Some Observations on Pollination and Compatibility in *Magnolia*

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The hypothesis that beetles were the pollinators of the earliest angiosperms was put forward by Diels in 1916. Grant (15) presented additional evidence for the primitiveness of beetle pollination and this view has recently been supported by Leppik (19), van der Pijl (26) and Eames (1961). *Magnolia* has not been the subject of detailed studies of its pollination since the time of Delpino (11) and his observations were made in Europe where no species of the genus occur naturally. Although Indiana is hardly the logical place to study pollination in *Magnolia* since only two species occur naturally in the state and these are quite rare, several species are cultivated in Bloomington and these afforded an excellent opportunity for some observations.

Magnolia tripetala L., a native of the southeastern United States, reaches its northernmost limit in southern Pennsylvania, Ohio and Indiana (10). Four trees are grown on the Campus of Indiana University. In 1961 the first flowers opened on May 8 and the trees continued flowering until June 10. A second burst of flowering occurred on one tree from June 28 to July 8. In 1962 the plants bloomed from May 2 to May 25. The flowers of *M. tripetala* have white petals, 10 to 15 cm. in length and a rather heavy odor which is frequently described as unpleasant. The flowers on first opening are trumpet shaped and the petals gradually spread so that on the second or third day after opening the flower becomes cup-shaped and finally saucer-shaped. The flowers are strongly protogynous and the stigmas, as determined by actual pollination tests, are normally receptive for a few hours to one day after the petals open. The stigmas then become appressed (Fig. 1) to the gynoecium as the petals open and the pollen begins to shed. The stamens are tardily dehiscent and fall to the base of the flower where they remain until the petals fall. So far as could be determined from observation no nectar-like secretions are produced on either the petals or gynoecium.

In 1961, it was observed that from May 8 to May 24 the stigmas of the flower were receptive only in the bud and that upon anthesis the stigmas were already appressed to the gynoecium. During this period no flowers produced fruits. The failure of normal "timing" of the flowers during this period may have been due to the exceptionally cool weather that prevailed in Indiana during the late spring of this year.

Daily visits were made to the flowers in 1961. No insects other than a few fungus gnats were observed before May 19. Flowers marked during the period from May 8 through May 17 did not set fruit. From only a small number of flowers contained beetles and never more than May 19 on a few beetles were found on the flowers, but at a given time

1. Several people have aided me in various ways in this study, and particular thanks are due Mrs. Zoe Chandik and Mr. Alvin Reeves.

two were observed on a single flower. Four flowers containing beetles on May 25 were tagged and later observed to set good fruits. Honeybees *(Apis mellifera)* were observed visiting the flowers on three occasions, and the two which were captured were found to have an abundance of *Magnolia* pollen on their bodies. It seems, unlikely, however, that bees could serve as important pollinators of this species, for they were observed to visit only fully opened flowers at which time the stigmas are not receptive. One trip was made to a natural stand of *M. tripetala* in Crawford County, Indiana and beetles were collected in two of the four flowers which were accessible.

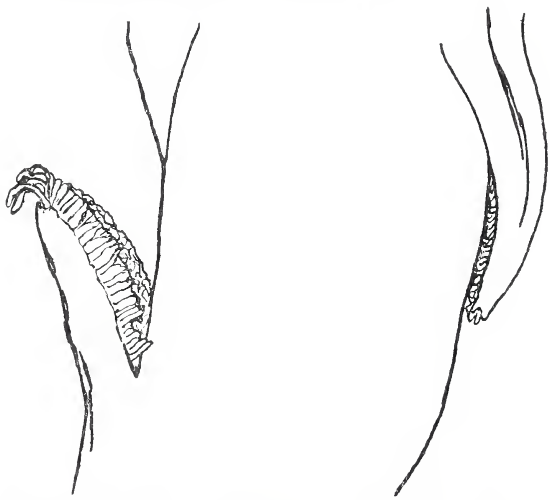

Figure 1. Stigma of *Magnolia virginica* before pollination (left) and after pollination (right) (X5.)

The following beetles were collected: Byturidae. *Byturus unicolor* Say; Coccinellidae, *Ceratomegilla maculata* De G.; Colletidae, Curulioidae, *Glyptobaris rugicollis* Lec.; Dermestidae, *Anthrenus vervasci* (L); Mylabridae, *Gibbobruchus mimus* (Say); Nitidulidae, *Carpophilus Lugibris* Morr., *Carpophilus sp., Epuraea sp.;* Staphylinidae, *Aleochara sp.* In addition to the bees, previously mentioned, a few small flies (Chloropidae, Sciaridae) were found in the flowers.[2]

Although the investigation is rather limited, it nevertheless seems reasonable to infer that *M. tripetala* is primarily, if not entirely, pollinated by beetles. Although perhaps no one beetle should be regarded as more important than the others, *Epuraea* was observed more than other species and it was found on both stigmas and stamens and was captured both at Bloomington and in Crawford County.

2. The preliminary identification of the insects for this study were made by Dr. David Wooldridge, and the insects were then sent to the Insect Identification Branch of the United States Department of Agriculture for verification or correction by Dr. W. H. Anderson and his staff. Their help is gratefully acknowledged. The insects are deposited in the entomological collections at Indiana University and voucher specimens of the plants in the herbarium of Indiana University.

Magnolia grandiflora L., which is native near the coast from South Carolina to Texas, has served as the chief example of beetle pollination in the Magnoliaciae. Delpino (11) reported that this species was pollinated by *Cetonia*, and this report has been widely cited, notwithstanding the fact that the study was made in Europe and that *Cetonia* is not known in North America. The flowers of *M. grandiflora* are white, quite large, cup-shaped and pleasantly odorous. The stigmas are receptive when the flower opens and drops of a nectar-like substance can be seen between the stigmas (11). After a few hours to one day the three inner petals, or rarely all the petals, close. The flower again opens on the following day, the anthers dehisce, and the readily deciduous stamens fall on the petals where they are visited by pollen gathering insects. The stigmas do not become appressed as in *M. tripetala* and it is conceivable that the stigmas could be pollinated with pollen from the same flower. Since all attempts at both self- and cross-pollination failed in this species, more specific information on this point is presently unavailable.

Insects were collected on trees cultivated in Bedford and Bloomington, Ind., Longwood Gardens, Pa., and Washington, D. C. during June and July of 1961, from flowers sent from Williamsburg, Ky. by Willard Yates, and in natural stands in Florida by Mrs. Zoe Chandik in May, 1962. Ten different beetles from six families were represented: Cantharidae, *Chauliognathus marginatus* Fab.; Dermestidae, *Anthrenus flavipes* Lec., *A. verbasci* (L.); Mordellidae, *Tomoxia sp.*; Nitidulidae, *Conotelus obscurus* Er.; Scarabeidae, *Macrodactylus subspinosus* (Fab.), *Trichiotinus bibens* (Fan.), *T. piger* (Fab.), *Popillia japonica* Newman; Staphylinideae.

Although large scarab beetles are found on this species, it again appears that the small beetles may be the more important pollinators. In Washington over 100 flowers on 15 trees were examined from June 23-25 and *Conotelus* was found in one-third of the flowers and was observed both on the gynoecium and the fallen stamens. In addition to *Conotelus*, the other beetles frequently observed on flowers in Bloomington were *Trichiotinus piger* and *Tomoxia*. The former belongs to the same family as *Cetonia* and behaves in the manner described by Delpino (11) for that species. Two specimens of *T. piger* were collected in natural stands of *M. grandiflora* in Florida and are recorded as pollinators of *Magnolia* in that state by Blatchley (5). The most frequently collected insect in Florida was an unidentified staphylinid which was not found in the collections from other areas. Honeybees, one carpenter bee, and flies (Syphidae, *Mesograpta marginata* (Say), *Metasyrphus, sp.*) were also taken. Honeybees are common visitors and it seems quite probable that they would have no difficulty in effecting pollination in this speices.

Magnolia virginiana L., another species of the southeastern United States extending as far north as Massachusetts, is cultivated in Indiana to a limited extent. The small white flower of *M. virginiana* is extremely fragrant. Its odor can be detected up to three fourths of a mile according to Peter Kalm (18). The flower buds open in the late afternoon, at which time the stigmas are receptive, and are closed by the next morning and remain closed for several hours. On the reopening the pollen is shed and the stamens fall onto the petals where the pollen is collected by insects. The stigma, although not becoming appressed to the gynoecium, is receptive only in the first stage so that this flower is protogynous.

At Bloomington from late May to mid July the following insects were collected on flowers of nine different plants: Coleoptera: Andremidae; Chrysomelidae, *Diabrotica undecimpunctata bowardii* Barber, *Metasyrphus sp.*; Coccinellidae, *Ceratomigilla Maculata* DeG; Mordellidae, *Mordellistema* sp.; Mylabridae, *Gibbrobruchus mimus* (Say); Nitidulidae; *Epuraea erichsoni* Reitter, *Gleschrochilus sp.*, *Pocadius belvolus* Er., *Stelidota geminata* (Say); Xylocopidae, *Xylocopa sp.* Diptera: Sphaeroceridae, Syrphidae, *Metasyrphus sp.;* Hemiptera: Anthocoridae; Hymenoptera: Andrenidae; Apidae, *Apis mellifera* L., *Bombus impatiens* Cr.; Lepidoptera. The two species of *Epuraea* and *Gibbrobruchus mimus* were the most frequently observed.

One of the plants studied was growing in the yard of Dr. B. A. Spencer and in the same yard 25 feet away grew a small tree of *M. grandiflora.* As can be seen from the lists of insects collected, the flowers of the two trees had almost completely different faunas.

At Longwood Gardens, Pa. individual flowers of this species were found containing as many as eight rose-chafers, *Macrodactylus subspinosus* (Fab.). Considerable damage to the petals was observed for which it may be assumed the rose-chafers were responsible. Riley (23) has previously referred to this species being found on *M. virginica.* In Georgia Mrs. Chandik collected on two plants occurring in natural stands and only staphylinids were found.

Flowers of *Magnolia macrophylla* Michx. were sent to the writer by Willard Yates, from Kentucky, which is in the natural range of this species, and they were found to contain *Trichiotinus bibens*, *Macrodoctylus subspinosus*, and *Epuraea sp.* Mrs. Chandik collected from one tree of this species in Kentucky and beetles of the families Cerambycidae, Chrysomelidae, and Curculionidae were present in the flowers.

Cross- and self-pollinations were attempted with *M. tripetala*, *M. grandiflora* and *M. virginiana* in Bloomington. Flowers which were to serve as male and female parents were covered with glacine bags prior to opening and following pollination the flowers used as the pistillate parents were rebagged for several days. All pollinations on *M. grandiflora* were unsuccessful. Self-pollination of the flower with its own pollen was found to be impossible in *M. tripetala* and *M. virginica.* Selfs were obtained, however, on three plants of these two species by using different flowers on the same plant as a source of pollen. These selfed-fruits were found to produce the same number of seeds found in open pollinated fruits of the same plants. In these two species it was found that emasculated flowers which were not pollinated failed to set fruit, and although the possibility of pseudogamous apomixis cannot yet be ruled out, it would appear that these species are self-compatible. The possibility that *M. grandiflora* is self-compatible also exists since isolated trees of this species are known to produce fruits with seeds.

Discussion

That *Magnolia* is primarily a beetle flower is substantiated by the observations on four species of *Magnolia*. Although no one beetle can be singled out as the principal pollinator, nitidulid beetles, in particular, and perhaps scarab beetles for *M. grandiflora* and *M. macrophylla*, are important pollinators. The pollen of all four species is readily accessible as is true of most beetle flowers. Visits to the gynoecium are rewarded by "nectar" in *M. grandiflora*, but no such substance appears present in *M. tripetala* and *M. virginiana*. The papillae of the stigmas bears a resemblance to the food-bodies (9) of certain beetle flowers, however, and although there is no evidence that they are eaten, they provide a possible explanation of the visits to the gynoecium. Delpino (11) suggested that *M. Yulan* was a pit-fall flowers for bees, although this was doubted by Dauman (9). It appears that the closing of the flower in *M. virginiana*, however, could serve as a temporary trap for beetles.

It has sometimes been assumed that since *Magnolia* flowers are dichomagous, cross-pollination is assured. Werth (27), for example, states that since in the first stage only the pistils are receptive, self-pollination is impossible, and that beetles, flying from flower to flower, cross-pollinate them. This is not necessarily true since beetles may fly from flower to flower on the same plant bringing about self-pollination. Dichomgamy does not necessarily lead to cross-pollination as is well known (8, 25).

Experimental evidence has been presented to show that selfing is possible in two species of Magnolia[3]. The question may be raised as to whether the first angiosperms, which are generally agreed to have been beetle flowers, were not also self-compatible. Although there is no evidence that the *Magnolias* were the first angiosperms, there is little question that they are primitive. As has been pointed out, however, by Canright (6) *Magnolia* has a number of advanced features. Obviously their compatibility could have changed since their origin. Whitehouse has written (28) that "if the original angiosperms had all possessed multiple-alleomorph incompatibility, then species which subsequently lost it would be expected to evolve more slowly and hence to show a greater range of ancestral characters than those species which retained it." This explanation could account for the primitive features of *Magnolia* and certain other angiosperms, but on the other hand the possibility that self-compatibility is a primitive feature that has been retained by certain groups deserves consideration.

Lewis (20), Stebbins (24) and Grant (15) have presented considerable evidence to show that self-compatible angiosperms are derived from self-incompatible ones, and the change is generally regarded as nearly irreversible. There can be little arguments with the examples that these authors have presented, but it does not necessarily deny the possibility

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3. Successful selfs were also obtained in *Michelia champaca* L., another member of the Magnoliaceae by crossing different flowers on the same plant. Carpenter and Guard (1950) however, secured only a very small number of seeds in selfs of *Liriodendron tulipifera* L., another magnoliaceous species.

that the earliest angiosperms were self-compatible. For example, Lewis and Crowe (21) state that they agree with Whitehouse that self-incompatibility has been established in the angiosperms *almost* from the time of their origin (italics mine). Fryxell, however (14), goes so far as to say, "Cross-fertilization is the 'normal' pattern of reproduction in most of the biological world, in the sense that it is the primitive, ancestral pattern."

It may have been advantageous for the first angiosperms, whether they were trees or herbs, to have been self-compatible, for many of the same reasons which have been postulated for the occurrance of self-fertilization as a derived condition in angiosperms today. Stebbins (24), for example, suggests that self-fertilization is an advantage where conditions are unfavorable for crossing. When the first angiosperms appeared, although they may have come from beetle pollinated ancestors, their pollination could have involved a considerable element of chance. Moreover, would seem more likely for the beetles to have moved from flower to flower on the same plant more frequently than from plant to plant. (This, of course, involves the assumption that the first angiosperms had more than one flower per plant.) Stebbins also points out that self-fertilization is an advantage for the colonization of new habitats in that it allows a few plants to rapidly build up a large colony of fit individuals, and Baker (2) has pointed out that self-compatibility is an advantage in long distance dispersal in that a single migrule can establish a colony. These advantages could have been especially important to the new angiosperms in allowing them to build up large colonies and spread widely.

Grant (16), following a discussion of the strong evidence that the change from open to restricted types of recombination systems are rare, writes, "There is also evidence for the view that recombination systems may become opened up during evolution. The earliest angiosperms were probably plants of the colonizing type. They existed as subordinate elements in Mesozoic forests until a series of climatic and biological changes opened up new habitats for which they were pre-adapted, whereupon they rapidly rose to dominance. These developments suggests a restricted recombination system in the early stages of angiosperm evolution." Self-pollination obviously would provide such a system of recombination.

Whitehouse (28) credits the abrupt world dominance of the angiosperms to the acquisition of multiple-alleomorphic incompatibility. Whether or not the rise to dominance was rapid (1), there can be little denying that this position was eventually achieved by securing favorable methods for outcrossing and certainly multiple-alleomorph incompatibility would provide an ideal method. Baker (3) recently has suggested that speciation would be relatively rapid after a change in the breeding system which might explain the successful adaptive radiation of the early angiosperms.

However, the change to self-incompatibility may not have occurred as one of the first steps in their evolution. The earliest flowers may have been homogamous (or synocomous, 25), such as is seen in *Paeonia* and certain members of the Ranunculaceae today (22), and self-compatible. In such types, however, some outcrossing can take place. An early development tending to promote more outcrossing may have been dichomogany. The question may be asked, however, whether or not the first angiosperms were already dichomoganous, this feature having been inherited from their progenitors. Obviously a definite answer can not be supplied, but one line of evidence suggests otherwise, for some angiosperms are protogynous and others are protandrous. Within the genus *Magnolia* where protogyny prevails, one species, *M. Delavazi* Franchet, (17) is protandrous. Dioecism also arose early in angiosperm evolution, if we can accept as evidence its occurrence in many members of the Magnoliales and Ranales. As Whitehouse (28) points out, however, dioecism is an expensive means of securing outcrossing since half of the population will not produce seed. Various types of incompatibility then later developed, perhaps independently in different lines (4). That multiple-alleomorph incompatibility comes late is suggested to me at least by the fact that some species which are dichogamous are also self-incompatible. In other words, a highly efficient method of outcrossing developed on top of a relatively inefficient method. As has been mentioned above, some self-incompatible types have since reverted to self-compatibility.

Grant (15) calls attention to the desirability of investigating the floral ecology of other primitive angiosperms. "Are the flowers of Winteraceae, *Degenaria* . . . . pollinated by beetles?" At the same time it would be interesting to learn if these primitive angiosperms are self-compatible or self-incompatible as well as to extend the observations on the Magnoliaceae.

Summary

Beetle pollination is thought to be primitive in angiosperms. *Magnolia* is generally considered a "beetle flower" but no detailed studies have been made on the genus since the time of Delpino (11) whose observations were made in Europe where no species occur naturally. Observations made on *M. grandiflora*, *M. macrophylla*, *M. tripetala* and *M. virginica* indicate that beetles are the most common visitors to the flowers. Successful selfs on *M. tripetala* and *M. virginiana* were secured by crossing different flowers on the same plant. It is pointed out that self-compatibility may have been the original condition in the angiosperms and possible advantages of a system of self-pollination, which does not exclude outcrossing, are presented.

Literature Cited

1. AXELROD, D. I. 1952. A theory of Angiosperm evolution. Evolution **6**:29-60.
2. BAKER, H. G. 1955. Self-compatibility and establishment after "long distance" dispersal. Evolution **9**:347-348.
3. ———. 1961. Rapid speciation in relation to changes in the breeding system of plants. Recent Advances in Botany **1**:881-885. University of Toronto Press.
4. BATEMAN, A. J. 1952. Self-incompatibility systems in angiosperms. Heredity **6**:285-310.
5. BLATCHLEY, W. S. 1930. The Scarabaeidae of Florida. Fla. Entomol. **14**:25-35.

6. CANRIGHT, J. E. 1960. The comparative morphology and relationships of the Magnoliaceae. III. Carpels. Amer. Jour. Bot. **47**:145-155. 1960.
7. CARPENTER, I. W. and A. T. GUARD. 1950. Some effects of cross pollination on seed production and hybrid vigor of tulip tree. Jour. Forestry **48**: 852-855.
8. DARWIN, CHARLES. 1877. The effects of cross and self fertilization in the vegetable kingdom. D. Appelton, N. Y.
9. DAUMAN, E. 1930. Das Blutennektarium von *Magnolia* und die Futterkorper in der Blute von *Calycanthus*. Planta **11**:108-116.
10. DEAM, C. C. 1953. Trees of Indiana. **3rd.** ed. Ind. Dept. of Conservation, Indianapolis.
11. DEFINO, F. 1875. Ulteriori osservazioni e considerazioni sulla Dicogamia vel regno vegetale. Milan.
12. DIELS, L. 1916. Kaferblumen bei den Ranales und ihre Bedeutung fur die Phylogenie der Angiospermen. Ber. Deu. Bot. Ges. **34**:758-774.
13. EAMES, A. J. 1961. Morphology of the Angiosperms. McGraw-Hill, New York.
14. FRYXELL, PAUL A. 1961. The evolutionary position of inbreeding systems. Recent Advances in Botany **1**:887-891. U. of Toronto Press.
15. *Grant, Verne.* 1950. The pollination of *Calycanthus occidentalis*. Amer. Jour. Bot. **37**:294-297.
16. ————. 1952. The regulation of recombination in plants. Cold Spring Harbor Symp. **23**:337-363.
17. JOHNSTONE, G. H. 1955. Asiatic Magnolias in Cultivation. Roy. Hort. Soc., London.
18. KENNEDY, G. C. 1916. Some historical data regarding the Sweet Bay and its station on Cape Ann. Rhodora **18**:205-212
19. LEPPIK, E. E. 1960. Early evolution of flower types. Lloydia **23**:72-92.
20. LEWIS, D. 1954. Comparative incompatibilty in Angiosperms and fungi. Adv. in Genetics **6**:235-285.
21. ———— and LESLIE K. CROWE. 1958. Unilateral interspecific incompatibility in flowering plants. Heredity **12**:233-256.
22. MULLER, H. 1883. The fertilization of flowers. Transl. by D'Arcy W. Thompson. London.
23. RILEY, C. V. 1890. The rose chafer. Insect Life **2**:295-302.
24. STEBBINS, G. L. 1957. Self fertilization and population variability in the higher plants. Amer. Natl. **91**:337-354.
25. STOUT, A. B. 1928. Dichogamy in flowering plants. Bull. Torrey Club **55**: 141-153.
26. VAN DER PIJL, L. 1960. Ecological aspects of flower evolution. I. Phyletic evolution. Evolution **14**:403-416.
27. WERTH, EMIL. 1956. Bau und Leben der Blumen. Stuttgard.
28. WHITEHOUSE, H. L. K. 1950. Multiple-allelomorph incompatibility of pollen and style in the evolution of Angiosperms. Ann. Bot., N. S., **14**: 199-216.