

- 3203 (1954); H. J. Dauben, Jr., F. A. Godecki, K. M. Harmon, D. L. Person, *ibid.* **79**, 4557 (1957).
56. R. Breslow and C. Yuan, *J. Am. Chem. Soc.* **80**, 5991 (1958); R. Breslow, J. T. Groves, G. Ryan, *ibid.* **89**, 5048 (1967).
57. G. A. Olah and J. S. Staral, *ibid.* **98**, 6290 (1976).
58. ———, G. Liang, *ibid.* **96**, 6233 (1974); G. A. Olah, J. S. Staral, R. J. Spear, G. Liang, *ibid.* **97**, 5489 (1975).
59. G. A. Olah, J. S. Staral, L. A. Paquette, *ibid.* **98**, 1267 (1976); G. A. Olah, J. S. Staral, G. Liang, L. A. Paquette, W. P. Melega, J. J. Carmody, *ibid.* **99**, 3349 (1977).
60. G. A. Olah, G. D. Mateescu, G. Sipos, P. v. R. Schleyer, in preparation.
61. G. A. Olah, G. Liang, P. v. R. Schleyer, E. M. Engler, M. J. S. Dewar, R. M. Bingham, *J. Am. Chem. Soc.* **95**, 6829 (1973).
62. G. A. Olah, G. Liang, P. v. R. Schleyer, W. Parker, C. I. F. Watt, *ibid.* **99**, 966 (1977).
63. S. Masamune, M. Sakai, A. V. K. Jones, T. Nakashima, *Can. J. Chem.* **52**, 855 (1974); G. A. Olah, G. K. S. Prakash, T. N. Rawdah, J. C. Rees, D. Whittaker, *J. Am. Chem. Soc.* **101**, 3935 (1979).
64. R. P. Kirchen and T. S. Sorensen, *J. Am. Chem. Soc.* **100**, 6761 (1978).
65. G. A. Olah, C. L. Jeuell, D. P. Kelley, R. D. Porter, *ibid.* **94**, 146 (1972); J. S. Staral *et al.*, *ibid.* **100**, 8016 (1978).
66. G. A. Olah, *Halonium Ions* (Wiley, New York, 1975).
67. H. Perst, in *Oxonium Ions in Organic Chemistry* (Academic Press, New York, 1971); in *Carbocation Ions*, G. A. Olah and P. v. R. Schleyer, Eds. (Wiley, New York, 1976), vol. 5, pp. 1961–2047.
68. G. A. Olah, D. H. O'Brien, C. U. Pittmann, *J. Am. Chem. Soc.* **89**, 2996 (1967).
69. R. J. Gillespie and T. Birchall, *Can. J. Chem.* **41**, 158 (1963); U. Müller and K. Dehnicke, *Angew. Chem.* **78**, 825 (1960); *Angew. Chem. Int. Ed. Engl.* **5**, 841 (1966).

The Rise of the Angiosperms: A Genecological Factor

The combination of insect pollination and closed
carpels may provide a unique selective mechanism.

David L. Mulcahy

To what factors do the angiosperms owe their preeminent position in present world floras? Numerous angiospermous characteristics have been suggested as being contributory toward, or even deci-

istics of the primitive angiosperms: insect pollination and the closed carpel. My hypothesis is that insect pollination and the closed carpel, in combination, provide a mechanism that greatly in-

Summary. In the primitive angiosperms, closed carpels are believed to have evolved as protection for ovules, which would otherwise be injured by animal pollinators. The hypothesis is presented that, whatever the origin and other functions of angiosperms, insect pollination and closed carpels may, in combination, reduce the influence of random variation on pollen tube competition, thus enhancing the ability of natural selection to act on the gametophytic phase of the life cycle. The microgametophytic phase represented by vast numbers of haploid individuals can then serve, by insect pollination and closed carpels, as a screen against any genome not functioning with a high degree of metabolic vigor. Poorly balanced genomes could thus be eliminated at relatively little cost. Insect-pollinated angiosperms would therefore benefit from positive aspects of sexual recombination. Such a system may have allowed the angiosperms to undergo their rise to dominance.

sive in, the evolutionary rise of this group. These include insect-pollinated flowers, closed carpels, double fertilization, true endosperm, vessel elements, broad leaves, defensive alkaloids, and bird-dispersed fruits (1–3).

There can be no doubt that many of these hypotheses contain more than a modicum of truth but, in this article, I propose yet another one, a hypothesis that depends on, and thereby adds significance to, two outstanding character-

tensified selection pressures among the microgametophytes. Thus, the microgametic phase of the life cycle served as a barrier against poorly functioning haploid genomes and hence benefited the remainder of the life cycle.

To understand the operation and the consequences of this mechanism, it is necessary to consider some characteristics of a wind-pollinated preangiospermous species, similar perhaps to those that presumably gave rise to the

early angiosperms. Typically vast numbers of pollen grains would have been produced since only a miniscule fraction of these randomly moving grains could ever reach a receptive surface. Those grains that did reach receptive surfaces would most likely have done so singly and, because such pollinations might have occurred over a long period of time, the first grains to arrive could have enjoyed a head start, compared to later arrivals. Thus, the success or failure of a particular microgametophyte was influenced by chance. Upon arrival, the wind-borne pollen was passively carried to the megasporangium either by falling upon or being drawn to it by contraction of a pollination droplet.

In each of these above-mentioned characteristics, an insect-pollinated angiosperm is in direct contrast with a wind-pollinated preangiosperm. In the angiosperm, for example, fairly large numbers of grains will have reached receptive surfaces, not by deposition of single grains, but rather by masses of pollen deposited simultaneously by insect visitors. Furthermore, upon reaching a receptive surface, pollen grains, because of the closed carpels, of necessity produce pollen tubes that grow through fairly long sections of stylar tissues.

While the transition from wind-pollinated preangiosperm to insect-pollinated angiosperm may have had many consequences, my hypothesis suggests some of the most significant effects may have been upon the nature of interactions between microgametophytes. For example, with insect pollinations, more pollen grains would reach receptive surfaces (stigmas) so that competition among microgametophytes would be intensified. Furthermore, the simultaneous arrival on the stigma of many pollen grains would generate, in itself, an episode of intense competition. Finally, the long passage through the style, as is explained below, would provide an ex-

The author is an associate professor of botany at the University of Massachusetts, Amherst 01003.

cellent opportunity for pollen tube competition.

Insect pollination and closed carpels thus provide a threefold mechanism for intensifying selection among microgametophytes. According to my hypothesis, the gametophytic phase of the life cycle serves as a screen against any haploid genome that does not function with a high degree of metabolic vigor. A further and essential part of the hypothesis is that the effects of this gametophytic screening are not limited to the gametophytic generation in that several studies have shown that pollen tube growth rate is significantly correlated with the quality of the resultant sporophytic generation (4-7). Consequently, gametophytic selection, intensified by the threefold effects of insect pollination and closed carpels, has a direct effect upon the sporophytic portion of the life cycle.

This sporophytic effect bestows great significance upon insect pollination and closed carpels. Through them, the angiosperm sporophyte is subjected to intense selection pressures usually thought to function only in microbial or microbial-like systems, such as pollen grains.

With such a selective mechanism, vast numbers of haploid genomes can be screened by intensified gametophytic selection, and poorly functioning individuals would be eliminated at relatively little cost to the organism. In this way, and perhaps only among vascular plants, the angiosperms may benefit from the positive aspects of genetic recombinations—that is, new and possibly adaptive recombinants—while, at the same time, partially avoiding the negative effects of poorly functioning recombinants (8). This system, I hypothesize, may have given the angiosperms an evolutionary plasticity that fueled their dramatic rise to dominance in the world flora. My hypothesis consists of three propositions:

1) Insect pollination and the closed carpel induced intensification of competition between microgametophytes.

2) Pollen tube growth rates exhibit significant differences; that is, some of the differences in growth rate among pollen tubes from a single pollen source reflect genetic differences among the individual microgametophytes.

3) Some of the genes expressed in the microgametophytes are expressed also in the sporophyte; otherwise, microgametophytic selection could not influence the quality of the sporophytic generation.

Each of these three propositions are presented below, along with supporting evidence and a brief discussion of the implications.

Competition Between Microgametophytes

The factors that influence the outcome of any competitive biological event may be grouped into two distinct categories. The first group includes requirements for viability, vigor, and all the other qualities in which individual organisms may be expected to vary. These first qualities are influenced by the genotypes of the individual. The second group includes random events in the environment before which the genotypes of the individuals are of little or no consequence. These events include, for example, dispersal in the wrong direction, severe flooding, and drought.

Interactions between these two types of factors have been examined by Wright (9), and more recently by others, perhaps less comprehensively, but more directly relevant to the thesis of this article (10, 11). As a very general conclusion, it may be stated that the first, or genetic, set of factors determines an average selective value for any particular genotype; while the second, or random, set of factors delimits, for each genotype, the variation around that average. The consequences of this interaction are illustrated in Fig. 1. As variance around averages becomes greater, it becomes progressively more difficult for statisticians (and presumably also for selective pro-

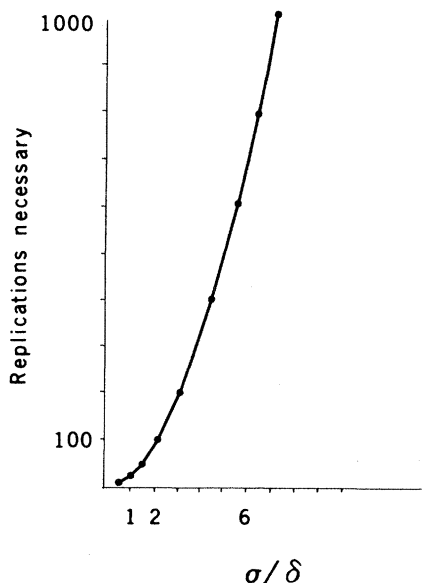


Fig. 1. The effect of increasing variation on the difficulty of distinguishing between two subpopulations. Standard deviation (σ) around the mean selective value of each population is assumed to be dependent upon random environmental factors. The means of the two subpopulations differ by δ . The vertical axis indicates the number of individuals which would have to be tested in order to allow a 90 percent probability of obtaining a statistically significant difference between the means of the two subpopulations (11).

cesses) to distinguish between the averages. Thus, we may assume that, in less than infinitely large populations, random environmental events may, in the long run, overwhelm genetically determined differences in selective values. Indeed, sufficiently random mortality could reduce the resolving power of natural selection to the point where only genetic lethals would be selected against. Thus, although stages in the life cycles of vascular plants frequently exhibit great surpluses of individuals (12), these provide opportunities for selection only if the effects of random events do not overwhelm genetically determined selective processes. Conversely, any selective system that reduces the influence of random events on the outcome of selection thereby increases the capacity of selection to respond to genetically determined differences between individuals.

Consider now my introductory statements about the contrasting effects of wind and insect pollination on the outcome of competition between microgametophytes. Many of the environmental hazards encountered by wind-dispersed pollen are independent of genetically determined pollen quality (13). In contrast is the statement by Baker that, because animals move between or within particular ecological habitats, random mortality of animal-borne seeds should be less than that of wind-borne seeds (14). In this same way, it may be assumed that insect-borne pollen should be less subject to random mortality than is wind-borne pollen (2).

A second aspect of insect pollination that serves to further reduce random variation in the outcome of microgametophytic competition is the simultaneous arrival, on the stigma, of large numbers of pollen grains. This would remove the variance introduced by single grains reaching receptive surfaces at widely disparate times. Under these conditions, the outcome of microgametophytic competition is more likely to reflect genetically determined differences in pollen tube growth rates than would be the case with wind-dispersed pollen.

Finally, when pollen grains reach a receptive stigma, they undergo processes of hydration and germination, and these represent still other opportunities for random events to increase variance of subpopulations. For example, if a pollen grain makes firm contact with the stigma, it may hydrate more rapidly than otherwise; and, if a germination pore is close to the stigma, the pollen tube may enter the style sooner than otherwise. However, as Correns first demonstrated (15),

Table 1. The influence of pollen quantity on the resultant sporophytic generation. The intensity of pollen competition is considered to be positively correlated with the quantity of pollen active in the pollination process (6).

| Item | Limited | Moderate | Excessive |
|------------------------------------|---------------|----------|-----------|
| Pollinations | 10 | 10 | 10 |
| Fruits (number) | 10 (one lost) | 10 | 9 |
| Mean number per fruit* | 112 | 221.3 | 245.9 |
| Mean weight (milligrams) per seed† | 0.095 | 0.089 | 0.088 |
| Seedlings | 878 | 2049 | 1913 |
| Germinate (percent)‡ | 87.10 | 92.59 | 86.44 |
| Mean number of leaves at day 51§ | 8.7480 | 8.2800 | 8.1317 |
| Mean weight (grams) | | | |
| Day 67‡ | 8.1001 | 8.1957 | 8.5833 |
| Day 92 | 32.2187 | 37.4576 | 39.2257 |

* $F = 8.84$, $P \leq .01$, d.f. = 2,25. †Limited versus excessive, $F = 6.42$, $P \leq .01$, d.f. = 1,16; limited versus moderate, $F = 5.73$, d.f. = 1,17; moderate versus excessive, $F = 1.48$, not significant, d.f. = 1,17. ‡No significant differences. §Limited versus moderate, $\chi^2 = 57.44$, $P \leq .01$, d.f. = 4; limited versus excessive, $\chi^2 = 28.61$, $P \leq .01$, d.f. = 4; moderate versus excessive, $\chi^2 = 28.38$, $P \leq .01$, d.f. = 4. || $F = 7.25$, $P \leq .01$, d.f. = 2,791.

passage through stylar tissues gives faster growing pollen tubes an opportunity to surpass slower tubes that may have, by chance, gained some initial advantage. This provides one more mechanism by which random effects may be moderated.

Thus, insect-pollinated angiosperms are shielded from random influences on pollen tube selection by three mechanisms: (i) nonrandomness in the direction of pollen dispersal, (ii) nonrandomness in the time of pollen arrival on the stigma, and (iii) nonrandomness in the outcome of pollen tube competition. Consequently, although many vascular plants undergo episodes of intense competition, pollen tubes in insect-pollinated angiosperms may be capable of reflecting genetically determined differences between individuals.

Pollen Tube Growth Rate: Influence of Genes Expressed in Pollen Grains

The potential efficacy of selection among pollen tubes would never be realized if the number of genes actually transcribed in the haploid generation is small (16). It is necessary, therefore, to consider this point.

For example, in *Zea mays* L., some genes are expressed in the pollen. These include waxy (17), alcohol dehydrogenase (18, 19), shrunken, and sugary (20) and several (six to nine) Ga (gametophytic) loci (21). Markers similar to waxy, Adh, and Ga are known from several taxa, as are examples of gametophytic self-incompatibility (22).

In addition to these single locus systems, there are also polygenic systems and, although these have not yet been subjected to extensive investigation, they may be important in adaptive processes. Sari-Gorla *et al.* (23), for example, compared pollen from hetero-

zygous plants (F_1 hybrids of *Zea mays*) with that from highly inbred lines of the same species. They found that lengths of pollen tubes from each hybrid, measured 2 hours after being sown on agar, were significantly more variable than those from the inbred plants. A hybrid, because of genetic segregation, should produce various pollen genotypes, whereas pollen grains from an inbred plant could produce identical genotypes. Thus, the greater variance in pollen tube lengths of genetically heterogeneous pollen indicates that pollen tube growth rate is indeed influenced by the gametophytic genotype.

A further indication that polygenic systems in the gametophyte influence pollen tube growth rates is provided by a comparison (24) of studies by Jones (25) and Pfahler (26). This comparison suggests that pollen of highly inbred plants has been selected, by many generations of selfing, for rapid growth through the stylar environment of that line. On the contrary, pollen of F_1 hybrids shows no unusual capability in the F_1 style, presumably because there has been no prior selection for that capability. This presumption has been tested and confirmed (27). Thus, pollen from single plants does indeed respond to selection for increased pollen tube growth rates. Since the only basis for response to selection is genetically determined variation (28), we may accept the response of pollen to selection as *prima facie* evidence for genetically determined variation among pollen grains from single plants.

Gametophytic Selection May Modify the Sporophytic Generation

It is, of course, certain that some of the genes expressed in the pollen will not be expressed in sporophytic tissues (29). This pattern of gene expression may be

referred to as the nonoverlapping model.

An alternative pattern of gene expression is shown in *Zea mays* by the alcohol dehydrogenase loci, Adh₁ and Adh₂, which are expressed in both the gametophytic (pollen) and sporophytic stages of the life cycle (19). This pattern of gene expression represents what may be referred to as the overlapping model. The relative importances of these two patterns, nonoverlapping versus overlapping, are of significance to my hypothesis. If, for example, gametophytic and sporophytic genes are separate (that is, nonoverlapping), then gametophytic selection cannot influence the quality of the sporophyte, except for transient effects of linkage. When, however, the gametophytic and sporophytic genomes do overlap, then selection in one phase will modify the genetic constitution of the other phase.

The overlapping model, moreover, would provide an explanation for the effect of pollen tube selection upon the resultant sporophytic generation. The best test for the functioning of this model is an empirical one. Selecting among gametophytes and searching for effects among the resultant sporophytes will not reveal which of the two model systems, overlapping or nonoverlapping, is more typical of gene expression, but will, however, indicate whether the overlapping model is sufficiently common to allow gametophytic selection to modify the sporophyte.

This type of empirical study was first performed by Ter-Avanesian (4), who found that sporophytes of *Gossypium hirsutum*, *Vigna sinensis*, and *Triticum aestivum* are modified by gametophytic selection. If the number of pollen grains used in pollinations was approximately equal to the number of ovules available for fertilization, the resultant sporophytic generation exhibited a relatively high range of phenotypic variations. With such limited pollinations, gametophytic competition and selection would necessarily have been at the lowest possible levels. When excessive quantities of pollen were used, however, only the fastest growing gametophytes were able to discharge their gametes into an unfertilized ovule; and, in those crosses, Ter-Avanesian found that the resultant sporophytes exhibited a relatively low range of phenotypic variation. These results indicate a significant presence of the overlapping model; genes that influence pollen tube growth rate and are therefore exposed to selection in the gametophyte, are expressed also in the sporophyte. Similar observations on the effect of gametophytic selection in *Lycopersicon esculentum* have been reported (5).

Whereas these studies did indicate that gametophytic selection could influence the quality of the resultant sporophytic generation, the method of varying the intensity of selection by varying the quantity of pollen introduces a confounding factor into the results; limited pollinations usually result in a few large seeds, but excessive pollinations result in a large number of small seeds. Because neither Ter-Avanesian (4) nor Lewis (5) considered this factor in much detail, additional studies were undertaken (6, 7).

The effect of varying the quantity of pollen in crosses between two clones of *Petunia hybrida* is shown in Table 1. As expected, limited pollinations resulted in relatively small numbers of large seeds. Consequently, seedlings from limited pollinations were significantly larger than others 51 days after planting. Such maternal effects are quite transient, however, in that they are statistically non-significant by day 67, and are finally reversed by day 92. Once maternal effects are outgrown (day 92, and perhaps sooner) plant weight should be a reflection of each sporophyte's genotype. The data obtained indicate that once this occurs, plants that result from the most intense gametophytic competition are significantly heavier than other plants. To ensure the total elimination of maternal effects, the above study was extended by self-pollinating samples of plants that had resulted from the three treatments. One fruit was randomly selected from each of three plants in each of the three treatments and seeds from these nine fruits were planted. The data obtained indicate that even in the F_2 sporophytes, the effect of gametophytic competition in the F_1 generation is still expressed (7).

When members of the Carophyllaceae are considered, an entirely different method of controlling the intensity of gametophytic competition is available. The method, devised by Correns (15), depends on the fact that, if a flower has elongated stigmatic surfaces (and many members of this family possess this characteristic morphology), pollen may be placed either proximal or distal to the ovary. In the first case, pollen tubes have only a short length of stylar tissue through which to grow, and thus there is little opportunity for the faster growing individuals to surpass the others. Gametophytic selection will thus be relatively modest. If, however, pollinations are made at the portion of the stigma that is distal to the ovary, there is a greater length of style to be penetrated and more opportunity for gametophytic selection

to occur, so that the effect of this selection will be greater.

The advantage of Corren's experimental system is that the intensity of gametophytic selection may be controlled without varying the quantity of pollen used in pollinations. Differences in seed weight and numbers are thus minimized. When this method was applied to clones of *Dianthus chinensis*, distal pollinations (intense gametophytic competition) resulted in seedlings that, 28 days after planting, were 15.49 percent heavier than those resulting from proximal pollinations (30). These several studies thus suggest that gametophytic competition can indeed modify the quality of the sporophyte.

Implications of the Proposed Hypothesis

The proposed hypothesis is related primarily to a genecological phenomenon, the intensification of microgametophytic selection, as a possible explanation for the adaptive success of the angiosperms. The hypothesis, however, holds implications for other subjects as well. For example, Maynard Smith (31) has concluded that sexual reproduction would provide a long-term beneficial effect only if population sizes were at least ten times the reciprocal of rates at which favorable mutations occur. Since mutation rates are often considered to approximate 1×10^{-6} per locus, sexual reproduction would be beneficial only in populations that contain 10×10^6 individuals or more. This would be a very large population of sporophytes, but not at all unusual for microgametophytes. Lewis (32), for example, was able to score 65×10^6 pollen grains of *Oenothera organensis* in his search for mutations in the self-incompatibility system of that species, and outcrossing species are reported to produce an average of 5859 ± 936 pollen grains for each ovule (33). These numbers may bear only a slight relation to those found in natural populations, but they do suggest an order of magnitude that could be expected to occur. Thus, Maynard Smith's criterion for the minimal population size that would allow sexual reproduction to provide a long-term benefit seems easily attainable in the microgametophytes of insect-pollinated angiosperms.

Another implication of my proposed hypothesis stems from the proposition that portions of the sporophytic genome are expressed in the gametophytic portion of the life cycle. This suggests that selection for microgametophytes that are resistant to extreme temperatures,

amino acid analogs, and other agents could result in sporophytes that are similarly resistant. This is already possible with the Adh system of *Zea mays* (19); but that is a single case, and the proposed hypothesis suggests that it may serve as a model for many such selective systems. If feasible, gametophytic selection may be a means of circumventing many of the technical difficulties involved in protoplast cultures (34) and other systems now used to develop resistant genotypes.

References and Notes

1. V. Grant, *Evolution* **3**, 82 (1949); H. L. K. Whitehouse, *Ann. Bot. (London)* **14**, 199 (1950); *Nature (London)* **188**, 957 (1960); G. L. Stebbins, *Evolution* **5**, 299 (1951); in *Origin and Early Evolution of Angiosperms*, C. B. Beck, Ed. (Columbia Univ. Press, New York, 1976), p. 300.
2. P. J. Regal, *Science* **196**, 622 (1977).
3. A. Manning, *Proc. R. Soc. Edinburgh* **25**, 67 (1957); A. Takhtajan, *Flowering Plants, Origin, and Dispersal* (Smithsonian Institution Press, Washington, D.C., 1969); P. R. Raven, *Evolution* **31**, 451 (1977).
4. D. V. Ter-Avanesian, *Bull. Appl. Genet. Plant Breeding Leningrad* **28**, 119 (1949); *Genetika* **5**, 103 (1969); *Theor. Appl. Genet.* **52a**, 77 (1978); *Bull. Torrey Bot. Club* **105b**, 2 (1978).
5. D. Lewis, *Annu. Rep. John Innes Hort. Inst.* **45**, 12 (1954).
6. D. L. Mulcahy, G. B. Mulcahy, E. Ottaviano, in *Gamete Competition in Plants and Animals*, D. L. Mulcahy, Ed. (Elsevier, Amsterdam, 1975), p. 227.
7. ———, *Societe botanique Francaise Actualites botaniques* 1-2, 57 (1978).
8. G. Williams, *Sex and Evolution* (Princeton Univ. Press, Princeton, N.J., 1975).
9. S. Wright, *Genetics* **16**, 97 (1931).
10. C. Wills and L. Nichols, *Nature (London)* **233**, 123 (1971); *Proc. Natl. Acad. Sci. U.S.A.* **69**, 323 (1972).
11. D. L. Mulcahy and S. M. Kaplan, *Am. Nat.* **113**, 419 (1979).
12. J. T. Buchholz, *Bot. Gaz.* **73**, 249 (1922).
13. D. R. Whitehead, *Evolution* **23**, 28 (1969).
14. H. G. Baker, personal communication.
15. C. Correns, *Handbuch der Vererbungswissenschaft Band II*, 1 (1928).
16. J. Heslop-Harrison, *Environ. Health Perspect.* **27**, 197 (1978).
17. G. F. Sprague, *Proc. Natl. Acad. Sci. U.S.A.* **19**, 838 (1933); O. E. Nelson, *Genetics* **37**, 101 (1952); G. Ericksson, *Heredity* **63**, 180 (1969).
18. M. Freeling, *Genetics* **81**, 641 (1975); **83**, 701 (1976); D. Schwartz, *ibid.* **67**, 411 (1971).
19. D. Schwartz and J. Osterman, *ibid.* **83**, 63 (1976).
20. P. L. Pfahler, in *Gamete Competition in Plants and Animals*, D. L. Mulcahy, Ed. (Elsevier, Amsterdam, 1975), p. 115.
21. A. Bianchi and C. Lorenzoni, in *Gamete Competition in Plants and Animals*, D. L. Mulcahy, Ed. (Elsevier, Amsterdam, 1975), p. 257.
22. C. E. Townsend, in *Pollen: Development and Physiology*, J. Heslop-Harrison, Ed. (Appleton-Century-Crofts, New York, 1974), p. 281.
23. M. Sari-Gorla, E. Ottaviano, D. Fiani, *Theor. Appl. Genet.* **46**, 289 (1975).
24. D. L. Mulcahy, in *Fertilization in Higher Plants*, H. F. Linskens, Ed. (Elsevier, Amsterdam, 1974), p. 27.
25. D. F. Jones, *Selective Fertilization* (Univ. of Chicago Press, Chicago, 1928).
26. P. L. Pfahler, *Genetics* **57**, 513 (1967).
27. C. M. Johnson and D. L. Mulcahy, *Theor. Appl. Genet.* **51**, 211 (1978).
28. W. Johannsen, *Elemente der Exakten Erblichkeitslehre* (Fischer, Jena, 1909).
29. O. E. Nelson and C. Y. Tsai, *Science* **145**, 1194 (1964).
30. D. L. Mulcahy and G. B. Mulcahy, *Theor. Appl. Genet.* **46**, 277 (1975).
31. J. Maynard Smith, *J. Theor. Biol.* **30**, 319 (1971).
32. D. Lewis, *Heredity* **2**, 219 (1948).
33. R. W. Cruden, *Evolution* **31**, 32 (1977).
34. D. N. Radin and P. S. Carlson, *Genet. Res.* **32**, 85 (1978).
35. I thank Drs. C. Johnson, R. Schuster, C. Swanson, J. Walker, J. Beach, and J. Heslop-Harrison for their many valuable suggestions. Supported by NSF grant DEB 76-82917.