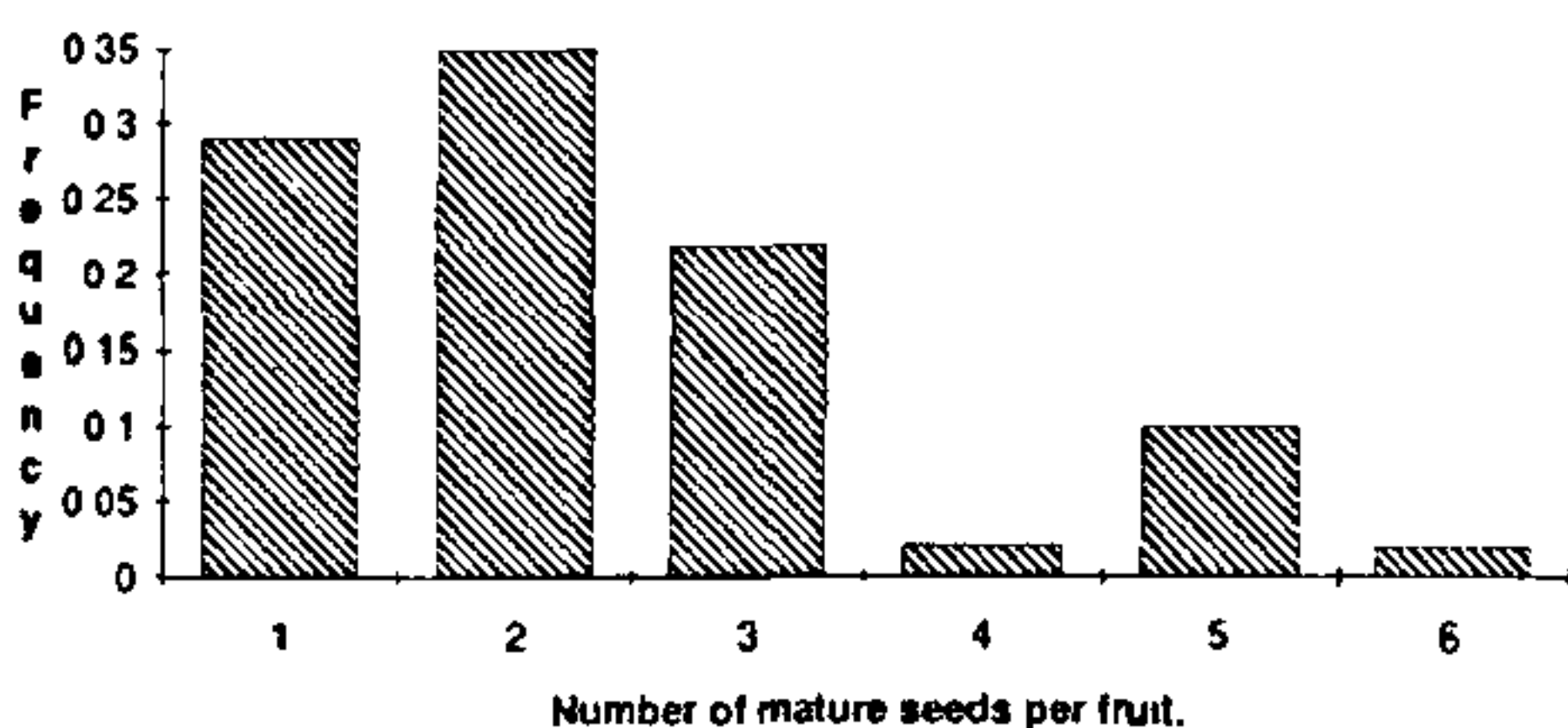


Figure 5. Variation in mature seed number in late developed fruits.

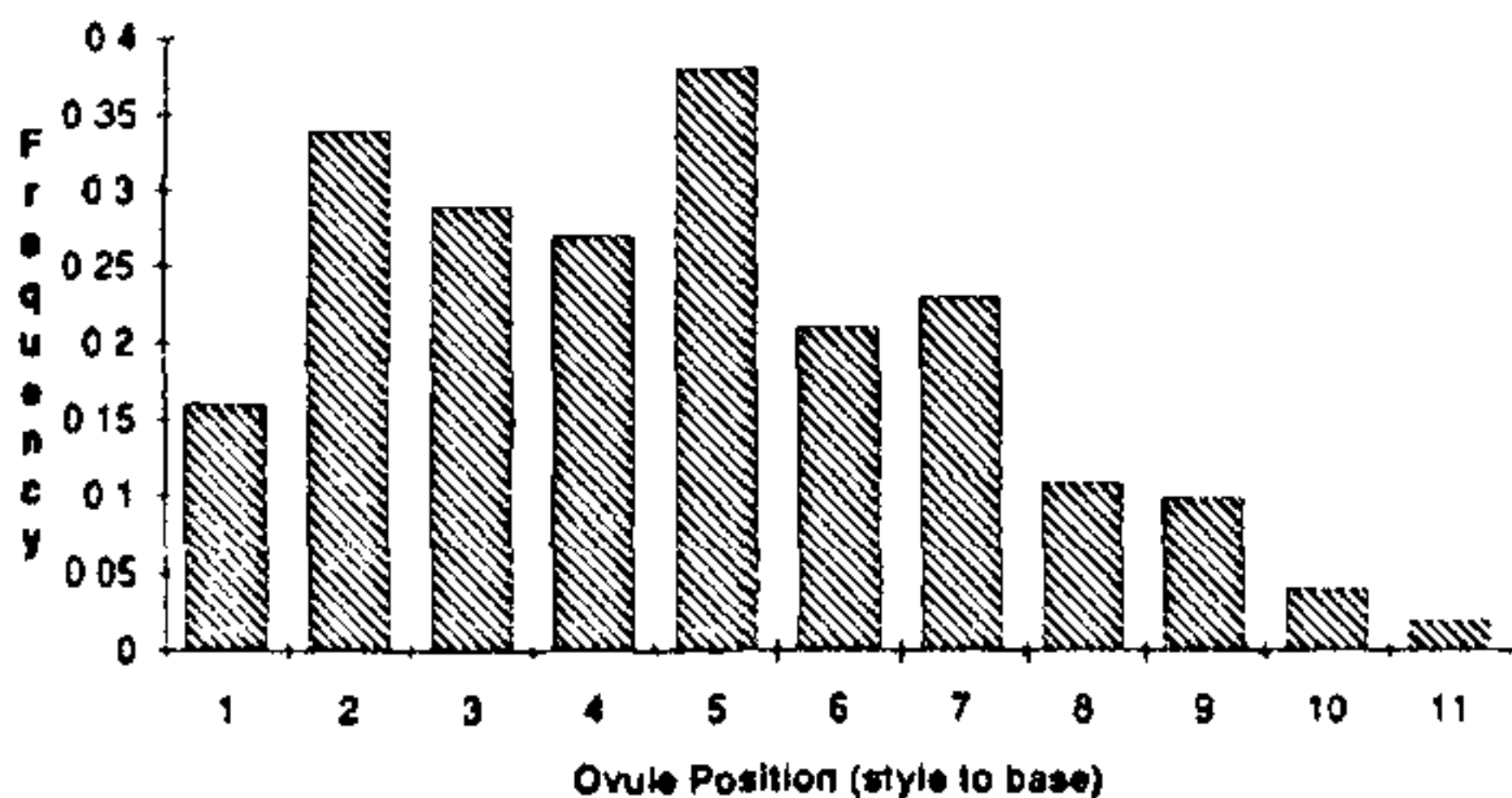


Figure 6. Probability of seed development at different positions in late fruits.

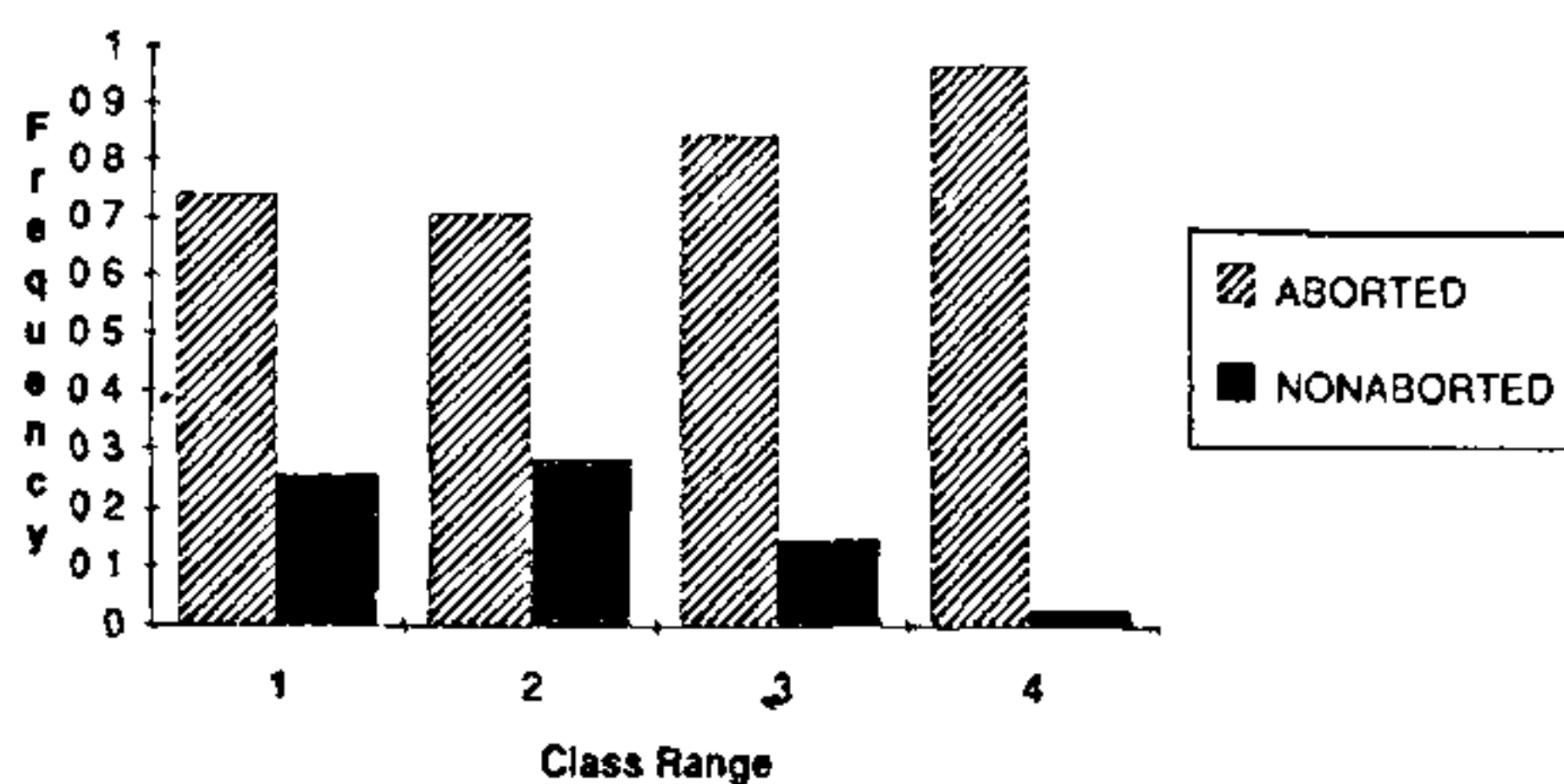


Figure 7. Variation in development (aborted versus nonaborted) for ovules classified into four position classes.

abortion in class I reflected the increase in ovule abortions at position one.

Discussion

The discussion below is confined to possible factors responsible for nonrandom patterns of abortion. The causes of abortion *per se* are not considered. There are many explanations for ovule and seed abortion, which have been recently reviewed by a number of investigators^{2-7,17-26}.

The average number of seeds (2.3) in fruit was less than the average number of ovules¹¹ per flower, thus indicating a high abortion rate in *S. japonica*. Specifically, the frequency of ovule abortion was 33% in young fruits and 24% in mature fruits. Apparently, many young fruits with a low number of maturing seeds are aborted. Ovules categorized as aborted did not develop into fully mature seed. These ovules may not have been fertilized or were aborted after fertilization.

The pattern of ovule abortion was nonrandom within fruits; the probability of an ovule aborting within an ovary increased from the style to basal end. This pattern was more evident in late developed fruits because size differences between aborted and nonaborted ovules were easier to distinguish in late fruits compared to mid-developed fruits. The exception to this pattern was the high incidence (84%) of ovule abortion in position one. There was also a general decrease in the number of mature seeds from the style toward the base of the fruit. Again, this pattern was more apparent in late developed fruits compared to mid-developed fruits. When ovule position was reclassified into four groups, seed set was highest in the second quarter of the ovary. As noted previously, this was due to the low probability of seed development in position one.

The gamete selection hypothesis suggests that ovules located near the point of pollen tube entry will be fertilized by the fastest growing pollen tubes. This fertilization pattern was observed in ovaries. Once pollen tubes enter the ovary, they pass

through the transfusion tissue and then fertilize ovules in the stylar end of the ovary first. As they grow toward the base of the ovary, the pollen tubes sequentially fertilize the remaining ovules. This was indicated by the high percentage (80%) of ovule fertilization in the stylar end of the ovary and the low frequency (12%) of fertilized ovules in the basal region. Occasionally, the bundle of pollen tubes bypassed one or two ovules along their growth pathway. We assume that these ovules remained unfertilized. Thus the fastest growing pollen tubes were able to access stylar ovules prior to slower growing pollen tubes.

This pattern of increased fertilization of ovules in the stylar region has been noted in several studies. For example, in alfalfa plants, although pollen tube growth was evident in the stylar and medial positions, it did not continue into the basal region¹⁰. In *Phaseolus coccineus* the stylar ovules are among the first to be fertilized and set seeds with a higher probability than basal ovules^{20,21}. A similar pattern has been observed in another legume, *Cassia fasciculata*^{27,28}. However, in *Lathyrus* ovules in the middle rather than the stylar end are the first to be fertilized and set seeds more often than either the stylar or the basal ovules.

In species other than legumes, patterns of fertilization and ovule abortion similar to *S. japonica* or *P. coccineus* have been noted in the common Zucchini, *Cucurbita pepo*²⁹. A greater percentage of ovules toward the stylar end were fertilized in the wild radish³⁰. However, in another cross, faster pollen tubes bypassed stylar ovules and fertilized basal ovules first, and the stylar ovules were then fertilized by the slower growing pollen tubes. Other studies have observed a fertilization pattern in which the ovules located near the point of pollen tube entry were not the first to be fertilized by pollen tubes. In wild radish, Marshall and Ellstrand³¹ noted that pollen donors differed in their ability to fertilize seeds. Two of the three pollen donors fertilized the highest proportion of seeds in the stylar end of the fruit. The third pollen donor fertilized the largest proportion of ovules in the middle region. All three of the donors fertilized the lowest proportion of seeds in the basal end. Mazer, Snow and Stanton³² examined pollen tube growth during two different time periods. Ten hours after pollination, 33% of the basal ovules were fertilized, 49% of the middle ovules and 35% of the stylar ovules. Forty-eight hours after pollination, pollen tubes had fertilized 63% of the basal ovules, 67% of the middle ovules and 63% of the ovules in the stylar position. After ten hours, the position of the ovules in the ovary significantly influenced the probability of fertilization. Ovules located in the middle of the ovary had the greatest chance of being fertilized. This influence was not apparent after a certain period of time. The fertilization of ovules in the middle region could not be explained

completely. It was hypothesized that ovules in this position may have emitted stronger chemicals which signalled their receptiveness to pollen tubes and early fertilization.

The gamete selection also suggests that a sequential pattern of ovule fertilization will produce a gradient of embryo quality in the ovary. Specifically, the gradient would range from the high quality stylar embryos sired by microgametophytes of superior genetic quality to low quality offspring sired by slower growing pollen tubes of inferior quality. Thus this prediction assumes that gametophytic qualities will be selected in the sporophytic generation. However, few studies have explored the relationship between the pattern of ovule fertilization and embryo quality. Seeds from stylar embryo have been shown to outperform other seeds in *P. coccineus*^{20,21} and *C. pepo*²⁹.

Although the high probability of seed set of ovules closer to the style may be attributed to gamete selection, the low probability of seed set at basal positions may be due to other causes. In *Kleinhovia hospita* reduced seed set was due to stylar plugging³³. Early fertilized ovules inhibited the growth of additional pollen tubes by secreting IAA into the style. Thus the pattern of ovule abortion is influenced by the lack of ovule fertilization. The lack of fertilization is not due to a shortage of pollen tubes but rather to the release of the inhibitor. In other species, not all ovules have been found to contain mature gametophytes at the time of pollination and the pollination process itself may promote³⁴ or inhibit maturation.

In short, there is now substantial evidence that sequence of fertilization, which itself is a function of gamete competition, plays a major role in generating nonrandom patterns of ovule abortion. This is particularly true for species in which the probability of abortion increases from the stylar to the basal end. In species with other patterns of ovule abortion, the point of pollen tube entry into the ovary and sequence of fertilization is generally not known. Such species will have to be examined before the process explored here can be assumed to have a general applicability.

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Pollination biology of Apiaceae

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Members of the family Apiaceae exhibit diverse breeding systems ranging from completely selfed to obligately outcrossed. While the former is accomplished by the dehiscence of anthers above the stigma of the same flower, the latter is brought about through structural dioecy and gynodioecy. Majority of the species of Apiaceae are monomorphic and are either hermaphrodite or andromonoecious. In this article we review briefly the various strategies adopted by the members of Apiaceae to promote cross pollination by insects.

ALL members of Apiaceae have simple or compound umbel, and reproduce sexually. Despite uniformity in structure of inflorescence and flower, they exhibit diverse breeding systems, probably because of the wide variation in the mode of pollination. A whole range of pollination systems, varying from completely self- to obligate cross-pollination occur within the family.

Obligate outcrossing in umbellifers is imposed by structural dioecy and gynodioecy¹⁻³. The dioecious species, e.g. *Aciphylla* and *Anisotome* bear male and female flowers on separate plants. In the gynodioecious taxa, e.g. *Gingidia*, *Scandia* and *Lignocarpa*, some plants carry female and others hermaphrodite flowers.

Taxa such as *Scandix pecten-veneris* which are completely self-pollinated represent the other extreme. Self-pollination is accomplished by dehiscence of anthers immediately above the stigma of the same flower⁴. That, such species are strictly autogamous is confirmed by the fact that the percentage seed set in bagged flowers is nearly equal to the control.

A few obligate self- or cross-pollinating taxa notwithstanding, majority of umbellifers exhibit a blend of self- and cross-pollination. All such species are monomorphic but are either hermaphrodite or andromonoecious. In the former all flowers are bisexual whereas in the latter some flowers are staminate and others bisexual. Proportion of the two types varies in umbels of different orders of an individual (Table 1). The male flowers in andromonoecious species produce pollen of which only a small part is used in pollinating hermaphrodite flowers, the rest is used as reward to pollinators visiting the flower.

The monomorphic species employ different contrivances for promoting cross-pollination such as dichogamy. Umbellifers exhibit protogynous and protandrous type of dichogamy. The Himalayan species follow protandrous dichogamy. In this type, insects get dusted with pollen during the first phase of flowering and in the second, the stigmas are exposed for getting dusted in return. This alternation leads to cross-pollination. The magnitude of cross-pollination is determined by degree of protandry (Table 2, Figure 1).

In the strongly protandrous taxa, the male phase lasts in an umbel till the flowers continue to open. Once the opening of flowers is completed, the female phase begins abruptly in all flowers of the umbel⁵⁻⁷. In the weakly protandrous forms, namely *Torilis arvensis*, dehiscence of anthers of the inner flowers and receptivity of the stigmas of outer flowers within the umbel overlap leading to geitonogamy⁸.

The phenological events in an individual are