

Pollen versus resource limitation of seed production: A reconsideration

Brenda B. Casper and Richard A. Niesenbaum*

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, USA

*Department of Biology, Swarthmore College, Swarthmore, PA 19081-1397, USA

Most empirical studies of pollination biology test exclusively for either pollen limitation or resource limitation of seed production. We make the assumption that both resources and pollen can limit seed production in an individual within a single flowering season. This is possible because the amount of pollen delivered by natural pollinators and the quantity of resources available to mature fruit are likely to vary among flowers, independently of each other. We discuss constraints on the temporal and spatial distribution of resources within plants and ecological factors that may cause variation in stigmatic pollen loads. We explain how independent variation in pollen and resources can have important fitness consequences by affecting both the quantity and genetic quality of seeds produced.

DETERMINING what factors limit female reproductive success in plants is a central goal of several different avenues of study in plant evolutionary ecology, including investigations of (i) competition among species for limited pollinators¹⁻⁴, (ii) gametophytic competition and selective fruit and seed abortion⁵⁻⁷, and (iii) the relationship between plant population structure and pollinator service⁸. Because seed production is often assumed to be limited by either pollen or resources but not some combination of these factors, empirical studies have been dominated historically by approaches that test exclusively for one or the other⁹.

Whether or not pollen availability limits seed production is known to differ among years, populations, or plants within populations¹⁰⁻¹⁴. The few studies examining pollen limitation under different resource conditions find its importance varying with the local environment¹⁵⁻¹⁹. Yet, little consideration has been given to how pollen and resources may limit seed production in the same plant over a single flowering season^{14, 18}.

Haig and Westoby²⁰ argue that selection should favor a pattern of allocation such that life-time seed production will be limited by both pollen and resources. They conclude that plants should allocate resources to flowers versus fruits so that pollen received by the plant and resources available to it limit fitness to the same degree. They recognize that an individual's seed production may be limited by either pollen or

resources in any particular year but suggest that if many individuals are examined over different years, pollen limitation and resource limitation will both occur.

We make the assumption that both resources and pollen can limit seed production in an individual within a single flowering season²¹. We explain that the amount of pollen delivered by natural pollinators and the quantity of resources available to any particular flower are likely to vary independently of each other. An uneven distribution of pollen and/or resources may occur among different parts of a plant or develop temporally as the flowering and fruiting season progresses. When a plant is unable to redistribute resources among flowers to match variation in stigmatic pollen loads, seed production can be pollen-limited in some flowers while resource-limited in others. We also discuss how the relative availability of pollen and resources can influence competition among fruits or seeds and their selective abortion.

Constraints on resource distribution

We know more about constraints on the distribution of resources within a plant than about temporal and spatial variation in the pollen received per flower. The probability an initiated fruit will mature often varies as a function of its location, the number of nearby developing fruits, and/or its sequence of fruit initiation²². The extent fruits influence each other should not depend simply on their spatial proximity, but whether they occupy the same integrated physiological unit (IPU), the semiautonomous plant sector over which assimilate is locally produced and translocated^{23, 24}. The organization of vegetative and reproductive structures into IPUs reflects underlying vascular architecture and varies greatly among species. An IPU may encompass, for example, a branch with several inflorescences, an inflorescence and all of its subtending leaves, or only a portion of an inflorescence and a particular subset of the associated leaves²³. Theoretically, when IPUs draw from largely separate resource pools, fruit and seed production can be resource-limited in some IPUs, while limited by pollen quantity in others.

Competition among fruits for resources and the potential for selective abortion of lower quality fruits or seeds^{22,25,26} could also vary among IPU's²⁷, depending on locally available resources and the number of pollinated flowers.

Temporal constraints on the distribution of resources among fruits also operate, even within IPU's. The probability an initiated fruit will mature often declines throughout the flowering season, particularly in plants with large inflorescences or terminal racemes whose basal flowers open first^{13,16,22,28-34}. In such plants fruit initiation sequence and position co-vary. Several nonexclusive mechanisms have been proposed to account for the apparent dominance of early fruits²⁶: (i) Fruits initiated first serve as stronger sinks and compete more effectively for resources^{33,35-38}, (ii) early fruits inhibit later fruits through phytohormones^{39,40}, and (iii) the distribution of resources or the development of supporting vascular tissue varies temporally and/or spatially over the plant^{22,41}. Several experimental studies support the generalization that resources become more limiting as the season progresses^{13,16,29,33,42}.

Whatever the mechanism, the presence of early fruits can greatly increase the probability that later fruits will abort²⁶. Successful pollinations early in the season have greater influence on the fates of later pollinated flowers than the converse. If fruit set in early flowers is sufficiently high, pollination levels of later flowers may have little effect on maximum seed production.

We also expect less than full pollination of early flowers to have more significant consequences for plant fitness than reduced pollination of later flowers. Fruits that normally abort in later flowers can develop if early flowers go unpollinated or if early fruits are removed^{22,36}, but complete compensation in seed numbers or seed mass often does not occur after early fruiting failures, even in plants with considerable spatial temporal integration of resources⁴²⁻⁴⁴. Consistent with this idea is House's⁴⁵ finding that total fruit set in the tropical dioecious tree *Neolitsea dealbata* is positively correlated with pollen quantity trapped in female canopies during the first six days of flowering but is unrelated to the amount measured over the entire flowering period. She suggests that effective fertilizations occur early in the season.

We can think of several possible reasons why compensation for the failure of early fruits and seeds could be incomplete even if later flowers are fully pollinated. First, leaf photosynthetic rate and/or overall plant vigor may simply decline with leaf or plant age⁴⁶, especially with biomass loss to herbivory. Secondly, fruits initiated earlier may have longer to garner resources. Thirdly, since photosynthetic rate increases with metabolic sink strength^{23,47}, the total resource pool available for reproduction might be increased by the presence of early fruits. Finally, fruits initiated later

may be located farther from the source of photosynthate, and supply may decrease with distance from source^{13,33}.

Variation in pollen delivery

We consider it likely that pollen deposition varies independently of resource distribution in most species. There may be a delay in pollinators locating or recognizing floral displays as flowering commences, and pollinator abundance and activity may change with weather conditions or the anthesis of other species⁴⁸. Pollen limitation should prove more important when resource levels are generally high.

Despite recognition that pollen limitation of seed production must be examined over the whole plant and not just in a subset of flowers²¹, few experimental studies have done that^{15-18,21}. Even fewer have paid attention to temporal or spatial changes within a plant in the importance of pollen limitation^{13,18,42,49}. Considerable variation in stigmatic pollen loads delivered by natural pollinators has been documented⁵⁰⁻⁵⁴, but such data are seldom collected as a function of the location of the flower or its position in the temporal flowering sequence.

Some studies provide at least indirect evidence that the importance of pollen limitation can vary spatially or temporally. Levin⁵⁰ found smaller stigmatic pollen loads later in the season in populations of *Phlox drummondii*, *P. cupsidea*, and their hybrids. In *Lindera benzoin*, fewer flowers opening in the first half of the flowering season receive pollen and those that do average fewer pollen tubes per style than those opening later; abortion of apparently viable fruits only occurs among flowers opening during the second half of the flowering season presumably due to resource constraints⁴⁹. Karoly¹³ demonstrated a seasonal decline in the degree pollen limits fruit set in *Lupinus nanus* even though supplemental pollination did not increase total fruit production. Hand pollination altered which fruits matured; more fruits developed from early flowers while fewer developed from later flowers, compared with plants pollinated naturally.

Consequences for selective abortion of seeds and fruits

The relative levels of pollen and available resources can affect fitness indirectly by influencing the success of different seed genotypes as well as directly through seed numbers or mass. Selective abortion of otherwise viable fruits or seeds, based on some criterion of quality and/or pollen parentage, may result from competition among reproductive structures for limited resources^{22,25,38}. Such selection can alter mean offspring fitness and genotype frequencies^{7,55-57}. Reflecting

temporal resource availability, plants may minimize abortions early in the season in order to maximize seed numbers. In *L. benzoin*, selective fruit abortion from flowers with fewer pollen tubes per style only occurs among later flowers even though early flowers receive, on average, less pollen⁴⁹. High abortion rates early in the season would be especially disadvantageous if pollination success later were uncertain.

Selective fruit and seed abortion should generally be more intense when resources constrain seed production, reflecting competition among fruits or ovules with different competitive abilities, and more lax when pollen is limiting²¹ (Figure 1). We also recognize that severe resource stress may accentuate the pattern that fruits in certain positions are more likely to mature because they have greater access to resources, irrespective of pollen identity. We are unaware of any studies of selective abortion that have incorporated the temporal patterns of pollen deposition by natural pollinators and some evaluation of resource availability or whole plant integration. Pollen donor studies conducted at different resource levels show overall maternal condition can affect the degree paternity is regulated through post-fertilization processes^{7,57}. In *Espelita schultzei*, fewer filled achenes develop from hand crosses between nearby individuals than between those more distant, but this difference is only apparent later in the season, as resources presumably become more limited and fruit set declines⁵⁸. Becerra and Lloyd⁵⁹ found abscission of selfed flowers in *Phorium tenax* increased in frequency with the proximity of outcrossed flowers on the same plant. Competition between these fruit types must increase when they are closer together.

The imperfect match between the spatial and

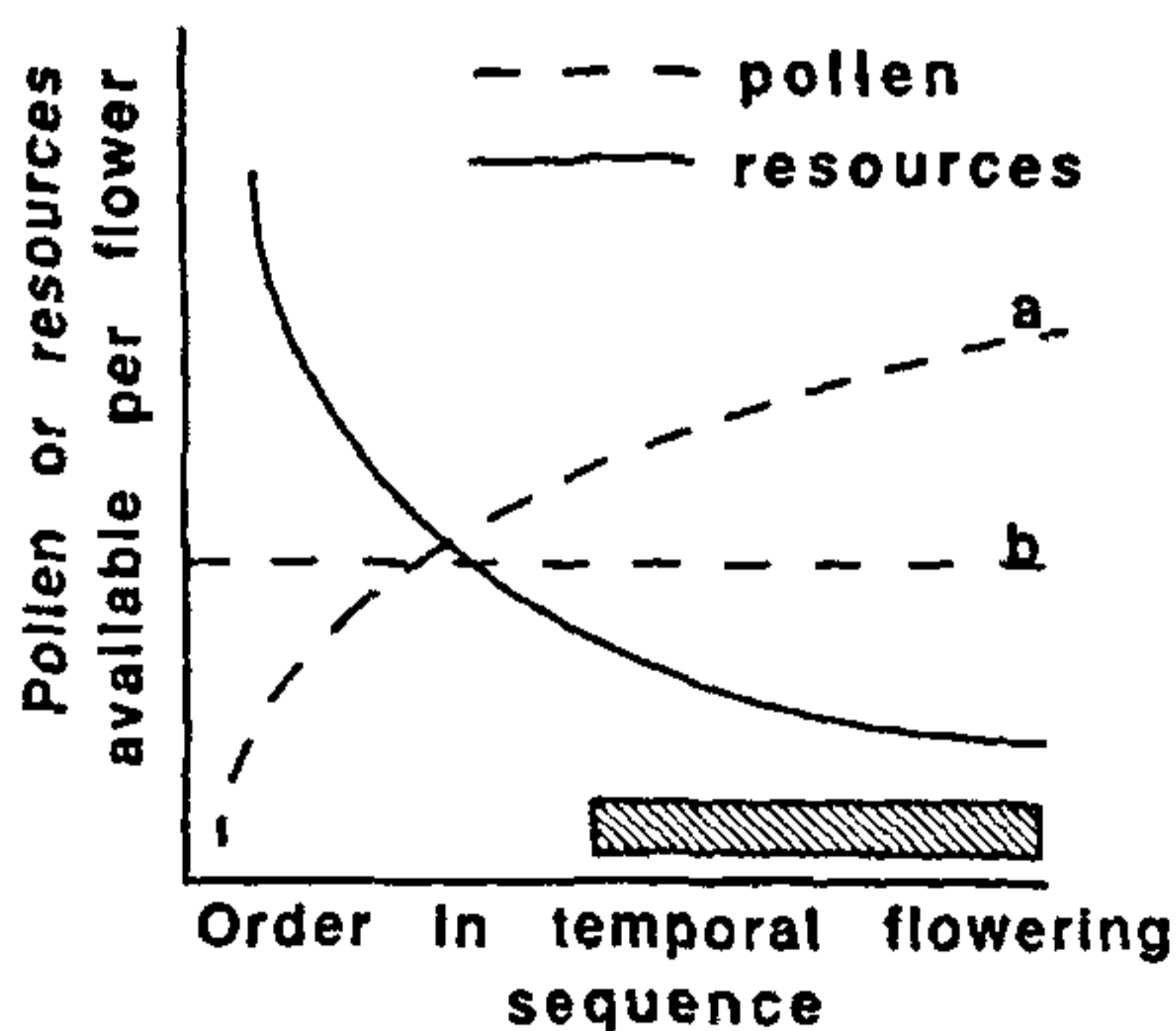


Figure 1. Graphical illustration of a likely temporal pattern of resource availability and two of many possible patterns of pollen availability (a and b). The period when seed production is resource-limited and selective abortion of fruits and seeds should be most likely is indicated by the striped bar.

temporal availability of pollen and the availability of resources and, theoretically, changes in the intensity of selection among reproductive structures, may help maintain genetic variation among the progeny, especially for paternal traits. For example, small stigmatic pollen loads and the absence of fruit abortion early in the season, as observed in *L. benzoin*⁴⁹, should allow pollen with slower pollen tube growth to sire successful seeds and thereby reduce selection on genetic components of pollen competitive ability. Selection on pollen tube growth rates may not be as strong under natural levels of pollination as sometimes interpreted⁶⁰, and this reduced selection may be important in maintaining genetic variation in this trait.

Importance of plant growth form

As noted earlier, the extent distributional constraints affect the amount of resources available for reproduction must differ greatly among species. In particular, intraseasonal pollen and resource limitations of seed production may well be expressed differently for species with indeterminate versus determinate flowering. In indeterminately flowering plants, low pollination levels can extend flower production⁴³ which permits seasonal adjustment in flower numbers in response to temporal availability of pollen and resources. Plants that regulate flower numbers in this way may continue to produce flowers until numbers of fertilized ovules more closely match resources available for seed maturation. In such plants, supplemental pollen may improve the percentage of early flowers maturing fruits and/or increase mean seed number per flower. Increased total seed production with supplemental pollen is especially likely if resources that would have been used to construct additional (later) flowers can be used for seed filling instead⁴³. This kind of flexibility probably reflects a high degree of spatial and temporal resource integration. In these species, supplemental resources could increase total seed production by increasing flower numbers even if the proportion of flowers pollinated remains constant. If so, one would have to conclude that seed production is simultaneously limited by resources and pollen. Campbell and Halama¹⁸ found this pattern in the monocarpic perennial, *Ipomopsis aggregata* which responded to nutrient addition by prolonging flower production and increasing seed number per flower after hand pollination. In unfertilized plants, hand pollination increased the proportion of flowers maturing fruits.

Plants with spatial constraints on resource distribution and whose flower numbers are not adjusted upwards during the flowering season should respond very differently to pollen limitation. Low pollination levels should have more severe fitness consequences,

particularly for the current year, if increasing flower numbers is not possible. The time between bud formation and anthesis can be considerable, and in many woody perennials, floral buds are laid down near the end of the previous growing season⁶¹. Moreover, branches of woody species are often autonomous resource producers and users²³, so that resource sharing among branches is limited.

Studies examining the consequences of adding pollen over the entire plant have mostly dealt with short-lived temperate herbs. While the size and longevity of woody plants prevent similar examinations of lifetime fitness effects, branch autonomy could validate parallel studies at the branch level⁴. We believe woody plants with biotic pollination systems and flower numbers determined before the flowering season, which must include many tropical species, would be especially likely to experience pollen and resource limitation within a season.

Conclusions

Based on known patterns of resource and pollen distribution, we make the following predictions regarding limitations to seed production, which should provide framework for future studies.

(1) In general, especially due to increasing constraints on resource availability later in the season, flowers opening early are more likely to be pollen-limited than are later flowers in the same plant.

(2) Because the plant may not be able to redistribute resources temporally, pollination failures in early flowers may be lost opportunities for reproduction even if seed production later in the season is resource-limited.

(3) Because abortion of seeds or fruits should become more selective during periods of resource limitation, selection would be intensive later in the season.

(4) Severe environmental stress may accentuate spatial patterns in the probability of fruit maturation, reflecting spatial constraints on the distribution of resources.

(5) Pollen of poor genetic quality will have a greater probability of success when seed production is locally or temporarily pollen-limited allowing for the maintenance of genetic variation in pollen, or other paternal traits. During periods of low pollen deposition, competition among seeds and fruits should be minimal.

We have confined our discussion to factors limiting seed quantity and quality, the female function of flowers. We are well aware that surplus hermaphroditic flowers may be important for male function^{62,63} and that fitness trade-offs in the two may occur⁴³. Surplus flower production is also viewed as possible bethedging against environmental variation^{24,64}. Serial adjustment

of reproductive structures to match resource or pollen levels is clearly advantageous⁶⁵. Because of resource distributional constraints we discuss here, we are suggesting that all flowers within a plant are not equally capable of producing seeds⁶⁶, which could limit their usefulness under a bethedging strategy. Combined studies of both resource distributions among flowers and variation in pollen loads delivered by natural pollinators should help in better understanding the adaptive significance of particular floral displays.

1. Zimmerman, M., *Ecology*, 1980, 31, 723.
2. Waser, N. M., *Handbook of Experimental Pollination*, (ed. Jones, E. C. and Little, R. J.), Van Reinhold, New York, 1983, pp. 227.
3. Campbell, D. R. and Motten, A. F., *Ecology*, 1985, 66, 554.
4. Rathcke, B., *Ecology*, 1988, 69, 446.
5. Willson, M. F. and Burley, N., *Mate Choice in Plants: Tactics, Mechanism, and Consequences*, Princeton, NJ, 1983.
6. Lee, T. D., *Am. Nat.*, 1984, 123, 427.
7. Marshall, D. L. and Folsom, M. W., *Annu. Rev. Ecol. Syst.*, 1991, 22, 37.
8. Handel, S., *Am. J. Bot.*, 1983, 69, 1538.
9. Bierzychudek, P., *Am. Nat.*, 1981, 117, 838.
10. Piper, J. G. et al., *Heredity*, 1986, 56, 207.
11. Campbell, D. R., *Am. J. Bot.*, 1987, 74, 269.
12. Johnston, M. O., *Ecology*, 1991, 72, 1500.
13. Karoly, K., *Am. J. Bot.*, 1992, 79, 49.
14. Lawrence, W. S., *Am. Nat.*, 1993, 141, 296.
15. Galen, C., *Ecology*, 1985, 66, 792.
16. Delph, L. F., *Oecologia*, 1986, 69, 471.
17. McCall, C. and Primack, R. B., *Oecologia*, 1987, 67, 403.
18. Campbell, D. R. and Halama, K. J., *Ecology*, 1993, 74, 1043.
19. Niesenbaum, R. A., *J. Ecol.*, 1993, 81, 315.
20. Haig, D. and Westoby, M., *Am. Nat.*, 1988, 131, 757.
21. Zimmerman, M. and Pyke, G. M., *Am. Nat.*, 1988, 31, 723.
22. Stephenson, A. G., *Annu. Rev. Ecol. Syst.*, 1981, 12, 253.
23. Watson, M. A. and Casper, B. B., *Annu. Rev. Ecol. Syst.*, 1984, 15, 233.
24. Ehrlén, J., *Am. Nat.*, 1991, 138, 918.
25. Stephenson, A. G. and Bertin, R. I., *Pollination Biology*, (ed. Real, L.), Academic Press, Orlando, FL, 1983, pp. 110.
26. Lee, T. D., *Plant Reproductive Ecology*, (eds. Lovett Doust, J. and Lovett Doust, L.), Oxford University Press, Oxford, 1988, pp. 179.
27. Schneider, G. W., *J. Am. Soc. Hortic. Sci.*, 1977, 102, 179.
28. Richardson, T. E. and Stephenson, A. G., *Oecologia*, 1991, 87, 80.
29. Schemske, D. W., *Bull. Torrey Bot. Club*, 1977, 104, 254.
30. Lloyd, D. G. et al., *New Phytol.*, 1980, 86, 81.
31. Bawa, K. S. and Webb, C. J., *Am. J. Bot.*, 1984, 71, 736.
32. Handel, S. N. and Mishkin, J. L., *Evolution*, 1984, 38, 1350.
33. Sage, T. and Webster, B. D., *Bot. Gaz.*, 1987, 148, 35.
34. Kwak, M. M. and Jennersten, O., *Oecologia*, 1991, 86, 99.
35. Adams, M. W., *Crop Sci.*, 1967, 7, 505.
36. Stephenson, A. G., *Ecology*, 1980, 56, 285.
37. Binnie, R. C. and Chifford, P. E., *J. Agric. Sci.*, 1981, 97, 397.
38. Lee, T. D. and Bazzaz, F. A., *Ecology*, 1982, 63, 1374.
39. Rawson, H. M. and Evans, L. T., *Aust. J. Biol. Sci.*, 1970, 23, 753.
40. Tamas, I. A. et al., *Plant Physiol.*, 1979, 64, 620.
41. Van Steveninck, R. F. M., *J. Exp. Bot.*, 1957, 8, 373.
42. Agren, J. and Willson, M. F., *Oecologia*, 1992, 92, 177.
43. Stanton, M. L. et al., *Oecologia*, 1987, 74, 68.
44. Garrish, R. S. and Lee, T. D., *Oecologia*, 1989, 81, 279.
45. House, S. M., *J. Ecol.*, 1992, 80, 57.
46. Salisbury, F. B. and Ross, C. W., *Plant Physiology*, 3rd edn. Wadsworth Pub., Belmont, CA, 1985, pp. 226.

47. Gifford, R. M. and Evans, L. T., *Annu. Rev. Plant Physiol.*, 1981, 32, 485.
48. Rathcke, B., *Pollination Biology*, (ed. Real, L.), Academic Press, Orlando, FL, 1983, pp. 305.
49. Niesenbaum, R. A., PhD Dissertation, University of Pennsylvania, Philadelphia, PA, 1992.
50. Levin, D. A., *Evolution*, 1970, 34, 367.
51. Casper, B. B., *Oecologia*, 1983, 59, 262.
52. Galen, C. and Newport, M. E. A., *Am. J. Bot.*, 1988, 75, 900.
53. Snow, A. A., *Am. J. Bot.*, 1986, 73, 39.
54. Snow, A. A., *Am. Nat.*, 1990, 136, 742.
55. Stephenson, A. G. and Winsor, J. A., *Evolution*, 1986, 40, 453.
56. Casper, B. B., *Am. Nat.*, 1988, 132, 318.
57. Marshall, D. L. and Ellstrand, N. C., *Am. Nat.*, 1988, 133, 751.
58. Sobrevila, C., *Am. J. Bot.*, 1988, 75, 701.
59. Becerra, J. X. and Lloyd, D. G., *Evolution*, 1992, 46, 458.
60. Walsh, N. E. and Charlesworth, D., *Q. Rev. Biol.*, 1992, 67, 19.
61. Ray, P. M. et al., *Botany*, Saunders College Publishing, Philadelphia, PA, 1983, pp. 39.
62. Willson, M. F. and Rathcke, B. J., *Am. Midl. Nat.*, 1974, 92, 47.
63. Bertin, R. I., *Plant Reproductive Ecology*, (eds. Lovett Doust, J. and Lovett Doust, L.), Oxford University Press, Oxford, 1988, p. 30.
64. Udovic, D., *Oecologia*, 1981, 48, 389.
65. Lloyd, D. G., *New Phytol.*, 1980, 86, 69.
66. Sutherland, S., *Evolution*, 1987, 41, 750.

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

Mary E. O'Donnell and Kamaljit S. Bawa

Department of Biology, University of Massachusetts, Boston, MA 02125, USA

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