Chapter 7

Pollination: costs and consequences

Chapter 5 discussed the evolution of the seed habit. I argued that pollination is the major adaptive character which distinguishes seed plants from pteridophytes. This chapter presents a miscellany of models that investigate some very general properties and consequences of pollination. The models are intended as simple heuristic devices to illustrate robust properties of pollination and reproduction by seeds. They are not intended to represent the many complexities of real pollination biology.

The meanings of some of the models' parameters "evolve". Thus, p starts off as a megaspore's probability of fertilization and ends up as the seed/ovule ratio. I have chosen to use parameters that shift in meaning from model to model, rather than use a new set of parameters for each model, because I wish to emphasize continuity in the evolutionary process.

I. When are adaptations for microspore capture advantageous?

Pollination must have evolved from a mating system in which most encounters between male and female gametophytes occurred after propagule dispersal. This required the acquisition of adaptations for microspore capture. Paleozoic ovules possessed a variety of mechanisms for pollen reception. The earliest was a funnel-shaped modification of the distal end of the megasporangium known as a salpinx or lagenostome (Taylor & Millay 1979). A salpinx presumably increased the probability of pollination but would also have increased the cost per ovule. Under what circumstances would natural selection favor ovules with a salpinx or similar structure?

Suppose that propagules of the seed plant ancestor usually encountered microspores after dispersal but occasionally encountered microspores before dispersal. Further suppose that the propagules had no special adaptations for microspore capture. Parental fitness w can be defined as the return in seedling

survival per unit cost,

$$w = qs/a \qquad (7.1)$$

where q is the probability of fertilization, s is the probability of seedling survival given fertilization, and a is the cost of a propagule ("propagule size").

Now suppose that a mutant sporophyte produced propagules of the same "size" a but that each propagule possessed some structure X (of additional cost b) that increased the probability of pre-dispersal encounter. Then,

$$w_X = ps/(a + b) \qquad (7.2)$$

where p is the probability of fertilization given structure X. X would increase parental fitness if (7.2) > (7.1). That is,

$$\frac{p}{q} > \frac{a + b}{a} \qquad (7.3)$$

In common language, X is adaptive if the proportional increase in the probability of fertilization is greater than the proportional increase in cost per propagule. I have talked about X as a structure, but X can represent any adaptation that increases the probability of pollination, provided that the adaptation has a constant cost per ovule. For example, b could represent the costs of producing a pollination droplet or the increased respiration costs from delayed dispersal.

To a first order approximation, the increased probability of fertilization for a structure X should be independent of propagule size a. For example, a salpinx of given size should be equally effective in trapping microspores whether it is attached to a large or small ovule. Therefore, p/q should be roughly constant for different ovule sizes, but the proportional increase in cost will decrease as ovules become larger. The consequence is that structures for microspore capture attached to each ovule are of greater advantage for species with larger ovules. This could help to explain why the earliest seeds were generally larger than

contemporary megaspores (see Chapter 1; Chaloner & Sheerin 1981). Adaptations for microspore capture might only have been economical above some minimum megaspore size.

II. How much should a sporophyte allocate to pollinated and unpollinated propagules?

Suppose that an ancestral seed plant had a pteridophytic mating system in which most propagules encountered microspores after dispersal but occasional propagules captured a microspore before dispersal. Then, a sporophyte would produce two types of propagules: "pollinated" propagules that were guaranteed fertilization, and unpollinated propagules that would not be fertilized unless they encountered a microspore after dispersal. From the sporophyte's perspective, pollinated propagules would be of greater value than unpollinated propagules because a larger proportion of pollinated propagules would be fertilized. In this section, I ask whether a sporophyte would benefit by supplying pollinated and unpollinated propagules with different amounts of resources.

This is a specific case of the general question, how much should a parent allocate to individual offspring when offspring differ in quality? In the Appendix to Chapter 2, I concluded that a parent should continue to invest in an offspring until the marginal return on investment equals the average return from all offspring. Further, the parent should abort all offspring whose expectation of fitness falls below some threshold. Here, I argue that this model predicts strong positive feedback favoring the evolution of an obligate pollination system from a pteridophytic mating system in which occasional propagules are pollinated.

I will make the simplifying assumption that the probability of success given fertilization is the same for pollinated and unpollinated (but otherwise identical) propagules. If the same allocation is made to pollinated and unpollinated propagules, a sporophyte's return on investment will be higher for pollinated propagules. Put in other words, the marginal return on investment in pollinated propagules is greater than the average return from all propagules. Conversely, the marginal return from unpollinated propagules is less than the average return. Therefore, the

sporophyte would benefit from allocating more to each pollinated propagule and less to each unpollinated propagule.

Thus, if a sporophyte can detect pollination, pollinated ovules should receive more resources than unpollinated ovules. This creates an advantage for microspores which encounter propagules before, rather than after, propagules are dispersed. As a consequence, sporophytes would be selected to produce microspores that are adapted for pre-dispersal encounters. Adaptations of microspores for pollination should decrease the likelihood of unpollinated propagules being fertilized after dispersal and favor complementary adaptations of propagules for microspore capture before dispersal. These processes are self-reinforcing.

Differential allocation could be achieved in one of two ways. All propagules could receive the larger amount and resources be withdrawn from unpollinated propagules, or all propagules could receive the lesser amount and pollinated propagules receive additional resources after pollination. The second method is more practicable and the mechanism adopted by seed plants. The optimal allocation to unpollinated propagules decreases as pollination becomes more common (Chapter 2, Appendix). These factors favor a progressive delay in the time of provisioning, relative to the time of pollination. Once the proportion of unpollinated propagules falls below some threshold, a sporophyte could obtain higher fitness by aborting rather than provisioning unpollinated propagules (Chapter 2, Appendix). Thus, a pteridophytic mode of reproduction can be replaced by an obligate pollination system.

III. How are seed size and parental fitness related?

The definition of parental fitness in equation (7.2) is not appropriate if unpollinated ovules are aborted. When an ovule is aborted, its parent incurs the cost of structures for pollen capture b, as well as some additional cost c for other resources (committed to the ovule) which cannot be recovered. Therefore, parental fitness can be represented in the form

$$w = \frac{ps}{p(a + b) + (1 - p)(b + c)} \qquad (7.4a)$$

where p is the proportion of provisioned ovules (i.e. the seed/ovule ratio), and s is redefined as the probability of seedling survival given provisioning. The numerator is the expected return per ovule and the denominator is the average cost per ovule. I defined p as the proportion of provisioned ovules rather than the proportion of pollinated ovules because I wish to emphasize that this equation also applies if some pollinated ovules are aborted. The equation can be rearranged to give the form

$$w = \frac{s}{(a - c) + (b + c)/p} \qquad (7.4b)$$

where the numerator is the expected return per seed (i.e. per provisioned ovule) and the denominator is the cost per seed. The denominator has two components: $(a - c)$ which is the additional cost of a provisioned ovule as compared to an aborted ovule, and $(b + c)/p$ which is the cost of an aborted ovule, $b + c$, multiplied by the number of ovules per seed, $1/p$.

These equations are not meant to imply that a, b, c, p, s, are mutually independent factors that jointly determine parental fitness. Some associations between the factors are obvious: seed size a and seed survival s are clearly related; the costs of pollen capture b determine an ovule's likelihood of being pollinated, and thus influence p. Other relationships are less obvious: if pollinated ovules are selectively aborted, p influences s; c affects the optimal value of b, because c is incurred whether or not an ovule is pollinated. The purpose of the various forms of equation (7.4) is to make the obvious point that the cost to a sporophyte of producing an additional seed cannot simply be measured by the energy content of the seed.

I will use another form of (7.4) to describe the optimal seed size $\hat{a}$ (given b, c, p) in terms of the Smith-Fretwell model. Suppose that s can be represented as a function of a. Then,

$$w = \frac{f(a)}{a + b/p + (1 - p)c/p} \qquad (7.4c)$$

The cost per seed (denominator) is expressed as the sum of three components: seed size, a; the cost per seed of pollen capture, b/p; and $(1 - p)c/p$, the cost per seed of aborted ovules. This equation is essentially the same as (2.4b), with the addition of b/p to the denominator. The optimal seed size $\hat{a}$ is given by the intercept of $f(a)$ with the tangent from a point k to the left of the origin (Figure 7.1) where $k = b/p + (1 - p)c/p$. I will refer to k as the supplementary cost of a seed.

An evolutionary innovation that reduced the supplementary cost per seed would be of greater advantage to species with small seeds than to species with large seeds. If k was reduced to half its previous value, this would have a large effect on the fitness of small-seeded species (k large relative to a) but little effect on large-seeded species (k small relative to a). Thus, supplementary costs can influence the relative fitness of species with different types of seeds (i.e. different $f(a)$). Figure 7.2 illustrates this effect. When k is large (Figure 7.2a), the species with the larger seeds has the higher return per unit investment but, when k is small (Figure 7.2b), the relative fitnesses are reversed.

The Smith-Fretwell model assumes that offspring fitness can be represented as a function of a single variable (in this case $s = f(a)$). For a particular relationship between seedling survival and seed size (i.e. for given $f(a)$), an increase in k has two effects: optimal "seed size" ($\hat{a}$) increases, and the parent's return per unit investment (the slope of the tangent at $\hat{a}$) decreases. This analysis implicitly assumes that the change in k does not affect seedling fitness. Otherwise, s would be a function of more than one variable. Some changes in supplementary costs will influence seedling fitness, particularly if these changes influence which offspring genotypes are provisioned. For example, selective seed abortion would decrease p but increase s.

In the discussion above, seed size is considered to be a variable within the constraints imposed by the function $f(a)$. Among seed plants, seed size varies over several orders of

Figure 7.1. A seedling's probability of survival given provisioning is a function of *a*, the provisioning cost of its seed. The cost to the parent of each seed also includes a supplementary cost (resources committed to pollen capture and to ovules that remain unpollinated). For a given supplementary cost *k* (see text), parental fitness (the return in offspring survival per unit cost) is maximized at $\hat{a}$.

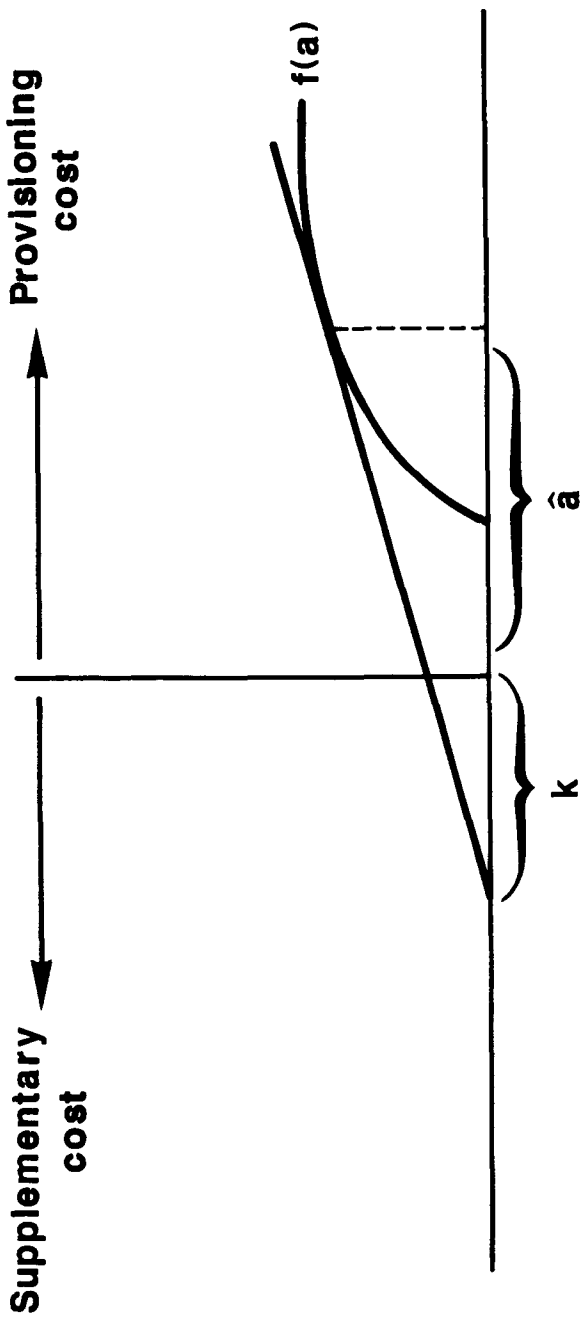
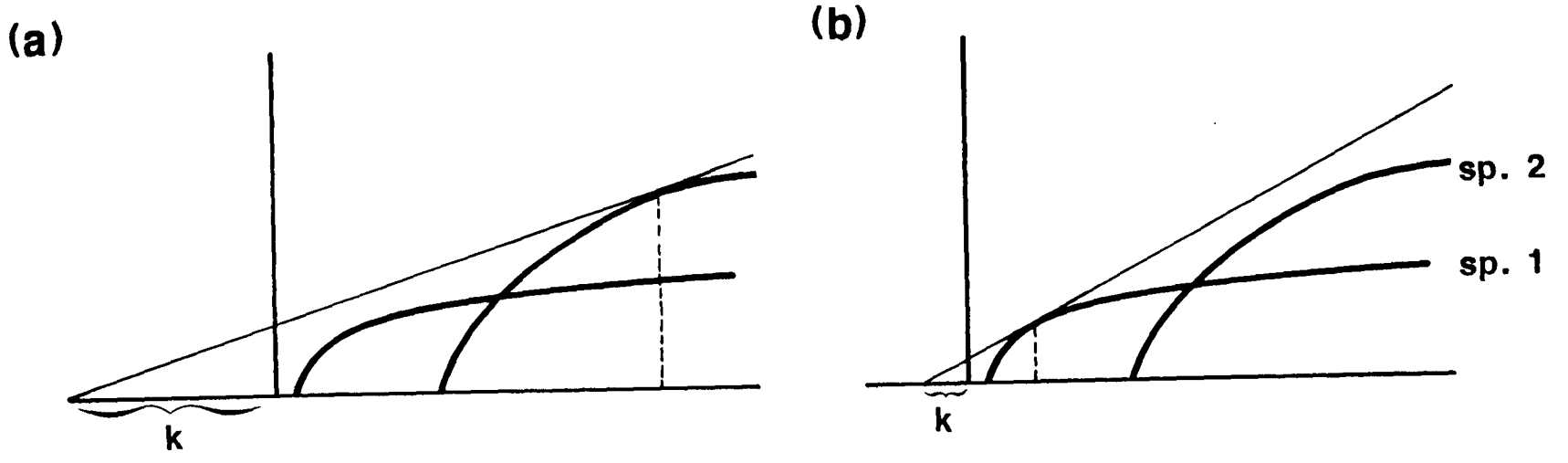


Figure 7.2. Species 1 produces many small seeds each with a low probability of survival given pollination. Species 2 produces fewer, larger seeds each with a high probability of survival given pollination. (a) If the pollination cost per seed is large, Species 1 has the lower relative fitness. (b) If the pollination cost per seed is small, Species 2 has the lower relative fitness.

The vertical axis gives the probability of seedling survival given provisioning. The horizontal axis gives the cost per seed. Distances to the left of the origin represent supplementary costs *k*, and distances to the right of the origin represent provisioning costs *a*. Relative fitness corresponds to the return in seedling survival per unit cost.



magnitude and this must represent different species having different forms of $f(a)$. What causes variation in the form of $f(a)$? Environmental factors obviously have a role but seed size varies markedly among species within the same environment (e.g. Mazer 1989). The crucial factor is undoubtedly the type of seedling that develops from the seed. An orchid and an avocado may grow in the same forest but their seedlings have very different growth forms. This is an extreme example but the same principle applies if two species produce seedlings with a lignified stem versus a herbaceous stem or a first pair of leaves that expand to cover 5 mm^2 versus 5 cm^2. The size-versus-number model assumes that it is meaningful to ask how an avocado seedling's fitness would be affected by receiving slightly less or slightly more nutrients in its seed.

IV. What is the relationship between seed size and the supplementary cost per seed?

The previous section showed that a parent's return per unit investment can be represented in the form

$$w = s/(a + k) \qquad (7.4d)$$

where s is the probability of seedling survival; a is the direct cost per seed ("seed size"); and k is the supplementary cost per seed. If k was constant for seeds of different sizes, species with larger seeds would spend a greater proportion of total reproductive resources on seed food reserves and a smaller proportion on the costs of pollination and seed abortion. Seed size varies over several orders of magnitude. Therefore, supplementary costs could become prohibitive for very small seeds. Clearly, it is important to know the relative contribution of direct and supplementary costs to the total cost of a seed, for seeds of very different sizes.

I propose that the proportion of a sporophyte's reproductive resources that must be committed to pollen capture and aborted ovules is, on average, greater for species with smaller seeds. This is because sporophytes cannot decrease the supplementary cost per seed in proportion to seed size. For purposes of

discussion, I will divide k into two components that will be discussed in turn. The components are b/p, the pollination cost per seed, and $(1 - p)c/p$, the abortion cost per seed.

Pollination costs should be determined primarily by characteristics of the pollen and its vector, rather than by seed size. One way to reduce the cost per ovule of pollination would be to use the same structure for more than one ovule. This strategy appears to be an effective method of reducing pollination costs in angiosperms, because a single stigma and perianth can service several ovules and the number of ovules in an ovary can be increased as seed size decreases. There is less potential for cost-sharing in gymnosperms because ovules receive pollen individually. In gymnosperms, adaptations for pollen capture (e.g. a pollination droplet) tend to be replicated for each ovule, and their effectiveness for pollen capture should be roughly independent of final seed size. Therefore, either the proportional cost of pollen capture increases (b constant) as seed size decreases or the sporophyte spends less per ovule on pollen capture but a lesser proportion of ovules are pollinated (b is reduced at the expense of a decrease in p). Gymnosperms are probably very limited in their ability to reduce b/p as seed size decreases.

The abortion cost per seed could be reduced by increasing the seed/ovule ratio (increasing p) or by reducing the cost per aborted ovule (decreasing c). An increase in the seed/ovule ratio appears to be the best option for decreasing abortion costs as seeds become smaller, because natural selection should already have brought c close to the minimum value set by developmental constraints. The seed/ovule ratio could be raised by increasing the proportion of pollinated ovules at the expense of increased expenditure on pollen capture, or by being less selective in which pollinated ovules are provisioned. Neither option is guaranteed to increase parental fitness because both have associated costs.

Thus, plausible arguments suggest that supplementary costs should be proportionally more expensive for species with smaller seeds. The hypothesis should be tested by comparing the relative allocation of resources to seed food reserves and to other

reproductive functions in species with very different seed sizes. The choice of monoecious and dioecious species would reduce complications arising from male function. The test is not ideal because it would be potentially confounded by trade-offs between increasing the seed/ovule ratio and reducing average seedling quality or reducing the buffer against years of poor pollination (see section VII). For example, species with small seeds could adopt facultative selfing to increase the seed/ovule ratio at the expense of reduced seedling quality. On the other hand, if aborted ovules are relatively less expensive for species with large seeds (as hypothesized), it might be economical for such species to decrease their seed/ovule ratio and be more selective as to which seeds are provisioned. (This does not even consider the feedback between different mating systems, genetic load, and offspring quality.)

V. For what types of propagule is gymnospermous reproduction superior to pteridophytic reproduction?

This section performs the thought experiment of comparing the return per unit investment for a heterosporous pteridophyte and a seed plant that produce similar propagules. The pteridophyte is assumed to lack adaptations for predispersal capture of microspores. Megaspores are dispersed and are either fertilized or not fertilized depending on their proximity to a microspore. On the other hand, the seed plant has adaptations for pollen capture and aborts unpollinated ovules. The model is a restatement of the model in Section I, except that in this model unpollinated ovules are aborted.

Compare a heterosporous pteridophyte and a gymnosperm that produce propagules of equivalent size a and equivalent probability s of producing a successful sporophyte given that a megaspore is fertilized or a seed is provisioned. For the same reproductive effort, the pteridophyte can produce more propagules because the pteridophyte does not incur the supplementary cost per propagule k. However, the pteridophyte's expected fitness gain per propagule will be less than that of the gymnosperm because megaspores, unlike seeds, are provisioned whether or not they will be fertilized. The pteridophyte's fitness (w_p) can be

represented in the form

$$w_p = qs/a \qquad \text{(see 7.1)}$$

where q is the proportion of megaspores that are fertilized (q is determined by the number and dispersal of conspecific microspores and should be independent of a). The gymnosperm's fitness (w_s) can be represented in the form

$$w_s = s/(a + k) \qquad \text{(see 7.4d)}$$

The gymnosperm will have the higher return per unit investment if $w_s > w_p$. That is, if

$$\frac{a}{(a + k)} > q \qquad (7.5)$$

The left-hand side of this inequality is the ratio of direct seed costs to total seed costs. As argued in the previous section, this ratio should decrease for smaller seeds. The proportion of a sporophyte's reproductive resources that are expended on supplementary costs should be greater for species with smaller seeds and the relative advantage of gymnospermous over pteridophytic reproduction should increase as propagule size increases. There is a possibility that, for small propagule sizes, reproduction by megaspores may be superior to reproduction by seeds, but this will depend on the relative values of q and k.

VI. Can the supplementary costs of seed production explain minimum seed size?

Seed production is subject to a size-versus-number trade-off in that more seeds can be produced if seeds are smaller but each seed has a smaller probability of successful establishment. Modern and fossil floras reveal that different species have adopted very different compromises between seed size and number (see Chapter 1). In this section, I am not concerned with why different species have different seed sizes, but with the reasons for the lower limit to seed size. I propose that minimum seed

sizes are determined by the supplementary cost per seed.

Supplementary costs have a significant effect on the size-versus-number trade-off. The number of seeds that can be produced from a given quantity of resources is proportional to $a + k$. Thus, if a is large relative to k, halving seed size will almost double the number of seeds produced. However, if a is small relative to k, halving seed size will have little effect on total number of seeds. Put another way, if a is small relative to k, a sporophyte can improve seedling survival by increasing seed size without a major decrease in seed numbers. In a previous section, I argued that supplementary costs are relatively more expensive for smaller seeds (i.e. a/k is a decreasing function of a). Therefore, as seeds become smaller, the same proportional decrease in seed size gives a smaller proportional increase in seed number. The same argument does not apply to spore size in pteridophytes because they do not incur the supplementary costs of pollination and seed abortion. Halving spore size doubles spore numbers for spores of all sizes (within a given reproductive investment).

By this argument, the minimum size of seeds can be explained because, below a certain size, there is little gain of increased numbers by producing smaller seeds. The minimum size would be determined by the ratio of provisioning costs to supplementary costs (a/k) which decreases with declining seed size. Clearly, any evolutionary innovation that substantially reduces k will decrease minimum seed size. This conclusion is significant because some seeds of early angiosperms were an order of magnitude smaller than the smallest gymnosperm seeds from earlier periods. This suggests that a reproductive advantage of early angiosperms was a smaller supplementary cost per seed than occurs in gymnosperms (see Chapter 8 for a fuller discussion).

The minimum seed size is the second critical value that is necessary to understand the correlation between different life cycles and propagule size. The first was the *heterospory threshold*, the critical spore size above which heterosporous reproduction becomes adaptively superior to homosporous reproduction (Chapter 4). If an evolutionary innovation in seed plants reduced k sufficiently, the minimum seed size could

converge on the heterospory threshold.

VII. Can supplementary costs explain changes in species diversity?

The adaptive radiation of angiosperms in the Cretaceous and early Tertiary was associated with a dramatic increase in within-floral diversity (Chapter 1; Knoll 1986). This section addresses the reasons for this increase in species diversity. The argument presented below is based on the elegant model of species-packing developed by Hopf & Hopf (1985) and Bernstein et al. (1985).

Sexual reproduction requires the coming together of two individuals to mate (e.g. an encounter between a male and female gametophyte). Such encounters become intrinsically less likely as the members of a species become more widely scattered. Thus, sexual species experience an inherent disadvantage at low population density. Members of a rare species must allocate a greater proportion of time and/or resources to obtaining mates than would members of a comparable common species. Hopf & Hopf (1985) and Bernstein et al. (1985) have argued that this cost of rarity imposes a limit on the number of species that can occupy an environment and a limit on fine-scale adaptation to the environment.

Hopf & Hopf (1985) developed a model in which similar species exploited different regions of a one-dimensional resource continuum. Each species was most efficient at exploiting one point on the continuum but could also exploit neighbouring points with lesser efficiency. The intrinsic ability of a species to exploit different points on the continuum was described by a "utilization function". For each species, this function was centered on a different point on the continuum but the functions were otherwise identical.

For a given species, the number of individuals that the environment could support was called the species' carrying capacity. This was determined by the amount of resources at each point on the continuum, the utilization function of the species and by the amount of resources consumed by neighbouring species. When a new species was introduced to the environment, this reduced the resources available to neighbouring species and

reduced their carrying capacity. If there was no cost of rarity, a potentially unlimited number of species could occupy the environment. A new species could invade the environment, provided that it could exploit some point on the continuum more efficiently than existing species. If there was a cost of rarity, this condition was no longer sufficient because the environment might be unable to support a viable population of the species. The greater the cost of rarity, the fewer species that could be accomodated on the continuum.

The models of Hopf & Hopf (1985) and Bernstein et al. (1985) assumed that all species experienced the same cost of rarity. What if this assumption were relaxed? Suppose that an environment was saturated with species with a high cost of rarity (call them gymnosperms). Not all parts of the environment would have been optimally exploited but the underexploited regions would not have had sufficient carrying capacity to support another species. A new species could only invade by displacing an existing species. Now suppose that a clade of species arose with a lower cost of rarity (call them angiosperms). These species would have been able to invade, thus reducing the carrying capacity of established species which would eventually be squeezed out of the environment. By this means, a flora with a small number of gymnosperm species could be replaced by a flora with a greater diversity of angiosperms. The replacement of gymnosperms by angiosperms in this model results from the angiosperms' lower cost of rarity. Angiosperms would replace gymnosperms even if they had identical utilization functions.

In seed plants, the cost of rarity is reflected in an increased supplementary cost per seed in sparser populations. As a species becomes rarer, either more resources are required to ensure pollination or the seed/ovule ratio declines as fewer ovules are pollinated. That is, $b/p + (1 - p)c/p$ decreases because there is an increase in b or a decrease in p. Fewer seeds can be produced from the same amount of resources and the ratio of provisioning costs to supplementary costs a/k increases.

Suppose that a decrease in abundance doubles k. This increase in costs will have a greater impact on species in which supplementary costs already comprise a larger proportion of total

seed costs (i.e. species in which a/k is already small). Therefore, the fitness of large-seeded plants is less affected by changes in density than the fitness of small-seeded plants, because species with large seeds tend to have higher a/k (Section IV above). Similarly, angiosperms appear to have higher a/k than gymnosperms with similar-sized seeds (Section V above). This may have contributed to a lower cost of rarity in angiosperms and the high diversity of angiosperm-dominated floras.

The initial radiation of gymnosperms was also accompanied by an increase in diversity. Here I consider whether early seed plants might have had a lower cost of rarity than contemporary pteridophytes. A pteridophyte's fitness (w_p) is proportional to the probability of fertilization (q). If q is halved, so is w_p (see equation 7.5). By contrast, a seed plant's fitness (w_s) is not proportional to the probability of pollination (p). If p is halved, w_s is reduced by less than half (see equation 7.4b). Therefore, a seed plant is less affected by increased rarity than is a pteridophyte. This is because a pteridophyte provisions all propagules regardless of fertilization but a seed plant provisions only those propagules that are pollinated. For simplicity, I have equated p with an ovule's probability of pollination and q with a megaspore's probability of fertilization. Much the same result applies if some pollinated ovules do not produce seeds and some fertilized megaspore's do not produce embryos because of genetic load.

Pollination may have allowed gymnosperms to persist at lower population densities than pteridophytes and, by this means, could have contributed to increased diversity. An alternative explanation should be mentioned. The origin of the seed habit was associated with the evolution of trees and the appearance of forests (Chapter 5). Increased diversity may have been a result of the greater structural complexity of plant communities.

VIII. When will seed production be pollen-limited?

The number of spores produced by a fern sporophyte is expected to be limited by the resources available to the sporophyte. What limits seed production, in any particular case, is less clear because a sporophyte might be unable to produce more seeds either

because it has insufficient resources or because insufficient ovules are pollinated. This section discusses the contrast between resource-limitation and pollen-limitation of seed production.

The model presented here is an extension of an earlier model developed by Haig & Westoby (1988d) in which we argued that a sporophyte's allocation of resources should be adjusted by natural selection to a point where seed production is equally limited by pollen supply and by resources. That model did not formally deal with unpredictable variation in pollen supply. The current model attempts to remedy that deficiency by considering the limits to seed production when pollen supply is uncertain at the time when ovule number is determined.

The model presented in this section is in some senses unsatisfactory, because it seeks an allocation strategy that maximizes the expected number of seeds (arithmetic mean) in a single breeding episode. The use of the geometric mean is usually considered to be a more appropriate measure of fitness in variable environments, but I believe there are also difficulties with using the geometric mean as the measure of fitness. A multiplicative model implicitly assumes that all of an individual's descendants in a future generation experience the same likelihood of pollination. If not, some form of arithmetic averaging would be necessary for seed production of different descendents in the same generation, and some form of geometric averaging to combine fitnesses from successive generations (cf. Venable & Lawlor 1980). An additive component to the model is also necessary if sporophytes are iteroparous, because life-time seed production is summed over a number of seasons with different (unpredictable) levels of pollen supply. I present the model here, despite its limitations, because I believe its qualitative features are essentially accurate.

The parameters used in this model are slightly different from the parameters used in previous sections. In particular, the cost of an aborted ovule in section (iii) was $b + c$ and the additional cost of provisioning was $a - c$. In this section, an aborted ovule is defined as having unit cost and the provisioning cost is m. Thus, m is equivalent to $(a - c)/(b + c)$. In this

section, p corresponds to the proportion of pollinated ovules rather than the proportion of provisioned ovules.

Suppose that a parent produces x ovules at unit cost out of a total reproductive resource of K units. The amount of resources remaining for seed provisioning is $K - x$, and the number of seeds that can be provisioned is

$$\alpha = (K - x)/m \tag{7.6}$$

where m is the cost of provisioning a pollinated ovule. If a proportion p of ovules are pollinated, the number of pollinated ovules is

$$\beta = px. \tag{7.7}$$

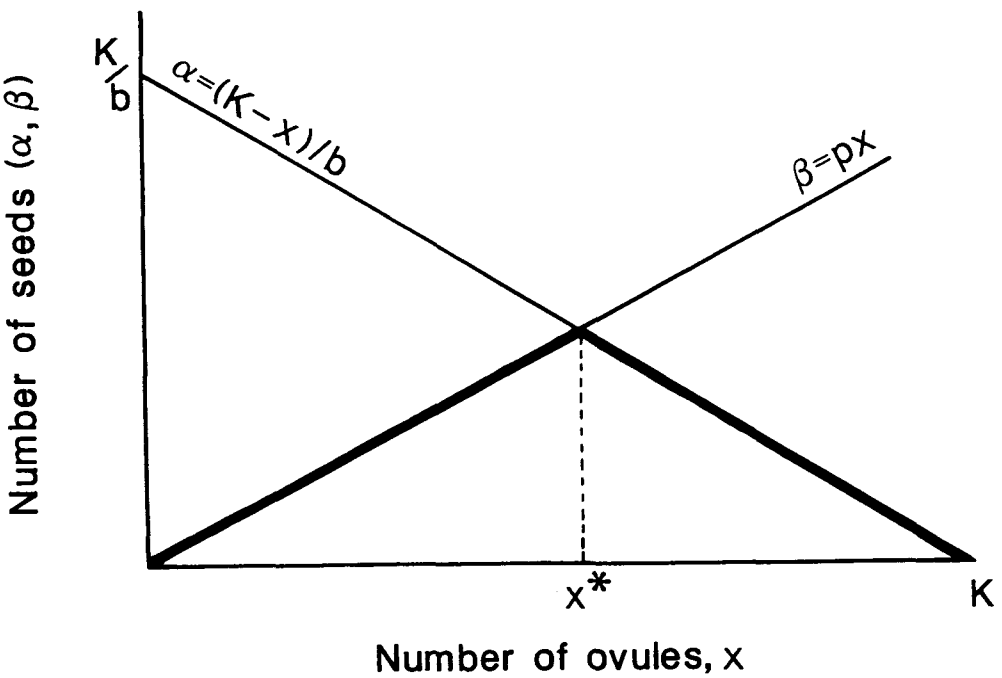
The number of pollinated ovules provisioned by a parent is the lesser of these two quantities. If $\alpha > \beta$, some resources remain uncommitted after all pollinated ovules are provisioned. The parent could have produced more seeds if some of these surplus resources had been used to produce additional ovules. If $\alpha < \beta$, there are insufficient resources to provision all pollinated ovules. The parent could have produced more seeds if fewer ovules had been produced, thus liberating resources to provision additional pollinated ovules. If $\alpha = \beta$, no resources remain after all pollinated ovules are provisioned and the parent could not have increased its number of seeds by producing a different number of ovules (Figure 7.3).

How many ovules should a parent produce if the proportion of ovules that will be pollinated is uncertain at the time when the number of ovules is determined? Suppose that p is a random variable with probability density function $\phi(p)$, where p is independent of x. For any given x, there exists a threshold value of p (call this threshold t) at which $\alpha = \beta$.

$$(K - x)/m = tx$$

$$x = K/(mt + 1). \tag{7.8}$$

Figure 7.3. The heavy line represents the function that relates number of seeds to number of ovules. The function is a maximum at x^*. Seed production is pollen-limited to the left of x^*, but resource-limited to the right of x^* (for details see text).



A parent that produces x ovules has sufficient resources to provision tx seeds, but the number of seeds produced will depend on p. Reproductive attempts are of two types. In *bad pollination years* ($p < t$) seed production is pollen-limited because some resources remain after all pollinated ovules are provisioned. In such years, the parent produces px seeds, and artificial pollination could increase seed set. In *good pollination years* ($p > t$), seed production is resource-limited because some pollinated ovules remain unprovisioned. In such years, the parent produces tx seeds, and artificial pollination does not increase seed set. The seed/ovule ratio is p in bad pollination years and t in good pollination years. The expected number of seeds is

$$\mu = x \left[\int_0^t p\phi(p)\ dp + t \int_t^1 \phi(p)\ dp \right] \qquad (7.9)$$

The set of alternative strategies consists of all possible values of x. Changes in x have opposite effects on α and β. An increase in x reduces the amount of resources for a parent to provision seeds but increases the number of pollinated ovules. Thus, a parent with a greater value of x can produce fewer seeds when seed production is resource-limited but more seeds when seed production is pollen-limited. A corollary is that seed production becomes resource-limited at a lower value of p. In other words, an increase in x reduces the pollination threshold t. Some years that were previously pollen-limited are now resource-limited. The seed/ovule ratio in good pollination years (which is equal to t) is also reduced.

The effect of producing more ovules (from a fixed total resource) is to increase a parent's seed production in years when pollination is poor, at the expense of reduced seed production in years when pollination is good. The strategy which maximizes the expected number of seeds can be found by differentiating (7.9) with respect to x or with respect to t. The two derivatives have the same stationary points. I choose to differentiate with respect to t for convenience. I will call this the maximal strategy rather than the optimal strategy, because μ is an unsatisfactory measure of fitness.

$$\frac{d\mu}{dt} = x \left[\frac{d}{dt}\int_0^t p\phi(p)\ dp + t\,\frac{d}{dt}\int_t^1 \phi(p)\ dp + \int_t^1 \phi(p)\ dp\right] + \frac{dx}{dt}\left[\int_0^t p\phi(p)\ dp + t\int_t^1 \phi(p)\ dp\right] \qquad (7.10)$$

Using Leibnitz's rule to evaluate the derivatives of integrals and substituting (7.8) for x gives

$$\frac{d\mu}{dt} = \frac{K}{mt+1}\left[t\phi(t) - t\phi(t) + \int_t^1 \phi(p)\ dp\right] - \frac{Km}{(mt+1)^2}\left[\int_0^t p\phi(p)\ dp + t\int_t^1 \phi(p)\ dp\right]$$

$$= \frac{K}{(mt+1)^2}\left\{\int_t^1 \phi(p)\ dp - m\int_0^t p\phi(p)\ dp\right\} \qquad (7.11)$$

There is a stationary point ($d\mu/dt = 0$) at which the expected number of seeds is a maximum ($d^2\mu/dt^2 < 0$) when

$$\int_t^1 \phi(p)\ dp = m\int_0^t p\phi(p)\ dp \qquad (7.12)$$

Equation (7.12) defines the maximal strategy in terms of t, the proportion of pollinated ovules at which seed production becomes resource-limited. The expected number of seeds is a maximum when the proportion of good pollination years (left-hand side) equals m times the average probability of pollination in bad pollination years (right-hand side). This is an implicit statement about x, because x defines t (equation (7.8)).

The maximal strategy depends on $\phi(p)$ and m. By definition, an ovule has unit cost. Therefore, m measures the cost of provisioning a seed relative to the cost of an ovule. This is not simply the ratio of seed dry weight to ovule dry weight, because each additional ovule has associated costs of floral attractants and the like. Nevertheless, species with a larger ratio of seed to ovule dry weight will usually have larger m. Consider the maximal strategies of two species with the same distribution of pollination probabilities $\phi(p)$, but with different relative seed sizes. The species with larger seeds (higher m) would be resource-limited in a greater proportion of years and would have a lower average seed/ovule ratio.

The model does not consider the possibility that resources

which remain uncommitted in poor pollination years could be used for reproduction in subsequent seasons. Iteroparity should reduce the fitness costs arising from underutilized resources in poor seasons. Its effect should be to increase the emphasis on reproduction in years when pollination is cheap. In other words, an iteroparous parent should produce fewer ovules than an (otherwise equivalent) semelparous parent and should be pollen-limited in a greater proportion of seasons.

In summary, a parent is predicted to be pollen-limited in some years and resource-limited in others because of uncertainty in pollen supply. If seeds are very expensive relative to ovules, the proportion of years in which seed production is pollen-limited may be small. If different modules (e.g. inflorescences) have independent resource pools, some modules could be resource-limited at the same time as other modules on the same plant are pollen-limited. The existence of "surplus" pollinated ovules in good pollination years would favor the evolution of any mechanism which ensured that pollinated ovules of lower quality are preferentially aborted.

This model has shown how the overproduction of ovules provides a buffer that partially compensates for variation in pollination success. Udovic (1981) and Sutherland (1986) have referred to this effect as *bet-hedging*. I prefer to call it a *buffer effect* because the extra ovules result in an increase in expected or arithmetic mean seed production. Seger & Brockmann (1987) defined bet-hedging as situations in which an individual experiences a loss of expected fitness in order to reduce the variance of fitness. My model does not consider the variance of expected seed production, but the effect of bet-hedging can be described. A sporophyte that produces more ovules from a fixed total resource reduces the variance of its expected number of seeds, because seed production is resource-limited in a greater proportion of years and the sporophyte produces the same number of seeds tx in all those years. Therefore, considerations of variance would predict lower seed/ovule ratios than are predicted on the basis of average fitness alone.

[Kozlowski & Stearns (1989) have recently published a model of "bet-hedging" where resources are unpredictable at the time

when zygote number is determined. This paper appeared during the final stages of my write-up and I have had insufficient time to study the reasons for the similarities and differences between our two models. Their random variable is resource supply rather than pollination level. In *poor resource years*, there are insufficient resources remaining after zygotes are produced to provision all zygotes. In *good resource years*, all zygotes are provisioned with resources to spare. The value to be optimized is the number of zygotes. Their model has a similar mathematical structure to the model presented here. Kozlowski & Stearns also maximized the expected number of offspring (arithmetic mean) by differentiating with respect to a limit of integration that defined which years were classified as poor resource years and which as good resource years. They also did not take account of the possibility that unused resources in good years could be used in subsequent years. Like my model, Kozlowski & Stearns also came to the (obvious) conclusion that a greater overproduction of zygotes/ovules is favored when the cost of abortion is small relative to the cost of maturing an offspring.]

IX. Should seed/ovule ratios be correlated with seed size?

The basic conclusion of the previous section that "larger" seeds favor smaller seed/ovule ratios and more frequent resource-limitation follows from the general principle that any benefits from the overproduction of ovules become more economical as the relative cost of additional ovules decreases. This principle applies to other hypothesized functions of surplus ovules. For example, selective abortion of ovules becomes more economical as the relative cost of aborted ovules decreases relative to the cost of a matured seed.

Statistical studies of seed/ovule ratios (Wiens 1984) or fruit/flower ratios (Sutherland 1986) have not considered seed size as a possible determinant of observed patterns. Wiens (1984) found that annuals had higher seed/ovule ratios than perennials (including woody perennials). He believed that perennials had breeding systems favoring genetic recombination. Thus, the high levels of abortion in perennials were a consequence of the elimination of lethal or sub-lethal allelic combinations, whereas

inbreeding annuals were more genetically uniform (see also Wiens et al. 1987). However, most inbreeding annuals are herbs, and herbs generally have smaller seeds than shrubs or trees (Harper, Lovell & Moore 1970; Baker 1972). Thus, differences in seed size are confounded with differences in life form and breeding system.

Sutherland (1986) found that herbaceous species had higher fruit/flower ratios than woody perennials. This relationship existed for self-incompatible species but not self-compatible species. Sutherland suggested that woody plants usually have a longer time span between flower initiation and fruit maturation. On this argument, fruit-set of woody plants is less predictable at the time of flower initiation and lower fruit/flower ratios reflect a greater emphasis on "bet-hedging". The model discussed above provides an alternative explanation, in that the same pattern is predicted if the herbs had smaller seeds than the woody plants.

These alternative hypotheses are presented to emphasize the need to consider seed size as a variable in studies of seed/ovule ratios, rather than to claim that explanations based on seed size are more plausible than the hypotheses of other authors.

Chapter 8

Adaptive explanations for the rise of angiosperms

Angiosperms are by far the most successful group of vascular plants in the modern flora. Their rapid rise to dominance during the Cretaceous and early Tertiary suggests that the group had some reproductive advantage (broadly defined) over earlier seed plants. I am using reproductive advantage to refer to adaptations that increase growth and the amount of reproductive resources accumulated, as well as adaptations that increase the efficiency with which a given quantity of reproductive resources is converted into successful seedlings. This chapter discusses the nature of this advantage.

Section I reviews some hypotheses from Chapter 7. In that chapter, I proposed that early angiosperms were able to produce smaller seeds than gymnosperms because angiosperms had a lower supplementary cost per seed. Smaller propagules probably allowed some angiosperms to adopt herbaceous growth habits that had previously been dominated by pteridophytes. Of greater significance, angiosperms could persist at lower population densities than could gymnosperms. In consequence, angiosperms were able to displace gymnosperms from many habitats, and angiosperm-dominated floras were more speciose than the gymnosperm-dominated floras they replaced. Section II discusses various hypotheses that have been proposed by other authors to account for the success of angiosperms. Section III is an overview. I conclude that there is insufficient evidence at present to unambiguously identify which characters were responsible for angiosperm success.

I. PATTERNS

A satisfactory theory explaining the reproductive advantage of early angiosperms would need to account for two curious patterns (see Chapter 1). (1) Angiosperm seeds from the Early Cretaceous

were uniformly small. The smallest angiosperm seeds were about an order of magnitude smaller (by volume) than the smallest gymnosperm seeds from previous periods. (2) Angiosperm-dominated floras were significantly more speciose than earlier gymnosperm-dominated floras.

In Chapter 7, I showed that a parent's return per unit investment can be represented in the form

$$w = s/(a + k) \qquad (7.4d)$$

where s is the probability of seedling survival; a is the direct cost per seed ("seed size"); and k is the supplementary cost per seed. The supplementary cost per seed k was a shorthand representation of $b/p + (1 - p)c/p$, where b is the cost per ovule of pollination, c is the cost of an aborted ovule, and p is the seed/ovule ratio. This simple model suggested explanations for the low minimum seed size of angiosperms and the high diversity of angiosperm-dominated floras.

I proposed that minimum seed size is determined by the ratio of the direct cost per seed to the supplementary cost per seed (i.e. a/k). I further proposed that supplementary costs become proportionately more important as seed size decreases. Thus, the total cost per seed becomes less sensitive to changes in seed size, as the ratio of direct costs to supplementary costs decreases. Therefore, a parent with very small seeds can increase seed size with little effect on the number of seeds produced. Or, to put it the other way round, once seed size becomes small enough, further decreases in size allow little increase in seed number. I proposed that this effect determines minimum seed size. The lower minimum size of angiosperm seeds suggested that angiosperms had a substantially lower supplementary cost per seed than earlier seed plants (see Chapter 7; V).

My discussion of species diversity was based on the model of Hopf & Hopf (1985). The supplementary cost per seed increases as a species' density decreases, because fewer ovules are pollinated. This cost of rarity sets a minimum viable density

below which a population cannot maintain its numbers. I proposed that angiosperms experience a lower cost of rarity than gymnosperms because their supplementary cost per seed is lower than that of a gymnosperm at the same population density. Therefore, more species of angiosperms can be "packed" into an environment, and gymnosperms are excluded from the environment as their numbers drop below the critical density (see Chapter 7, VI).

There appear to be two major ways in which angiosperms could have reduced the supplementary cost per seed relative to gymnosperms. Either pollination was more efficient (and b/p smaller), or, aborted ovules were produced more cheaply (c smaller). The next section reviews some of the many hypotheses that have attempted to explain the evolutionary success of angiosperms.

II. A REVIEW OF HYPOTHESES

I will discuss existing hypotheses under six headings: (a) cheaper ovules; (b) improved pollination efficiency; (c) faster growth rates; (d) superior chemical defences; (e) selective improvement of offspring quality; and (f) higher speciation rates.

One problem with any hypothesis that attempts to identify the characters responsible for the rise of the angiosperms is to explain why angiosperm-like plants first appear in the Cretaceous rather than at some earlier time. Either the success of angiosperms was dependent on environmental factors that were not present in previous periods or angiosperm success was dependent on difficult-to-evolve characters which made their first appearance in the Cretaceous. In the first view, angiosperm-like plants would not have been successful prior to the Cretaceous whereas, in the second view, angiosperm-like plants would have been successful whenever they arose. The second alternative has the advantage that it can easily explain the present dominance of angiosperms in a wide variety of environments. Of course the distinction between extrinsic (environmental) and intrinsic

(character-based) explanations is a rhetorical device. Environmental hypotheses implicitly or explicitly presume that some character will explain why angiosperms and not other groups were able to successfully respond to the particular environmental conditions.

A. Cheaper Ovules

Takhtajan (1976) and Stebbins (1974, 1976, 1981) have emphasized the small size and rapid development of angiosperm ovules as crucial factors in the group's evolutionary success. The female gametophyte of angiosperms is greatly reduced and double fertilization ensures rapid development after fertilization. However, the direct comparison of angiosperm and gymnosperm ovules at the time of fertilization is potentially misleading. Gymnosperm ovules often increase markedly in size between pollination and fertilization but this growth may be contingent on pollination and thus only take place in ovules that will be provisioned (Chapter 6). If it can be shown that angiosperms commit fewer resources to each unprovisioned ovule, Takhtajan's and Stebbins' hypothesis is compatible with lower supplementary costs per seed, and this of itself would contribute to a lower cost of rarity in angiosperms.

The long-delayed appearance of angiosperm-like plants could be explained if there were strong developmental constraints on the evolution of the angiosperm ovule. For example, the extreme reduction of the female gametophyte may have required major developmental changes. Stebbins (1974) suggested that rapid development of angiosperm seeds was an adaptation for climates with marked seasonal drought, but such conditions are likely to have existed prior to the Cretaceous.

B. Improved Pollination Efficiency

A number of authors have argued that insect pollination is more efficient than wind pollination at low population densities, thus allowing insect-pollinated angiosperms to persist as populations of widely dispersed individuals (Raven 1977; Regal 1977; Burger

1981). This, they argue, was a crucial factor in the greater adaptability and resistance to extinction of angiosperms. Their argument clearly ascribes a lower cost of rarity to angiosperms and is, therefore, closely related to the scenario presented in Section VI of Chapter 7. However, there are differences in emphasis. In my scenario, angiosperms displaced gymnosperms because seeds were cheaper to produce as a result of a smaller supplementary cost per seed. On the other hand, Regal (1977, 1982) emphasized genetic factors such as the kind of pollen received. He believed that insect pollination allowed greater genetic exchange between distant individuals or small populations, and that angiosperms were more adaptable than gymnosperms because of enhanced sexual recombination. However, electrophoretic studies suggest that there is a greater incidence of long-distance pollen dispersal in wind-pollinated species than in animal-pollinated species (Hamrick & Godt in press).

Supplementary costs will increase at low population densities because fewer ovules are pollinated or because more resources are expended on pollen capture. Encounters between ovules and wind-borne pollen grains should approximate a Poisson process. As the density of pollen grains decreases, the proportion of ovules that remain unpollinated should increase. The costs of insect pollination should also increase at low densities. However, insect pollination differs from wind pollination because pollen can exploit the muscular and sensory systems of its vector. Pollinators can detect ovules at a distance and fly towards them. Moreover, pollinators can adopt a systematic search pattern in contrast to the non-systematic movements of wind-dispersed pollen. These differences are suggestive but I know of no explicit model that compares the relative efficiency of wind and insect pollination at different densities. Such a model would need to consider the costs of attracting pollinators.

Midgley & Bond (1989) questioned the belief that wind-pollinated gymnosperms are restricted to communities of low species richness because wind pollination becomes inherently

inefficient as the distance between conspecifics increases. *Podocarpus falcatus* (a dioecious wind-pollinated conifer) is able to persist in populations of widely scattered individuals, and Southern African forests with conifers are no less species rich than Southern African forests without conifers. These observations suggested that wind-pollination may be effective at low population densities (Midgley & Bond 1989).

An important point should be made. Southern African conifers exist as members of species rich communities, but these communities are not particularly rich in wind-pollinated species. An uncommon, wind-pollinated species could be at a disadvantage in a community of other wind-pollinated species because many pollinations would be with non-specific pollen. Reproductive interference could account for a high cost of rarity and low species diversity in wind-pollinated floras. A couple of examples will illustrate the potential for reproductive interference. Most pollen chambers of *Pinus sylvestris* have a maximum capacity of 2-3 pollen grains (Chapter 6; Sarvas 1962). Pollination could be very inefficient if *P. sylvestris* pollen was a minority component of a diverse pollen cloud. Only 18% of pollen recovered from pollination droplets of *Ephedra trifurca* came from an *Ephedra* (Buchmann, O'Rourke & Niklas 1989).

Reproductive interference may be less of a problem in floras that are predominantly insect-pollinated because different species can specialize on different pollinators or different parts of pollinators. Moreover, the evolution of a closed carpel with stigmatic germination of pollen grains may have allowed effective sorting of specific and non-specific pollen at the stigma or in the style. Pollen rarely germinates on the stigmas of distantly related species (Martin 1970).

Insect pollination *per se* cannot account for the rise to dominance of angiosperms because it is not an exclusively angiospermous character. Bennettitales from the Jurassic have fructifications that are clearly adapted for insect pollination (Crepet & Friis 1987; Gottsberger 1988), and several modern cycads are known to be insect pollinated (Norstog 1987; Norstog,

Stevenson & Niklas 1986; Tang 1987a, 1987b) as is *Ephedra aphylla* (Bino, Dafni & Meeuse 1984; Bino, Devente & Meeuse 1984). Moreover, the great radiation of angiosperms during the Albian-Cenomanian occurred within a subset of the insect-pollinated angiosperms already existing at that time (Crane 1987; Crepet & Friis 1987).

A possible resolution of these difficulties would be that insect pollination in non-angiosperms is comparatively costly and that the success of insect-pollinated angiosperms was due to the evolution of particular kinds of interactions with pollinators. Crepet (1984) argued that the appearance of advanced pollinators, belonging to the Apoidea and Lepidoptera, was roughly contemporaneous with the major radiation of angiosperms. Crepet inferred the presence of eusocial bees in the Cretaceous from biogeographic evidence, though at the time there was no fossil evidence for this contention. Since his review, a fossil *Trigona* has been reported from the late Cretaceous (Michener & Grimaldi 1988). Bee-pollination appears to have evolved several times among primitive angiosperms from a more generalized insect-pollination syndrome (Bernhardt & Thien 1987).

Raven (1977) proposed that insect-pollinated angiosperms were favored during the Cretaceous by an expansion of equable tropical climates. Climate may have had a role in the timing of the angiosperm radiation but climatic factors do not appear to be a sufficient explanation as to why angiosperm-like plants did not arise at an earlier period. Regal (1977) proposed that angiosperm dominance resulted from an interplay between seed and pollen dispersal systems. The diversification of birds and mammals during the Cretaceous allowed long distance seed dispersal and plant populations of widely scattered individuals. This population structure favored insect-pollinated angiosperms over wind-pollinated gymnosperms. Herrera (1989) conclusively rejected this hypothesis. Many gymnosperms have animal-dispersed seeds and angiosperm families with fleshy fruits are not particularly speciose. Moreover, early angiosperms were small-seeded and abiotically dispersed. Larger, biotically dispersed seeds only

appear during the latest Cretaceous well into the major radiation of angiosperms (Tiffney 1984). It could be argued that the diversification in dispersal mode at this later stage was an epiphenomenon of the diversification in seed size.

C. Faster Growth Rates

Cronquist (1988, p. 132) and others have argued that angiosperms are competitively superior to gymnosperms because they possess a more efficient vascular system (vessels rather than tracheids), which allows faster transport of water and higher rates of photosynthesis. The superior vascular system and more flexible growth patterns of angiosperms may be of particular advantage during seedling establishment. Bond (1989) noted that the productivity of adult conifers often equals, or exceeds, that of potentially competing angiosperms, but that angiosperm seedlings have much higher relative growth rates than gymnosperm seedlings. Adult gymnosperms can achieve high productivities by accumulating more than one yearly cohort of leaves, but seedlings only have a single cohort. Therefore, he argued that gymnosperms are inferior competitors as seedlings and juveniles, even though they may be superior competitors as adults. As a result, competition with angiosperms during seedling establishment restricts gymnosperms to environments where conditions for rapid vegetative growth are poor.

Three kinds of evidence support Bond's hypothesis. First, experimental studies show angiosperm seedlings have higher relative growth rates. Second, foresters observe that conifer seedlings are suppressed by faster-growing angiosperms. Third, conifers are most abundant at high elevations or latitudes where vegetative growth is limited by cool temperatures and short growing seasons. Outside these regions, conifers are generally restricted to infertile soils (Bond 1989). Some highly diverse, angiosperm-dominated communities occur on nutrient-poor soils. Examples are eastern Australian sclerophyllous scrub, southwestern Australian heath, and South African fynbos (Rice & Westoby 1983). Conifers would be excluded from such habitats

because there is insufficient time between disturbances (e.g. fires) for conifers to reach maturity (Bond 1989).

Bond (1989) ascribed angiosperm dominance to increased seedling survival given pollination, rather than to increased efficiency of pollination. He emphasized that there is almost no direct evidence to support the competing hypothesis (discussed above) that gymnosperms are restricted to relatively pure stands because of the inherent limitations of wind pollination. His measure of success was relative cover or biomass, rather than number of species. His hypothesis does not address why there are so many species of angiosperms.

The hypothesis that angiosperms have higher productivity than gymnosperms does not require a higher return per unit investment in seed production, because angiosperms could produce greater total reproductive resources from the same growing season. On the other hand, Bond (1989) disputed whether angiosperms really have higher productivity as adults. In his hypothesis, angiosperms obtain a higher return per unit investment because their seedlings have a higher probability of survival than gymnosperm seedlings from seeds of the same size.

D. Superior Chemical Defences

Kubitzki & Gottlieb (1984b) have suggested that the initial radiation of angiosperms was facilitated by a greater flexibility in defensive chemistry. In their view, pteridophytes and gymnosperms rely on a costly *general defence* against herbivores. Tissues are impregnated with substantial quantities of lignins, silica or condensed tannins which reduce the tissues' digestibility. In contrast, many angiosperms rely on a *specialized defence* in which tissues contain much lower concentrations of toxic micromolecules. Such a defence is energetically less costly, but is vulnerable to the evolution of specific detoxification mechanisms by herbivores.

I prefer to view the different patterns of defensive chemistry in angiosperms and gymnosperms as a consequence rather than a cause of the angiosperm radiation. Among modern

angiosperms, most woody species contain tannins or analogous compounds that reduce plant digestibility. Species that do not produce such substances are predominantly (if not exclusively) herbaceous and are believed to rely on "escape in time and space" to avoid destruction by specialist herbivores (Feeny 1976; Rhoades & Cates 1976). The statement that a host plant without digestibility-reducing substances is able to persist because it escapes its enemies in time and space is another way of saying that herbivores regulate the host population at relatively low densities. Specialized defences are probably incompatible with a high cost of rarity.

E. Selective Improvement of Offspring Quality

Whitehouse (1950), Mulcahy (1979), and Zavada & Taylor (1986) considered prezygotic selection of male gametophytes (in the carpel) to be an important factor in the evolutionary success of angiosperms. Westoby and Rice (1982) argued that the success of angiosperms was a result of more effective postzygotic selection of offspring. I include self-incompatibility under the heading of selective offspring improvement because it is a process that eliminates selfed embryos.

According to Whitehouse (1950), self-incompatibility controlled by multiple alleles was the critical innovation that enabled efficient outcrossing in angiosperms and thus ensured the greater adaptability of angiosperms relative to gymnosperms. In Whitehouse's view, multi-allelic incompatibility was a highly advantageous, but difficult-to-evolve, character that arose only once in the history of seed plants. Bernhardt & Thien (1987) reviewed reports of self-incompatibility from families of "primitive" angiosperms and concluded that gametophytic incompatibility probably arose only once. Other workers suggest that self-incompatibility may have had multiple origins among angiosperms (Endress & Lorence 1982; Barrett 1988).

The primary evidence that self-incompatibility is a difficult-to-evolve character is its absence in gymnosperms. Could this have an alternative explanation? Monoecious

gymnosperms eliminate selfed embryos by a combination of simple polyembryony and the production of empty seeds (see Chapter 6). It could be argued that self-incompatibility would be superfluous in gymnosperms or impractical in situations where a mixture of self-pollen and outcross pollen are present in the same ovule for months, or even years, before fertilization. Angiosperms lack simple polyembryony. Could self-incompatibility have evolved in response to the loss of simple polyembryony, or did the evolution of self-incompatibility make simple polyembryony redundant?

Mulcahy (1979) argued that insect pollination and the closed carpel greatly intensified reproductive competition among male gametophytes. This resulted in superior quality offspring because more-vigorous male gametophytes produce more-vigorous sporophytes. Mulcahy contrasted insect-pollinated angiosperms with wind-pollinated gymnosperms. In angiosperms, there is intense competition among pollen grains because insects deposit masses of pollen simultaneously on receptive surfaces and because pollen tubes must grow through long sections of stylar tissues. By contrast, wind pollination usually delivers pollen grains singly to receptive surfaces and the first grain to arrive enjoys a head start over later arrivals. In consequence, the success or failure of a particular pollen grain is primarily influenced by chance.

This comparison underestimates the potential for prezygotic selection in gymnosperms. In most gymnosperms, ovules are not ready for fertilization at the time of pollination. Male gametophytes must survive for considerable periods surrounded by, and nutritionally dependent on, maternal sporophytic tissues. Pollen chambers frequently contain more than one pollen grain and the period between pollination and fertilization could provide ample opportunity for male gametophyte competition. Several species are known to abort poorly pollinated cones and simple polyembryony provides an opportunity for postzygotic selection among embryo genotypes. The angiosperm system may be more energetically efficient, particularly in low density populations, but this requires more detailed arguments than provided by

Mulcahy (1979).

Zavada & Taylor (1986) argued that the evolution of prezygotic mate assessment necessitated the concomitant evolution of sporophytic structures (carpel and stigma) to separate ovules from male gametophytes. Their paper discusses fossil evidence and is complementary to Mulcahy (1979).

Westoby & Rice (1982) argued that double fertilization and the formation of triploid endosperm allowed efficient postzygotic selection of offspring. Angiosperms commit few resources to ovules until after fertilization, and are, therefore, able to selectively abort fertilized ovules of low quality for little cost. Westoby & Rice believed that double fertilization allowed maternal sporophytes to accurately assess offspring quality because the nutrient-acquiring tissue (endosperm) was qualitatively identical to the embryo. The addition of a second maternal genome to the endosperm allowed the sporophyte more effective control of resource allocation than would be the case if the endosperm contained an equal dosage of maternal and paternal genomes. Selective seed abortion in angiosperms and gymnosperms are compared in Chapter 6 (Section V). The reasons for the second maternal genome in endosperm are discussed in Chapter 9.

Gymnosperms possess mechanisms of postzygotic selection not present in angiosperms. Female gametophytes of gymnosperms select among embryo genotypes by means of simple polyembryony (see Chapter 6). The loss of simple polyembryony in the angiosperm lineage may be a consequence of lower supplementary costs per seed and small seed size of early angiosperms. First, the cost of producing an additional embryo should be roughly independent of the provisioning cost of a seed. Thus, as seeds become smaller, the proportional cost of simple polyembryony should increase. There seems no reason to assume that the benefits of simple polyembryony should be greater for embryos from smaller seeds. Therefore, small-seeded early angiosperms may have lost simple polyembryony because the benefits were not worth the costs. Second, lower supplementary costs mean that pollinated ovules are

cheaper to produce. This should increase the relative merits of developmental selection among ovules relative to developmental selection within ovules. One possible scenario is that an ancestral angiosperm with small seeds lost simple polyembryony and its large-seeded descendents evolved mechanisms for the selective abortion of pollinated ovules. Efficient selection among ovules would make simple polyembryony redundant.

F. Higher Speciation Rates

Doyle & Donoghue (1986) suggested that the success of angiosperms was "due not to any competitively advantageous feature(s) common to all angiosperms, but rather to the fact that they consist of such a wide array of adaptive types, as a consequence of high speciation rates." They suggested that the critical character responsible for increased speciation may have been closure of the carpel, because this allowed experimentation with new means of dispersal independent of changes in seed structure. Moreover, germination of pollen on the stigma may have increased the probability of mutations causing blocks to the growth of pollen from partially differentiated populations.

Olmstead (1989) believed that "angiosperm success may be a consequence of a greater propensity on the part of angiosperm populations to inbreed and, therefore, to differentiate, rather than a consequence of any adaptive functional morphology that allowed them to outcompete their gymnospermous predecessors." In Olmstead's view, insect pollination was the critical character responsible for inbreeding within small local populations. Thus, Olmstead believed that insect pollination caused a lack of genetic exchange between populations, whereas Regal (1977) believed that insect pollination had the opposite effect and promoted genetic recombination between populations. Allozyme data supports Olmstead. Wind-pollinated species have higher levels of genetic variation within populations, and a smaller proportion of total variation between populations, than animal-pollinated species (Hamrick & Godt in press).

I have proposed that angiosperms can persist at lower

population densities than gymnosperms. This low cost of rarity would undoubtedly influence speciation and extinction rates. Small local populations would go extinct less readily and this might contribute to longer persistence of geographical isolates and genetic differentiation among populations.

III. SUMMARY

The unparalleled evolutionary success of angiosperms could be explained by a number of different types of hypothesis. I will present a classification into four types. The classification is not claimed to be exhaustive, nor are the categories claimed to be mutually exclusive.

(1) Angiosperms obtained a similar return per unit investment to other seed plants, but were more effective at accumulating reproductive resources. This could be because adult angiosperms were absolutely more efficient than other species, or were superior competitors for limited resources. Hypotheses of this type are the proposals that adult angiosperms have faster growth rates than gymnosperms or that angiosperms suffer less from herbivory because of superior chemical defences.

(2) Angiosperms were more efficient at converting a given quantity of reproductive resources into successful seedlings because angiosperm seedlings could obtain a higher probability of seedling survival s, given the same food reserves a. Hypotheses of this kind are Bond's (1989) proposal that angiosperms are so successful because their seedlings have much faster growth rates than gymnosperms and the various proposals of more effective prezygotic or postzygotic selection in angiosperms.

(3) Angiosperms were more efficient at converting a given quantity of reproductive resources into successful seedlings because angiosperms had a smaller supplementary cost per seed k than gymnosperms with equivalent-sized seeds. Hypotheses of this kind propose that angiosperms produce cheaper ovules than

gymnosperms or that pollination is more efficient in angiosperms.

(4) Angiosperms had faster speciation rates.

I have argued that angiosperm success is, at least in part, due to a smaller supplementary cost per seed. My support for category (3) is based on the lower minimum size of angiosperm seeds, which suggests a shift in the size-versus-number trade-off. However, I have not yet addressed whether the other categories of hypothesis can account for this pattern.

If angiosperms accumulate greater reproductive resources (category 1), this would result in more seeds being produced but should not have a direct effect on the size-versus-number trade-off. If angiosperms produce better quality seedlings (category 2), this could influence the size-versus-number trade-off in the appropriate direction, provided that the proportional increase in fitness is greater for seedlings from smaller seeds. Thus, Bond's (1989) hypothesis might be compatible with smaller minimum seed sizes. Hypotheses based on speciation rates (category 4) do not suggest any particular reason why minimum seed sizes should be smaller, except for Doyle & Donoghue's (1986) proposal that higher speciation rates allowed angiosperms to "experiment" with different adaptive types.

Two factors possibly contributed to lower supplementary costs in angiosperms. First, the small size and rapid development of angiosperm ovules suggests that ovules were cheaper to produce. Second, insect pollination may be more efficient than wind pollination at low population densities. This does not preclude other factors from having an important role in angiosperm success. The rise of the angiosperms is a unique event that occurred comparatively late in the fossil record. Therefore, the possibility that angiosperm dominance resulted from the occurrence within a single lineage of several, individually unimportant, characters cannot be dismissed simply on the grounds of parsimony.

The next two chapters discuss developmental processes in

angiosperm seeds. Chapter 9 discusses adaptive explanations for the triploid endosperm. Chapter 10 discusses the development of the angiosperm female gametophyte.