Chapter 5

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Pollination and the origin of the seed habit

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Der Embryosack der Coniferen lässt sich betrachten als eine
Spore, welche von ihrem Sporangium umschlossen bleibt.

[The embryo sac of conifers can be considered to be a spore which
remains enclosed within its sporangium.]

Wilhelm Hofmeister 1851.

The evolution of the seed is one of the major events in the
history of land plants. In this chapter, I consider the suite of
characters that define the seed habit, and discuss the probable
selective pressures that produced each character. My major
conclusion is that most characters are a direct consequence of
the origin of heterospory (discussed in Chapter 4) and of natural
selection for propagules with larger food reserves.

Seeds are traditionally defined by the possession of
integuments. However, some heterosporous pteridophytes possess
integument-like structures. Therefore, integuments cannot explain
the evolutionary success of seed plants. Rather, I believe that
the decisive character in this success is related to pollination.
Seed plants differ from other heterosporous lineages in the
capture of microspores before dispersal of the "megaspore".
Modern gymnosperms all possess mechanisms whereby the maternal
sporophyte withholds resources from potential propagules that
have not been pollinated and/or fertilized. This represents an
increase in efficiency over pteridophytic reproduction. Wind-
pollination means that the propagule is vulnerable to pathogens
that mimic pollen, and pathogen pressures may have contributed to
some seed characters.

I. INTRODUCTION

Vascular plants have either a homosporous or a heterosporous life cycle. Heterospory has evolved from homospory on several separate occasions. Most of these heterosporous lineages are now extinct or represented by a relatively small number of species. By far the most successful group of heterosporous plants are those that produce seeds.

Homosporous land plants are known from the mid-Silurian, approximately 420 Myr ago (Edwards & Feehan 1980). Heterosporous plants are known from as early as the Middle Devonian (Andrews, Gensel & Forbes 1974) and the earliest known seeds come from the Famennian of the upper Devonian (Gillespie, Rothwell & Scheckler 1981). Thus, on a geological time-scale, seed plants closely follow the origin of heterospory (Middle Devonian: c. 380 Myr ago; Famennian: c. 365 Myr ago; 1 Myr is a million years, dates from Harland et al. 1982).

Chaloner & Sheerin (1981) proposed that megaspores and seeds evolved as a consequence of reproductive strategies that favored greater investment in each of a smaller number of propagules. Such new strategies were necessary because of the origin of forest communities with low light intensities at ground level. These ideas were further developed by Chaloner & Pettitt (1987). The size distribution of Middle Devonian spores suggests that an increase in spore size preceded the origin of heterospory (Turnau & Karczewska 1987). Haig & Westoby (1988a; Chapter 4 this thesis) developed a model for the origin of heterospory under which increases in spore size eventually led to a fission of spore sizes, with smaller microspores specialized for male reproduction introduced into the spore population.

In this chapter I assess adaptive explanations for the origin of the seed. Because I deal with adaptive rather than phylogenetic explanations, I am not directly concerned with which taxa evolved from which other taxa nor whether seed plants are monophyletic or polyphyletic. My concern is the transition from a free-sporing heterosporous pteridophyte to a plant with gymnospermous reproduction. The change from gymnospermous to angiospermous reproduction is not considered in this chapter (see Chapter 8). I will argue that heterospory made possible the

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origin of the seed, and that many seed characters are adaptive consequences of larger propagule size.

The origin of the seed is not a simple problem and I will consider several issues. What characters, or combinations of characters, define seed plants? What selective factors would have favored each character? Is the proposed advantage of a character credible in general, or does it depend on some other character being present? On which genotype -- maternal sporophyte, gametophyte, offspring sporophyte etc -- would the putative selection pressure have operated? By considering these questions I hope to approach three more synoptic issues. Could the distinctive features of seed plants have evolved in any sequence, or are only one or a few sequences credible? Do these features only make adaptive sense in the context of each other, or is the fact that they are found together an accident of phylogenetic history? And what explains the success of seed plants relative to other heterosporous taxa?

II. EVOLUTION OF SEED CHARACTERS

The following characters are typical of modern seed plants:-

(1) The megasporangium (nucellus) contains a single functional megaspore. This megaspore is usually one member of a linear tetrad formed by the meiotic division of a single megaspore mother cell.

(2) The megaspore is retained within the megasporangium.

(3) The megasporangium is enclosed by a sporophytic structure known as an integument.

(4) The megaspore exine is thin or absent.

(5) The megaspore and megasporangium are united histologically.

(6) The female gametophyte develops while retained and nourished by the maternal sporophyte.

(7) Microspores (pollen grains) are captured before dispersal of the megasporangium.

(8) Fertilization and formation of an embryo usually occur before dispersal of the megasporangium.

(9) Resources are only committed to pollinated ovules or to ovules that have been fertilized.

(10) Microspores germinate distally to form pollen tubes that

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grow through sporophytic tissues to reach the female gametophyte.

The next four sections will present hypotheses as to why these characters evolved and how they are interrelated. The section headings and the characters dealt with in each section are listed below.

Retention of the megaspore	(1),(2)
Integuments	(3)
Seed nutrition	(4),(5),(6)
Pollination	(7),(8),(9),(10)

Before commencing these sections some comment should be made on my use of morphological evidence. Logically, this evidence is of three kinds. Firstly, the fossil record of early seed plants can suggest the order in which seed-characters were acquired and can suggest intermediate stages in the evolution of a character. This is evidence from (possible) homology. Secondly, the appearance of seed-like characters in some heterosporous pteridophytes suggests natural selection has acted similarly in more than one group. This is evidence from convergent evolution rather than homology. In a sense, heterosporous pteridophytes provide replication. Thirdly, consistent associations among characters in seed plants and heterosporous pteridophytes may suggest causal relationships. The heterosporous pteridophytes used in my comparisons are listed in Table 5.1. These taxa were chosen because of the availability of evidence, rather than as a random sample.

A. Retention of the megaspore

A single-spored megasporangium has evolved in several separate lineages. A common belief is that the smaller the number of spores in a sporangium the more nutrients are available for the remaining spores (Sussex 1966; Pettitt 1970; Niklas, Tiffney & Knoll 1980). This belief attributes the single-spored condition to natural selection for larger megaspores. So long as a sporangium contains more than one spore, individual dispersal of spores requires that the sporangium sheds its contents. However, once a sporangium contains a single spore, spore and sporangium can be shed as a unit (Coulter 1898).

This argument is strengthened by comparative morphology.

TABLE 5.1

Presence/absence (+/-) of single-spored megasporangia and of spore retention in Carboniferous and modern pteridophytes.

	Single-spored megasporangia	Spore retention	Source
Carboniferous taxa			
Lepidostrobus	–	–	(1)
Mazocarpon	–	–	(1)
Achlamydocarpon	+	+	(1)
Lepidocarpon	+	+	(1)
Miadesmia	+	+	(2)
Calamocarpon	+	+	(3)
Stauropteris	–	+	(4)
Modern taxa			
Selaginella	–	–	(5)
Isoetes	–	–	(5)
Platyzoma	–	–	(6)
Marsilea	+	–	(7)
Azolla	+	+	(8)
Salvinia	+	+	(9)

Sources: (1) Phillips 1979; (2) Benson 1908; (3) Baxter 1963; (4) Chaloner 1958; (5) Bold 1973; (6) Tryon 1964; (7) Machlis & Rawitscher-Kunkel 1967; (8) Herd, Cutter & Watanabe 1986; (9) Lasser 1924.

Multi-spored sporangia usually shed their spores whereas most single-spored sporangia retain their spore (Table 5.1). I know of two exceptions. In *Marsilea*, a sporocarp contains several megasporangia, each containing a single functional megaspore. When a megasporangium is removed from its sporocarp and placed in water, the megaspore is forcibly ejected from the sporangial wall (Machlis & Rawitscher-Kunkel 1967). In the Carboniferous fern *Stauropteris burntislandica*, megasporangia contained two megaspores but apparently lacked a dehiscence mechanism. The megaspores were bound together and apparently dispersed as a unit (Chaloner 1958).

B. Integuments

1. Integument-like structures in heterosporous pteridophytes

The ovule/seed has traditionally been defined by the possession of an integument. Three types of function have been invoked to explain the evolution of integuments. (1) Integuments evolved to protect the contents of the megasporangium (e.g. McLean & Ivimey-Cook 1951; Sinnott & Wilson 1963; Taylor 1981). (2) Integuments evolved to assist the capture of wind-born microspores (Niklas 1985). (3) Integuments evolved to limit offspring access to maternal resources (Westoby & Rice 1982).

In assessing these functional interpretations it is important to appreciate that some heterosporous pteridophytes have sporophytic structures that enclose, and are dispersed with, a single-spored megasporangium. I do not wish to debate whether such structures ought properly to be called integuments, but adaptive explanations for seed plant integuments ought to apply to these structures as well.

Structures which fit this definition are known from two groups of Carboniferous lycopods. *Lepidocarpon* was the propagule of an arborescent lycopod (Phillips 1979). *Miadesmia* was a herbaceous lycopod (Benson 1908). The micropyle was slit-like in *Lepidocarpon* but circular in *Miadesmia*. In both groups, the integument was a modified sporophyll. Nothing definite is known of the integument's function in *Miadesmia* and *Lepidocarpon* though the literature assumes them to have been protective structures (Benson 1908; Phillips 1979). Propagules of *Lepidocarpon* are

usually more than twice as large as those of the unintegumented
but similar *Achlamydocarpon* (Phillips 1979). This is consistent
with the protection hypothesis because the advantages of
protection should increase with propagule size (see below).

The sporocarps of heterosporous water-ferns enclose one or
more sporangia and, thus, are sporophytic structures with some
functional resemblance to integuments. In the Marsileales, the
sporocarp contains both microsporangia and megasporangia. In the
Salviniales, microsporangia and megasporangia occur in separate
sporocarps. The megasporocarp of *Azolla* contains a single
megasporangium and forms a cap which remains attached to the
megaspore until after fertilization. The sporocarp of the
Marsileales is believed to be a folded pinna; that of the
Salviniales, a modified indusium (G. Smith 1955; Bold 1973).
Sporocarps are perennating structures (Eames 1936; Bold 1973;
Konar & Kapoor 1974; Johnson 1985) and in this respect resemble
many modern seeds.

2. Integuments in early seed plants

The integument of seed plants is believed to have originated in
the fusion of a whorl of sterile axes subtending a megasporangium
(Andrews 1963; Smith 1964). Devonian and Lower Carboniferous
ovules show a variety of forms with varying degrees of fusion of
the "integumentary lobes". These ovules can be arranged in a
sequence such that an ovule with a complete integument and
circular micropyle can be derived by stages from an "ovule" in
which the individual lobes are attached only at the base of the
megasporangium. However, this is an artificially constructed
rather than phylogenetic sequence (Andrews 1963; DiMichele, Davis
& Olmstead 1989).

Paleozoic ovules not associated with leaf or stem material
are commonly assigned to one of three form orders:
Lagenostomales, Trigonocarpales or Cardiocarpales (see Rothwell
1981). The integument of the Lagenostomales is often described as
being fused to the nucellus (Figure 5.1a). From a developmental
perspective, "fusion" seems to have been the result of
intercalary growth of the ovule below the juncture of the
megasporangium and integument rather than of the actual fusion of

two distinct structures (Figure 5.1d; Sporne 1965; Singh 1978).
Where nucellus and integument are fused, there is no clear
distinction between these structures. Setting aside the
micropylar region, the major difference between a lagenostomalean
ovule and a naked megasporangium is the possession of an
integumentary vascular system. There seems no reason to believe
this difference represents an increase in protection, in the
capacity to acquire pollen, or in the capacity to control the
offspring's access to maternal provisioning. The apex of the
megasporangium usually possesses a complicated structure, known
as a lagenostome or salpinx. This is thought to have had a role
in pollination, but it is not part of the integument, nor does
there appear to be any reason an integument is necessary to allow
a lagenostome to be developed. Lagenostomalean ovules are often
surrounded by a cupule.

The Trigonocarpales are radially symmetrical and have a
vascularised nucellus which lies free of the integument (Figure
5.1b). Some authors have suggested that the "nucellus" is
homologous to the fused integument/nucellus of the Lagenostomales
and the "integument" is a modified cupule (Walton 1953; Sporne
1965; Meyen 1984). Ovules of the Cardiocarpales are bilaterally
symmetrical (Figure 5.1c). As in the Trigonocarpales the
integument is free and the nucellus vascularised, though
tracheids are usually restricted to the chalaza. If the nucellus
of the Trigonocarpales and Cardiocarpales is actually a fused
integument/nucellus, then these ovules have two integuments and a
different adaptive explanation may be necessary for each
structure. (The same difficulty applies to the two integuments of
most angiosperms.)

There is currently no consensus as to whether the
integuments in the different groups of early seeds are homologous
structures. Meyen (1984) has recently argued for a biphyletic
origin of the integumented megasporangium but this interpretation
has been criticized by other paleobotanists (Beck 1985; Miller
1985; Rothwell 1985). However, even if a monophyletic origin is
accepted there is still uncertainty as to whether the outer
covering of some ovules should be interpreted as a cupule or an
integument, and whether the nucellus is the strict homologue of a

Figure 5.1. Ovule structure in the Paleozoic form orders (a) Lagenostomales; (b) Trigonocarpales; and (c) Cardiocarpales. Dotted lines are vascular traces. (d) Schematic diagram showing how intercalary growth below the juncture of the integument and megasporangium results in a "fused" integument/nucellus. A young ovule is on left and a mature ovule on right. (a-c: modified from Rothwell 1981; d: modified from Singh 1978).
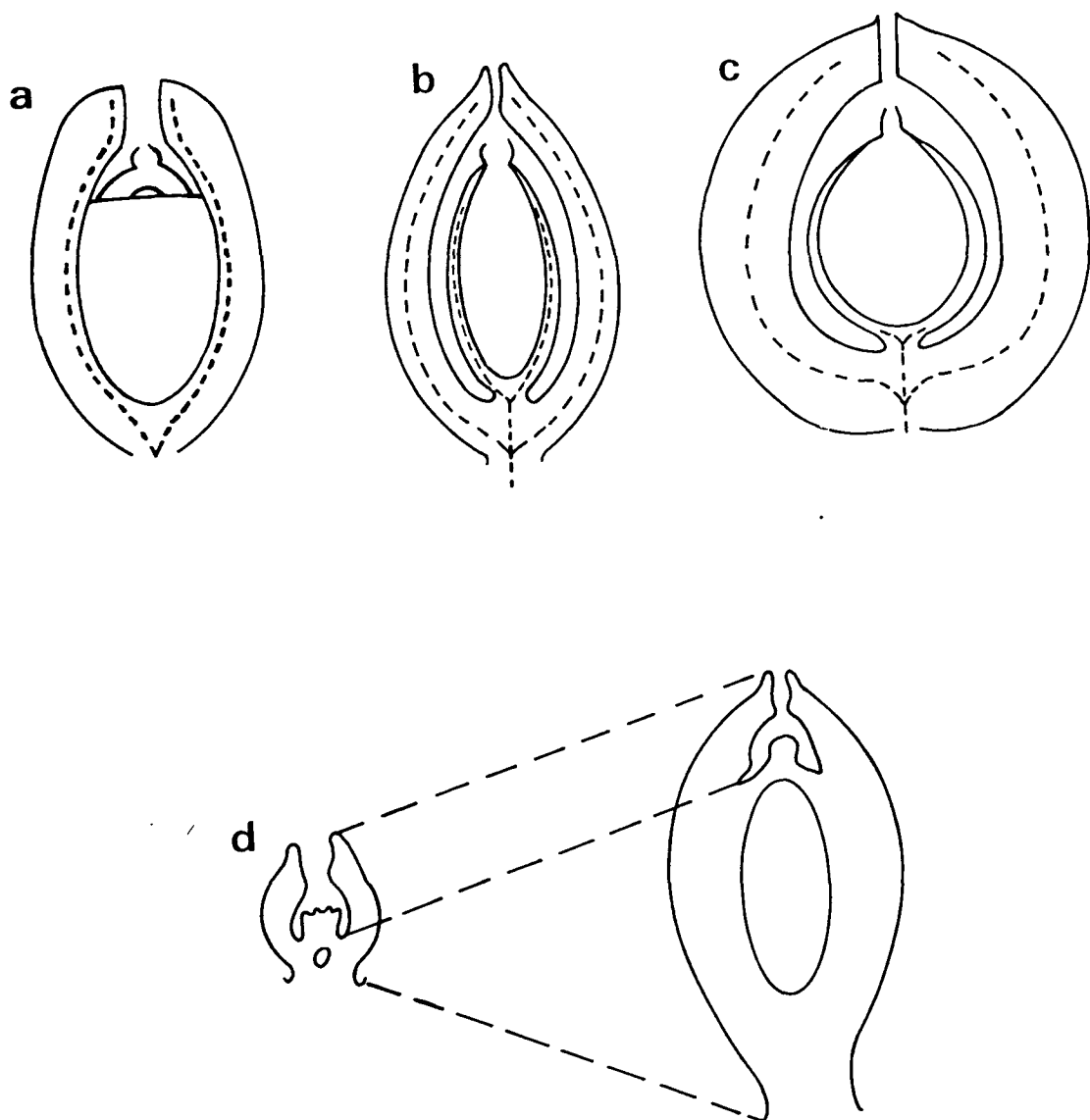
megasporangium or a composite structure of megasporangium and
integument.

3. Adaptive interpretations of the integument

Protection of the megasporangium has been the most frequently
proposed function for the integument of seed plants. This
hypothesis actually has two components: that the offspring should
be protected, and that the protection should be constructed of
maternal tissue (Westoby & Rice 1982). Protection would seem to
be of advantage to any propagule. Therefore, the restriction of
integuments (or similar structures) to seed plants and a few
heterosporous pteridophytes requires explanation. I suggest that
protection is associated with heterospory because as propagule
size increases, the relative costs of protection decrease because
of a reduced surface area to volume ratio. Larger propagules
might also be at greater risk from predators, increasing the
benefits of protection. Protective structures would be of
maternal origin because heterospory is associated with retention
of the megaspore (see above), so that protection constructed
around the offspring would necessarily be sporophytic.

The protection hypothesis does not explain why the
protective function is taken by a new structure rather than by
the sporangium itself. The megasporangium of Achlamydocarpon
varius is naked, but its outer wall contains specialized thick-
walled cells that probably had a protective function (Leisman &
Phillips 1979). To describe the seed coat as derived from the
integument rather than the nucellus appears to be little more
than a convention in groups where the integument is "fused" to
the nucellus. These include the cycads, Cephalotaxus and some
members of the Pinaceae as well as exclusively fossil forms such
as the Lagenostomales (see Singh 1978).

Niklas (1985) has challenged the protection hypothesis on
the grounds that partially enclosed ovules would not be
effectively protected. Instead he proposed that integuments
evolved to facilitate wind-pollination. He used the results of
experiments with model ovules in wind-tunnels to support this
hypothesis. However, the experiments did not, in fact, offer an
explanation for partial enclosure of the ovule. Generally,

microspores tended to be removed from the air-flow in regions of turbulence. Capture of microspores by the apex of the ovule was increased by localising turbulence around the apex and streamlining the remainder. This could be done by fusion of the integumentary lobes and adduction of their free ends to form a micropyle. Free integumentary lobes, cupules, hairs and other intervening structures interfered with the delivery of microspores because they broadened the region of turbulence. Therefore, Niklas' experiments provide a possible adaptive reason why integumentary lobes should fuse but do not explain why the megasporangium should be surrounded by lobes in the first place. Indeed, Niklas' results suggest that a naked megasporangium with a salpinx would capture microspores more effectively than would the same structure surrounded by integumentary lobes.

Westoby & Rice (1982) argued that integuments evolved in response to provisioning of propagules after meiosis. Female gametophytes should be selected to procure more provisions from their mother than the mother should be selected to provide. Therefore mothers which commit provisions to gametophytes (or endosperms) rather than to megasporangia might be expected to evolve machinery capable of restricting offsprings' access to their resources. Integuments might be part of that machinery, since they are of maternal genotype and they surround the offspring. Westoby & Rice rejected the protection hypothesis because it did not seem to explain why protective structures only appeared when provisioning was delayed until after meiosis. However, increased protection and delayed provisioning are possibly both associated with an absolute increase in the quantity of provisions provided to individual offspring. As well, provisioning after meiosis is found in some pteridophytes to a greater extent than Westoby & Rice appreciated. Parent-offspring conflict and the timing of investment will be taken up at greater length in the next section.

Retention of the megaspore within the megasporangium meant that sporophytic tissues replaced the megaspore exine as the outer covering of the propagule. Once this had happened, natural selection for protection would necessarily act on the outer covering. However, this does not preclude other factors from

having a role in the evolution of integuments. Modifications to
the outer surface which improved pollination or dispersal would
be positively selected provided they did not have greater
deleterious effects on other functions. It would be interesting
to know the role of the integumentary vascular system in the
nutrition of early seeds.

C. Seed nutrition

Westoby & Rice (1982) believed that pteridophytes differed from
seed plants because the pteridophyte sporangium already contained
all the food reserves of the future spores before meiosis whereas
seed plants supplied the bulk of food reserves to ovules after
meiosis. Theoretically, food reserves could accumulate in
sporocytes before meiosis but the evidence reviewed below
suggests that post-meiotic provisioning is the rule in both
pteridophytes and seed plants.

Marengo (1949) described the growth of *Onoclea sensibilis*
isospores. In his figures spore diameter doubles after meiosis.
Moreover, the spores are highly vacuolate during enlargement but
fill with cytoplasm after growth ceases. Kremp (1967) gives
further examples of isospore growth. Among heterosporous
pteridophytes, megaspores of *Selaginella* (Sievers & Buchen 1970;
Pettitt 1971), *Marsilea* (Bell 1985) and *Azolla* (Konar & Kapoor
1974) increase markedly in size after meiosis. The post-meiotic
growth of ovules is well known.

The large size of seeds relative to isospores strongly
suggests that there is a greater total transfer of resources in
seed plants. A number of seed characters can plausibly be related
to the increased transfer of resources into propagules after
meiosis.

The "exine" of modern gymnosperm ovules is a thin membrane
closely associated with the peripheral cells of the female
gametophyte (Pettitt 1966a, 1977). However, the Paleozoic seeds
Trigonocarpus and *Taxospermum* have spore walls that more closely
resemble those of heterosporous pteridophytes than those of
modern gymnosperms (Pettitt 1966b). The spore walls of these
early seeds were "spongy" and porous, and in this respect similar
to the exine of *Cystosporites* (the megaspore of *Lepidocarpon*).

Schopf (1938) suggested that the *Cystosporites* exine could have been "an adaptation for food transfer between the sporophyte and the enclosed and retained gametophyte." Pettitt (1966b) disputed this interpretation because equally porous exines surround the gametophytes of *Selaginella*, *Isoetes* and *Laevigatisporites* (the megaspore of *Mazocarpon*). However, his own discussion mentioned the post-meiotic growth of megaspores from *Selaginella* and *Isoetes*, and post-meiotic growth is probable for *Mazocarpon*.

Ramanujam & Stewart (1969) compared the spore walls of the different spore types in a *Cystosporites* tetrad. The large functional megaspore had a thin wall (1-3 µm) composed of matted fibrils whereas the three small abortive spores had granular walls that were very thick (18-25 µm). These observations are consistent with the hypothesis that thin porous exines are an adaptation for food transfer after meiosis because the thick-walled abortive spores are not provisioned by the sporophyte. In fact, spore abortion may be a consequence of isolation from nutrient supplies (Haig 1986). In summary, the reduced exine of modern seeds probably evolved because a well-developed exine would have been an impediment to nutrition of the gametophyte and because many of the exine's former functions had been assumed by the integument.

Martens (1966) identified the histological union of megaspore and megasporangium as the distinctive feature of seed plants and claimed that megaspores of pteridophytes always lie free within the megasporangium. Martens' generalisation does not apply to fossil forms however. Megaspores of the lycopod *Mazocarpon* (Phillips 1979) and the sphenopsid *Calamocarpon* (Baxter 1963) are not separated from their megasporangia by maceration. The more intimate association between megaspore and nucellus in seed plants may be an adaptation for post-meiotic provisioning. It could also have contributed to new arrangements of the megaspore tetrad. So long as the tetrad is formed free within the lumen of a megasporangium, the simplest geometric arrangement of four spores is a tetrahedron. When the megaspore mother cell is no longer free, other arrangements become likely. Paleozoic seeds are known with the tetrahedral tetrad typical of pteridophytes rather than the linear tetrad typical of modern

seed plants (Pettitt 1969; Schabilion & Brotzman 1979).

The female gametophyte of modern gymnosperms develops while the ovule is still being provisioned. In homosporous pteridophytes, however, the gametophyte develops after spore dispersal. Precocious development probably allows more rapid establishment after dispersal. In addition, a gametophyte (with several nuclei) may be more efficient at storing food reserves in a large propagule than would a megaspore (with a single nucleus). Gametophytes have been found in fossil cones of *Mazocarpon*, *Achlamydocarpon*, *Lepidocarpon* (Phillips 1979) and *Miadesmia* (Benson 1908). Development was probably precocious because gametophytes are present in undispersed propagules. Among modern pteridophytes, the megaspore of some *Selaginella* species contains a multicellular gametophyte at the time of release (G. Smith 1955; Bold 1973).

Westoby & Rice (1982) were concerned with the stage at which resources are supplied to propagules because of the genetic implications of post-meiotic provisioning. When offspring are provisioned after meiosis the tissue receiving resources (the female gametophyte in gymnosperms) differs genetically from the tissue supplying resources (the sporophyte). This might have implications of two sorts. If some offspring are provisioned while others are aborted, provisioning after meiosis could be associated with an increase in the average genetic vigor of the set of offspring which is provisioned. The second implication is that natural selection acting on genes expressed in the gametophyte should favor the acquisition of more resources than the sporophyte is selected to supply (Westoby & Rice 1982; Queller 1983). For this reason sporophytes seeking to abort offspring after meiosis might need to overcome some resistance from those offspring.

Abortion of seeds and redistribution of resources is well documented in seed plants (Stephenson 1981) but little is known about the possible reallocation of resources among sporangia in pteridophytes. The abortion of entire sporangia in pteridophytes has almost no potential for increasing spore quality. This is because each sporangium contains several spores and there would be little variance in quality among sporangia. Similarly, there

is little or no scope for genetic conflict over abortion between genes expressed in the mother and genes expressed in the spores. This is because all four meiotic products of each spore mother cell usually form functional spores. In each sporangium, there will be equal numbers of haploid spores carrying each of the two maternal alleles at a locus. Therefore, the abortion of entire sporangia does not redistribute resources between the two alleles. There is, however, potential for conflict between the two alleles over the distribution of resources within sporangia.

D. Pollination
1. Microspore capture before propagule dispersal
In modern seed plants, fertilization requires pollination. That is, a male gametophyte must encounter a female gametophyte before the latter disperses from its parent sporophyte. However, in homosporous pteridophytes, "male" gametophytes encounter "female" gametophytes after both have been dispersed. In what follows, I assume that pollination evolved from a system in which megaspores and microspores were independently dispersed and fertilization was effected by free-swimming sperm. Fertilization would usually occur on the ground after megaspore dispersal but wind-dispersed microspores would probably have settled on most surfaces with which they came in contact. Occasionally, a microspore would have settled near a megaspore that was still attached to its parent sporophyte. Fertilization would have been in the interests of both spores, because neither could be guaranteed fertilization at a subsequent encounter. Thus, a minority of fertilizations would have been the result of encounters which occurred before megaspore dispersal. An obligate pollination system could have evolved by such encounters gradually replacing encounters occurring after dispersal as the major cause of fertilization.

The probability of encounters before megaspore dispersal could have been increased (1) by modifications of the megasporangium (or surrounding structures) to trap microspores; (2) by changes to the location of megasporangia with respect to air-flow; (3) by the longer retention of megasporangia; (4) by the earlier release of microspores; or (5) by changes to the aerodynamic properties of microspores such that they remained

air-borne longer or moved at a height at which encounters with undispersed megaspores were more likely. These characters are largely under the control of the sporophyte genome. Therefore, my arguments are phrased in terms of selective advantages to individual sporophytes. The first three characters would increase the probability of pre-dispersal encounters by a sporophyte's megaspores, whereas the others would favor pre-dispersal encounters by the sporophyte's microspores. I will assume that innovations which changed the likelihood of pre-dispersal encounters by a sporophyte's megaspores did not affect the kind of encounters experienced by the sporophyte's microspores, and vice versa. This assumption allows natural selection on encounters by megaspores to be considered separately from natural selection on encounters by microspores. The assumption would be satisfied by a new "mutant" in a large out-breeding population.

Encounters by megaspores will be considered first. Some female gametophytes would have failed to reproduce because they did not encounter a male gametophyte. Changes which increased the probability of pre-dispersal encounter need not have reduced that of post-dispersal encounter. Therefore, natural selection should have tended to favor adaptations for microspore capture provided their cost in terms of fewer megaspores produced by the sporophyte was less than their benefit in terms of more fertilizations. As a first-order approximation, the cost per megaspore of structures ensuring a given level of pre-dispersal encounter should be independent of propagule size. Therefore, a shift to pre-dispersal encounters would be expected to accompany an increase in propagule size because the proportional cost of microspore capture would decrease as propagules became larger (see Chapter 7).

Natural selection on encounters by microspores is less straightforward. Any change that increased a microspore's chances of pre-dispersal encounter would be likely to reduce the chances of post-dispersal encounter. Therefore, the nett effect on encounter rates is unclear. However, not all encounters are equal. A megaspore may encounter more than one microspore, in which case microspores compete for fertilizations. (This can also be viewed as competition among the parent sporophytes of the

microspores.) If the first microspore to reach a megaspore has an advantage over later arrivals, competition among male parents would have favored earlier encounters by microspores and natural selection should have shifted the time of encounter to the earliest stage at which there was an advantage of priority.

In summary, adaptations for microspore capture would probably have been a consequence of selection to minimize the number of megaspores that failed to encounter microspores, whereas adaptations of microspores for pre-dispersal encounter would probably have been a consequence of competition for fertilizations. The strength of these forces might have been negatively correlated because competition among microspores should have been greater when fewer megaspores failed to encounter any microspore. However, so long as some megaspores remained unfertilized and some microspores competed for fertilization, there would have been scope for both forces.

Another factor may have been important in the evolution of obligate pollination. If a sporophyte produces some propagules that are pollinated and others that remain unpollinated, the optimal allocation of parental resources is to supply extra nutrients to pollinated propagules at the expense of unpollinated propagules. If pollinated propagules received additional resources, this would be another reason favoring pre-dispersal encounters by microspores (see Chapter 7).

The scenario I have sketched has potential for positive feedback. At first very few microspores would land within fertilizing distance of megaspores before the megaspores had dispersed. Once significant adaptations for capturing wind-borne microspores had been established, selection on microspore characteristics would be increased. Conversely once many microspores passed near megaspores before dispersal, selection for microspore capture would accelerate. Thus, once wind-pollination had become a significant minority route of fertilization, it could be expected to rapidly become the dominant route. Because of these positive feedback characteristics, one would not expect to see many plants occupying intermediate stages along this evolutionary sequence. Rather one would expect to see a clear demarcation between plants

with predominantly post-dispersal encounter and plants with fully-developed pollination systems.

A difficulty with the argument is that pre-dispersal encounters would be more likely to be with "self" microspores than would post-dispersal encounters. This difficulty applies to almost any model of the evolution of pollination. A couple of suggestions can be made. Firstly, a sporophyte can limit self-pollination by separating the maturation of its microsporangia and megasporangia in time or space. Secondly, simple polyembryony could allow the preferential maturation of outcrossed embryos if both self and non-self microspores are encountered by an ovule (Haig & Westoby 1988b; Chapter 3 this thesis).

Pollination and the precocious development of the female gametophyte enabled fertilization to occur before dispersal. The presence of an embryo is the formal distinction between an ovule and a seed though this distinction is usually not made in the paleobotanical literature. A seed that contained an embryo at the time of dispersal could respond more rapidly to favorable germination conditions than a seed that was yet to form its embryo. This would only have been a significant advantage in species where favorable germination conditions are temporary. Embryos are rare in Paleozoic seeds. Stidd & Cosentino (1976) report an embryo within a Carboniferous seed. Mapes, Rothwell & Haworth (1989) report embryos in seeds from a conifer cone found near the Pennsylvanian-Permian boundary. Embryos within Permian seeds are slightly more common (Miller & Brown 1973; Smoot & Taylor 1986). Stewart (1983) has described the paucity of embryos in Carboniferous seeds as an "enigma". He suggested two possible explanations: either embryo development occurred outside the seed or only a very small percentage of ovules developed embryos. Among modern gymnosperms, fertilization in *Ginkgo* may occur after the ovule is detached from the sporophyte (Favre-Duchartre 1958).

Pollination is often assumed to be an adaptation for terrestrial existence because it allows eggs to be fertilized in the absence of surface water, but most seed plants have surface water in their environment occasionally and fertilization is not extremely time-consuming. If there is sufficient water for seed germination, there should be sufficient water for fertilization.

However, the seed habit does allow greater independence from surface water than is possible for homosporous life cycles. The female gametophyte of seed plants develops while supported by the mother's vascular system. Therefore, the gametophyte has access to water that is unavailable to homosporous gametophytes growing on the surface. After dispersal, the seed's larger food reserves allow the rapid establishment of an extensive root system during brief periods of ample water.

The earliest known seeds had a nucellar apex that was modified into a salpinx-like tube (Gillespie et al. 1981). By implication, pre-dispersal encounter was already established at this time (Famennian c. 365 Myr ago). Though the nucellar apex was initially responsible for pollen reception, the evolutionary fusion of pre-integumentary lobes transferred this function to the micropyle (Taylor & Millay 1979). By mid-Pennsylvanian times (c. 300 Myr ago), *Callospermarion* had a pollination-drop mechanism which closely resembles that in many modern gymnosperms (Rothwell 1977). Galtier & Rowe (1989) have recently reported an integumented megasporangium of Middle Tournaisian age (c. 355 Myr ago) that lacks a pollen chamber and has no obvious adaptations of the nucellar apex for pollen capture. This fossil is problematical, because it is unclear as to how and when microspores gained access to the female gametophyte within the megasporangium.

In most modern gymnosperms, pollen is received at the micropyle. Pollination drops are common (Owens & Molder 1980; Owens, Simpson & Molder 1981a; Owens, Simpson & Caron 1987; Friedman 1987) but not universal. Some members of the Pinaceae possess "stigmatic" surfaces that receive pollen and are drawn into the micropyle (Owens & Molder 1977b, 1979b; Owens, Simpson & Molder 1981b). In *Araucaria* pollen grains germinate on the ovuliferous or bract scale and pollen tubes enter the micropyle (Haines, Prakash & Nikles 1984).

Reproductive systems of heterosporous pteridophytes are poorly known. Megaspores of some species of *Selaginella* and *Azolla* are regularly shed with attached microspores (Chaloner & Pettitt 1987). Fertilization is reported to occur before dispersal in two species of *Selaginella* (Lyon 1901; Geiger 1934).

Microspores and megaspores are probably produced by the same
sporophyte in all these cases, and outcrossing still depends on
post-dispersal encounters (Chaloner & Pettitt 1987). Among fossil
forms, *Miadesmia* might have had a pollination system (Benson
1908). Whether *Lepidocarpon* encountered microspores before or
after dispersal is disputed (Thomas 1978, 1981; Phillips 1979).

A surprisingly large proportion of modern heterosporous
pteridophytes are aquatic. The Salviniales are floating ferns and
most members of the Marsileales and Isoetales are submerged at
some stage in their life-cycle. The prevalence of aquatic forms
probably is related to encounter rates. On land, a microspore and
a megaspore must settle in each other's immediate vicinity if
fertilization is to occur. However, a floating microspore can
"search" a much larger area for megaspores. Therefore, the post-
dispersal encounter rate for aquatic pteridophytes is likely to
be high. This is particularly the case if encounters occur in a
single plane such as the water surface (see Cox 1983). The
higher the probability of post-dispersal encounter, the less the
benefit of microspore capture before dispersal. Therefore in
aquatic pteridophytes selection for pre-dispersal encounter ought
to be relatively weak.

2. Delayed resource commitment

Pollination made possible a major adaptive advance, because
resources need only be committed to those propagules that receive
pollen. (Resources are only "committed" to a propagule when they
can no longer be withdrawn and reallocated to other propagules or
functions.) Modern gymnosperms fall into two groups: those that
commit resources to propagules before fertilization and those
that commit the bulk of provisions after fertilization. Most
modern gymnosperms belong to the second group. *Ginkgo* and cycads
are probably the only members of the first group.

In *Ginkgo*, ovules are fully provisioned before
fertilization, and fertilization has no effect on gametophyte
food reserves. Therefore, sterile ovules accumulate similar
reserves to fertilized ovules. The same is true for sterile
ovules of *Cycas, Encephalartos, Macrozamia* and *Bowenia* (Favre-
Duchartre 1958). However, *Ginkgo* and cycads abort unpollinated

ovules before major resource commitment (*Ginkgo biloba*, Lee 1955; Favre-Duchartre 1958; Friedman 1987; *Macrozamia reidlei*, Baird 1939; *Zamia furfuracea*, Norstog, Stevenson & Niklas 1986; *Zamia pumila*, Tang 1987a). Thus, provisioning is only inefficient to the extent that some pollinated ovules remain unfertilized or to the extent that all embryos die within a fertilized ovule.

Most (if not all) other gymnosperms supply the bulk of resources to ovules after fertilization (Schnarf 1933; Favre-Duchartre 1958). A distinction must be made between the size of an ovule and the amount of its food reserves. Ovules of *Cephalotaxus drupacea* have reached almost maximum fresh-weight at fertilization, but their greatest increase in dry-weight occurs after fertilization (Favre-Duchartre 1958). *Picea glauca* provides another example. Ovules are almost full-size before fertilization but food reserves only accumulate once an embryo is present (Owens & Molder 1979a).

Despite the claim that gymnosperm ovules are usually full-sized at fertilization (Johansen 1940) there are so many exceptions that this generalization may not be helpful. In *Podocarpus falcatus* (Osborn 1960) and *P. gracilior* (Konar & Oberoi 1969) the ovule increases in size after fertilization. Post-fertilization ovules also enlarge in *Agathis robusta* (Kaur & Bhatnagar 1986), *Araucaria bidwilli* and *A. hunsteinii* (Haines 1983). In *A. cunninghamia* the female gametophyte enlarges after fertilization though the ovule does not increase in size (Haines 1983). In *Taxus* (Favre-Duchartre 1984), *Torreya taxifolia* (Coulter & Land 1905), *Ephedra trifurca* (Land 1907), *Gnetum* spp (Maheshwari & Vasil 1961) and *Welwitschia mirabilis* (Pearson 1929) the female gametophyte is very small at fertilization and almost all growth occurs after fertilization.

Some of the gymnosperms which provision ovules after fertilization are known to abort unpollinated ovules (*Podocarpus falcatus*, Osborn 1960; *Juniperus communis*, Sarvas 1962; *Pinus* spp, Buchholz 1946; Sarvas 1962; Sweet 1973; *Picea* spp, Sarvas 1968; Mikkola 1969). However, female gametophytes of *Metasequoia* (Engels & Gianordoli 1983), *Araucaria* (Haines 1983) and *Agathis robusta* (Kaur & Bhatnagar 1986) develop to the archegoniate stage without pollination. Whether or not unpollinated ovules are

aborted, seed food reserves only accumulate in fertilized ovules. Unfertilized female gametophytes degenerate and their ovules often persist as "empty seeds" (e.g. Sarvas 1962, 1968; Mikkola 1969; Sweet 1973; Haines 1983; Engels & Gianordoli 1983; Kaur & Bhatnagar 1986). It is possible that resources already supplied to gametophytes can be retrieved and allocated elsewhere. For these reasons, seed provisioning is potentially more efficient than in *Ginkgo* and cycads.

Studies of ovule ontogeny in early gymnosperms show that delayed resource commitment evolved early in the history of seed plants. Ovules of *Elkinsia* (Famennian: c. 365 Myr ago) appear to have undergone their major growth after pollination (Rothwell, Scheckler & Gillespie 1989). The same is true of *Callospermarion* (mid–Pennsylvanian: c. 300 Myr ago) (Rothwell 1977). These studies show that pollination preceded substantial growth of the ovule, but they do not show whether unpollinated ovules were aborted.

All modern gymnosperms have evolved mechanisms for terminating investment in unpollinated or unfertilized propagules. Mechanisms for early termination can serve a number of functions. The most obvious is that resources need not be committed to propagules with no chance of reproductive success. A less direct advantage is that mothers can initiate more propagules than they are feasibly capable of provisioning. The actual number provisioned can then be adjusted to variation in resource availability, pollination, or losses due to predation ("bet-hedging hypothesis"). If mothers initiate more propagules than are provisioned, a mother can selectively provision propagules of higher expected fitness ("selective abortion hypothesis"). These hypotheses have been used to explain low seed set in angiosperms (see Stephenson 1981; Stephenson & Bertin 1983; Sutherland 1986). Seed and ovule abortion in gymnosperms is discussed at length in Chapter 6.

Facultative abortion required the evolution of new controls on ovule development. For example, those gymnosperms which abort unpollinated ovules must be able to recognize appropriate pollen or male gametophytes. The best studied system is found in *Pinus*. Some interspecific pollinations prevent ovule abortion whereas

others result in early abortion (McWilliam 1959; Hagman 1975;
Kormutak 1984). The causal mechanisms are unknown.

3. Male gametophytes and pollen tubes

Pollen is usually received at an early stage of the female
gametophyte's development. This necessitates a delay between
pollination and fertilization. During this period the male
gametophyte must support itself using its own food reserves or
resources obtained from the host sporophyte. There are
considerable advantages to a male gametophyte that can obtain
additional resources from its host. The gametophyte might thereby
attain an advantage in competition for fertilizations with other
male gametophytes in the same ovule (see below). Moreover, the
pollen grain could afford to be smaller at dispersal, allowing
its paternal sporophyte to produce more (gibling) pollen grains.

Pollen tubes may originally have evolved as haustoria to
assist in the nutrition of the male gametophyte and at some
subsequent stage acquired the additional function of delivering
sperm to archegonia (siphonogamy). Most isospores, and
microspores of heterosporous pteridophytes, germinate proximally;
that is from the spore's surface that developed nearest the other
members of the tetrad. In contrast, pollen grains of most modern
gymnosperms are said to germinate distally, because the pollen
tube develops from the opposite face of the spore (Kuprianova
1967; Chaloner 1970). This change is explicable in terms of a
two-stage evolution of the pollen tube. In this scenario, the
proximal face originally retained its ancestral function of
gamete release and the distal face acquired the novel haustorial
function. This situation is found in modern cycads (Chaloner
1970). At a later stage, and not in all gymnosperms, the pollen
tube came to deliver sperm to archegonia and proximal germination
was completely lost.

Among modern gymnosperms, the pollen tubes of *Ginkgo* and
cycads are strictly haustorial and do not participate in sperm
delivery. The pollen tube is assumed to have a nutritive function
but this has never been proved. At fertilization, flagellated
sperm are released from the non-haustorial end of the gametophyte
and swim to archegonia (Favre-Duchartre 1958; Friedman 1987).

This mode of fertilization is known as zooidogamy.

Probably the most remarkable feature of zooidogamous gymnosperms are their massive spermatozoids. These can reach 400 μm in diameter amd may have over 10,000 flagella (Norstog 1975). Their evolution can be explained in terms of competition between male gametophytes for fertilizations. In *Ginkgo*, the sudden release of liquid from nucellar cells allows spermatozoids to swim across the pollen chamber to archegonia. Each male gametophyte produces two spermatozoids; there may be several male gametophytes in the pollen chamber; but there are only two archegonia (Favre-Duchartre 1958). As a result, more than one spermatozoid may enter a single archegonium (Lee 1955). Clearly, there is competition for fertilizations and an advantage to faster and stronger spermatozoids. *Ginkgo* sperm are miniature power-boats in a sprint to an egg.

In siphonogamous gymnosperms, the pollen tube delivers sperm directly to the female gametophyte. However, the pollen tubes probably also have a nutritive function, especially in those species with a long delay between pollination and fertilization. Siphonogamy is often claimed to be the final step in the evolution of fully terrestrial reproduction, freeing the reproductive process from the uncertainties of fertilization by free-swimming sperm. This explanation is far from convincing. The fertilization liquid in zooidogamous forms does not appear to be a prohibitive cost and can probably be resorbed. Moreover, fertilization by free-swimming sperm in the enclosed pollen chamber does not seem to be inherently more risky than the delivery of sperm by a pollen tube. Perhaps siphonogamy evolved because it was of advantage to male gametophytes in sexual competition, allowing sperm to reach archegonia before the breakdown of the micropylar nucellus. Once siphonogamy was established it may have had advantages to the host sporophyte because it allowed the female gametophyte to be surrounded by maternal tissues throughout development. This could have protected the food reserves of the propagule from ready access by pathogens (see below).

Fertilization in *Ephedra* is unusual. There is only a brief interval between pollination and fertilization. Pollen grains are

deposited at the base of the pollen chamber in direct contact with the female gametophyte. The archegonial neck is unusually long, and the pollen tube grows through gametophytic, rather than sporophytic, tissues to reach an egg (Land 1907; Singh 1978).

Not all fossil seed plants produced pollen tubes. Stewart (1951) observed microspores in the pollen chamber of a *Pachytesta* ovule. The microspores lay directly above the megaspore membrane in close proximity to archegonia. One microspore contained two cells that resembled the spermatozoids of modern cycads. The formation of a pollen tube seems unlikely. The microspores were large, with an average diameter of 365 µm. Similar monolete microspores can reach 600 µm in diameter (Taylor & Millay 1979). How such microspores were dispersed is problematical, but their size may reflect the lack of haustoria and reliance on their own food reserves (Millay & Taylor 1976). The earliest known pollen tube comes from a microspore in a *Callospermarion* ovule (Rothwell 1972). Pollination preceded ovule growth in *Callospermarion* (Rothwell 1977).

4. Wind-pollination and pathogens

Pollination probably had non-adaptive as well as adaptive consequences. Structures which capture wind-borne microspores would also capture wind-borne pathogens. Such pathogens would be selected to mimic pollen's dispersal timing and aerodynamic behaviour. Several seed characters may reduce this risk and assist in excluding, recognizing or eliminating "counterfeit" pollen. These include the enclosure of the megaspore within sporophytic tissues and an extended period during which the male gametophyte must coexist in intimate association with its host. Post-pollination provisioning might allow sporophytes to abort parasitized ovules, and pathogen pressure may have favored the ability to distinguish between same-species pollen and other materials. Strong similarities have been recognized at genetic and biochemical level between host-pathogen interactions and pollen-stigma interactions (Bushnell 1979).

Paleozoic ovules evolved a number of mechanisms for closure of the pollen chamber following pollination. The micropyle was variously sealed by the proliferation of integumentary tissues

(Stewart 1951); of female gametophyte tissues (Taylor & Millay
1981); or by the resinous pollination-drop (Taylor & Millay
1979). Foreign pollen has been reported in the pollen chambers of
fossil and modern gymnosperms (Sahni 1915; Lee 1955; Konar &
Oberoi 1969; Taylor & Millay 1979; Rothwell 1972). Insect eggs
enter the ovules of *Picea abies* (Sarvas 1968) and *Larix
occidentalis* (Owens & Molder 1979b) by the normal pollination
mechanism. Closure of the pollen chamber would have limited the
period of gametophyte exposure to pathogen propagules. An
alternative explanation is that closure prevented desiccation.

III. DISCUSSION

An evolutionary trade-off exists between propagule size and
number. Larger propagules enable a young plant to develop more
extensive structures for collecting sunlight, water or nutrients
before the plant becomes nutritionally self-sufficient. Thus, a
young plant's expectation of survival should tend to increase
with propagule size but the number of propagules produced by its
parent should tend to decrease. The optimal compromise between
propagule size and number should be determined by ecological
factors.

Many factors may favor larger propagules. I will emphasize
three: dry conditions, establishment in shade, and intense
competition among young plants. Large food reserves may be of
particular benefit when water is limited because they enable a
young plant to develop a more extensive root system or to
complete vulnerable juvenile stages during brief wet periods.
When light is limiting, large food reserves may allow greater
leaf area or longer persistence until light becomes available.
Under competitive conditions, larger food reserves may give a
head-start in competition with other plants germinating in the
same place. Among modern seed plants, larger seeds are associated
with drier habitats (Baker 1972) and with low light (Foster
1986).

After the first colonization of land, vascular plants would
have radiated into increasingly xeric habitats. At the same time,
improved conducting systems allowed increases in plant height,
and possibly greater shading at ground level. For these reasons

one would expect a progressive increase in maximum propagule size
during the Devonian, and such an increase has been documented
(Chaloner 1967; Chaloner & Sheerin 1981).

The present paper has explicitly considered the origin of
individual seed characters. If my assessment of the credible
selective pressures is accepted, the first generalization which
emerges is that selection for larger propagules lies behind most
of the evolutionary steps which separate seed plants from
pteridophytes. The second generalization is that the features of
seed plants arose in two major sequences, running roughly down
the right and left-hand sides of Figure 5.2. Those on the left
(2-12) are concerned with ovule structure, while those on the
right (13-22) are concerned with the pollination system. Within
each sequence, the order in which features should have arisen is
largely (though not completely) fixed, in that many features are
only selected for, or only possible, after other features have
arisen. But there are few such links between the two sequences.

The two sequences differ in the nature of selection. The
right-hand sequence involves selection on maternal genotypes. The
left-hand sequence involves both maternal and paternal genotypes.
An important factor in selection on paternal genotypes is inter-
male competition. Pollination (predispersal encounter) was
probably favored by selection on male sporophytes to produce
microspores that reached megaspores before competitors. The
evolution of pollen haustoria and siphonogamy was probably
favored by competition among male gametophytes to fertilize the
limited number of eggs within a single ovule.

Along the left-hand sequence, various steps have been taken
by a number of heterosporous lineages without this having led
automatically to the full complex of adaptations found in seed
plants. Reduction to a single megaspore per megasporangium,
enclosure of the megasporangium by "integuments", and post-
meiotic provisioning are found in various combinations among
pteridophytes. Seeds have traditionally been defined by the
possession of integuments, but I see no reason to believe that
the integuments of seed plants have adaptive significance
essentially different from analogous structures surrounding the
megasporangia of some pteridophytes. Integuments do not appear to

be the decisive adaptive innovation of seed plants.

I propose that the success of seed plants is associated with the right-hand sequence (pollination). The reception of microspores before propagule dispersal allowed resource commitment to become contingent on either pollination or fertilization. The selective advantage for the mother is obvious: resources need no longer be wasted on unfertilized propagules. Thus, conditional provisioning would have greatly increased the efficiency of sexual reproduction. However, the evolutionary change may have been far from trivial. Development that is contingent on pollination requires pollen recognition, and new developmental controls. Such capabilities are difficult to determine from the fossil record but, as far as I know, they are restricted to seed plants.

Wind-pollination would seem to offer easy access for pathogen spores to the food reserves of the propagule. Several seed characters may have a role in reducing this risk. These include pollen-recognition, enclosure of the female gametophyte, and the commitment of resources after pollination. Little is known about chemical recognition of same-species pollen by gymnosperms, or the fate of pathogen spores which enter pollen chambers. These seem promising areas for empirical study.

How do changes in ovule structure (left-hand side of Figure 5.2) relate to the evolution of a pollination system? As already pointed out, none of the changes on the pollination side seem directly necessary as precursors to changes in the other sequence. I suggest that the two sequences are related in a looser way, in that both are associated with continuing quantitative increases in propagule size. In each sequence, further steps are encouraged by selection to increase propagule size, and in turn many of the steps make further increase in maternal provisioning possible. For this reason the two sequences ought to be mutually reinforcing.

Figure 5.2. Adaptive interrelations among seed characters -- a summary of hypotheses. Names are given to characters for short reference; the exact nature of the characters is spelled out in the text. A broken arrow connecting two characters indicates that the presence of the first feature allowed the evolution of the second; a solid arrow indicates that the first feature actively favored the evolution of the second. This distinction is rarely clear. Numbers refer to selection pressures as follows (discussed at greater length in the text):

1) More difficult conditions for early establishment favored increased provisioning of offspring.

2) One means by which larger megaspores were achieved was to mature only one megaspore per megasporangium.

3) Once a sporangium contained a single spore, megaspore and sporangium could be dispersed together.

4) Protection became relatively cheaper, and the risk of predation may have increased, as propagules became larger.

5) Retention of the megaspore within the sporangium enabled the sporangium to be surrounded by protective structures that were dispersed with the propagule.

6) Exine functions were assumed by the new outer layers of the propagule.

7) Food reserves are most easily accumulated after the meiotic divisions.

8) Provisions could not be transferred across an impermeable exine.

9) Histological union of megaspore and sporangium was possible because the megaspore no longer required to be shed from its sporangium.

10) Provisions could be transferred more efficiently when the whole surface of a megaspore was in intimate contact with its sporangium.

11) Histological union between the megaspore mother cell and the megasporangium meant that a tetrahedron was no longer the most natural arrangement of the megaspore tetrad.

12) Provisioning of the megaspore after meiosis allowed the contemporaneous development of the female gametophyte.

13) Selection on male parents and/or microspores to reach megaspores first. This assumes that there was competition amongst

microspores and that first arrival was a significant factor in determining which microspore was successful. The putative selection pressure is associated with heterospory because it implies sexual specialization among spores, and because greater investment in each offspring via female function relative to male function implies more microspores than megaspores.

14) Selection on female parents and/or megaspores to reduce the probability of not being fertilized: selection will be stronger, and costs relatively less, when investment in each female-line offspring is greater.

15) Positive feedback.

16) Adaptations for pollen capture created a serious hazard of being infected by pathogens via the same route.

17) Commitment of resources to propagules became conditional on microspore capture or fertilization, thus avoiding expenditure on ovules which were not fertilized. Delayed commitment may also have contributed to reducing the pathogen hazard.

18) Post-meiotic provisioning allowed provisioning to be terminated if the propagule was not pollinated or fertilized.

19) Resources were conserved by provisioning only those propagules that were pollinated or fertilized.
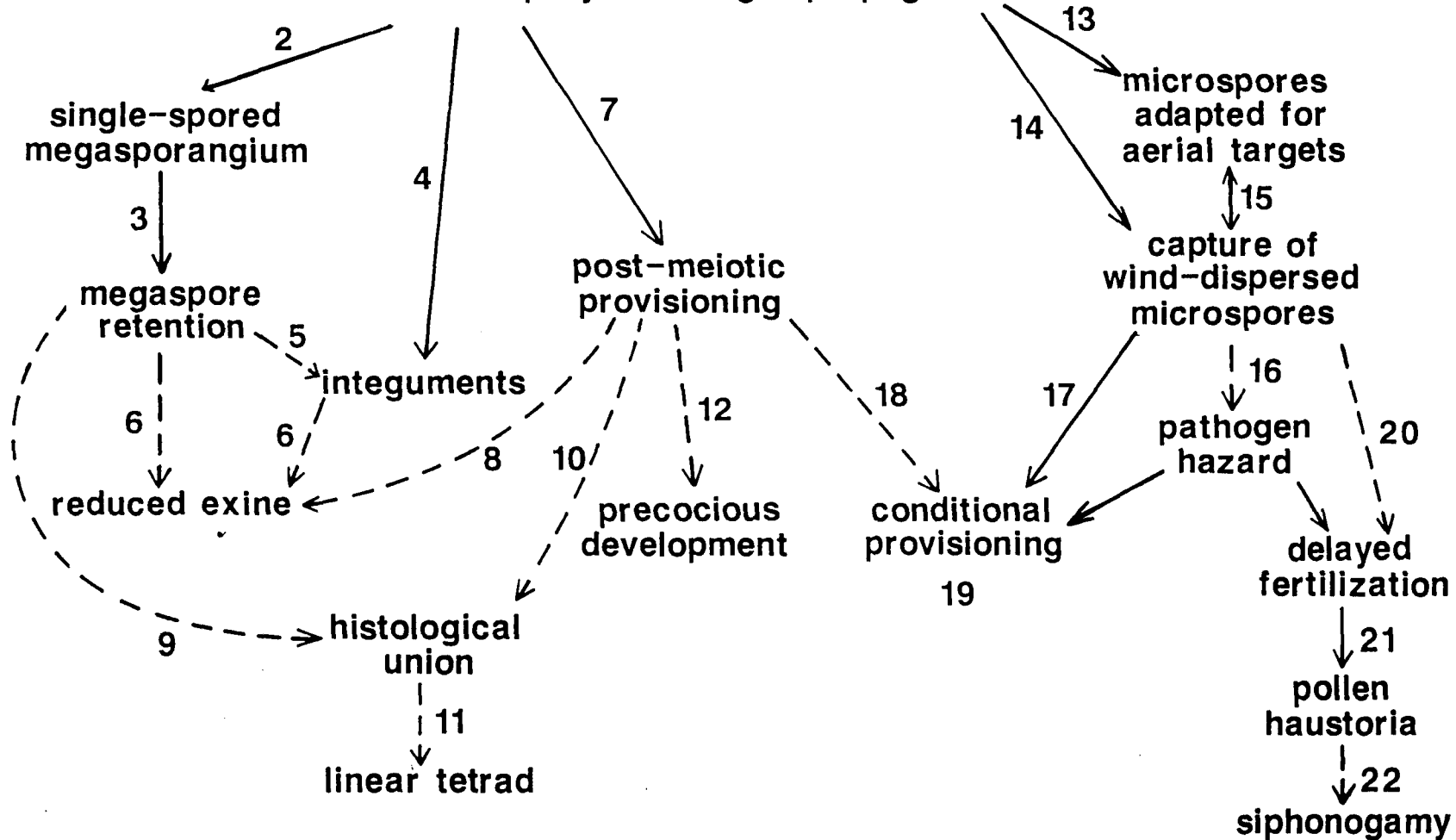
20) Pollination occured early during gametophyte development. This resulted in a delay between pollination and fertilization.

21) Male gametophytes held in the pollen chamber for extended periods developed haustoria to acquire nutrients from the host sporophyte.

22) Pollen haustoria provided a mechanism preadapted for delivering sperm. Siphonogamy allowed the female gametophyte to be enclosed by sporophytic tissues throughout development.

1
Heterospory and larger propagules

2

single-spored
megasporangium

3

megaspore
retention

5

integuments

6

6

reduced exine

4

7

post-meiotic
provisioning

12

precocious
development

8

10

9

histological
union

11

linear tetrad

13

microspores
adapted for
aerial targets

14

15

capture of
wind-dispersed
microspores

16

17

pathogen
hazard

18

conditional
provisioning

19

20

delayed
fertilization

21

pollen
haustoria

22

siphonogamy

Chapter 6

Brood reduction in gymnosperms

Chapter 5 discussed the evolution of the seed habit. I concluded
that a major advantage of seed plants, as compared to
pteridophytes, was the ability to abort unpollinated ovules for
less than the cost of a mature seed. Non-pollination is not the
only cause of seed or ovule abortion. In this chapter, I address
the mechanisms and functions of brood reduction in gymnosperms,
and then compare these processes to fruit and ovule abortion in
angiosperms. I emphasize gymnosperms rather than angiosperms
because brood reduction in angiosperms has been extensively
reviewed elsewhere (Stephenson 1981; Lee 1988). The chapter has
five major sections: Section I introduces the major features of
gymnospermous reproduction, by giving an overview of the
reproductive cycle in *Pinus*; Section II discusses seed and ovule
abortion; Section III discusses polyembryony and developmental
selection within seeds; Section IV considers whether seed
abortion could function to improve offspring quality; Section V
compares brood reduction in gymnosperms and angiosperms.

For simplicity, I will refer to plants by their generic name
and, in most cases, delete the specific name. The species on
which an observation is based can be found from the citation.
Strictly, the observation only applies to this species and may
not extend to other members of the genus, many of which probably
remain uninvestigated.

I. REPRODUCTIVE CYCLE OF *PINUS*

In this section, I describe the life cycle of a "typical"
temperate *Pinus* with a two-year reproductive cycle. The
description is a composite picture pieced together from studies
on several different species and may not correspond in all
details to any particular species. My purpose is to provide a
general overview of gymnosperm reproduction, before discussing
particular stages in greater detail. *Pinus* has been especially
well-studied because of its commercial importance and will serve

as a useful reference to identify similarities and differences
among gymnosperms.

Pines release their wind-dispersed pollen during spring.
Pollination occurs when one or more pollen grains are captured by
the pollination drop that is exuded from the micropyle of an
ovule. When the pollination drop is withdrawn, pollen is carried
into the micropyle and settles on the nucellus. Pollen germinates
within the ovule and forms a haustorial pollen tube that
penetrates the nucellus. Fertilization does not occur until the
next spring. Therefore, the male gametophyte must persist in the
ovule for about a year, during which time it is "parasitic" on
the maternal sporophyte.

Female cones and ovules are poorly developed at the time of
pollination. Shortly after pollination, unpollinated ovules
abort, as do conelets with many unpollinated ovules. Growth of
pollinated ovules and development of female gametophytes pauses
during the winter and resumes in the following spring, at which
time archegonia are formed and fertilization occurs. By this
stage, seeds have reached their final size, but seeds only
accumulate food reserves after fertilization. Unfertilized
ovules, and ovules with non-viable embryos, do not accumulate
reserves. In these ovules, the nucellus and female gametophyte
degenerate, leaving a full-sized empty seed.

Embryos grow at the expense of food reserves stored in the
female gametophyte. Starch begins to accumulate in the female
gametophyte during the earliest stages of embryo development.
However, it is not until the seed is almost mature that female
gametophyte cells become packed with their final complement of
lipids, protein and starch (Lill 1976; Owens & Molder 1977a;
Owens, Simpson & Molder 1982). In mature seeds of ponderosa pine,
the embryo represents about 10% of seed volume and 5% of seed
weight (Buchholz 1946). Most of the remainder consists of the
food stores of the female gametophyte. These reserves are used
during germination.

I will adopt Buchholz's (1918) terminology to describe the
post-fertilization development of a fertilized archegonium (for
alternative terminologies see Singh 1978). The zygote divides
four times to produce a 16-celled proembryo that consists of four

horizontal tiers of four cells. The basal tier is open to the archegonium and soon degenerates. The other tiers are (in order) the rosette, suspensor and embryonal tiers. Elongation of the suspensor cells forms the primary suspensor, which pushes the embryonal tier and its derivatives into the nutritive tissue of the female gametophyte. Each cell of the embryonal tier is the apical cell of an embryo. Each apical cell divides to produce a compact mass of cells which forms the embryo proper and one or more basal cells which elongate to form the secondary suspensor. Thus, each embryonal complex consists of four embryos attached to a common suspensor system (Figure 6.1). Sometimes, the rosette tier divides to produce additional "embryos" but these show very limited development (Berlyn 1962).

Two or more archegonia are often fertilized within an ovule, and each fertilized archegonium forms an embryonal complex with multiple embryos. Therefore, developing pine seeds usually contain several embryos. As a rule, however, only one seedling germinates from each seed. Thus, there must be some mechanism whereby all but one embryo is suppressed.

According to Buchholz (1918), a corrosion cavity is initiated in the female gametophyte, even if there is no fertilization. However, the subsequent enlargement of the cavity is due to digestive enzymes secreted by the developing embryos. An "embryo is first pushed as far as possible into the corrosion cavity by the mechanical action of the suspensor; later it remains nearly stationary in the lower end of this cavity, but continues to give off the suspensor by the successive elongation of cells from the radical end of the embryo" (Buchholz 1918). Usually one embryo attains a dominant position and pushes smaller embryos back towards the archegonium with the twists and coils of its suspensor (Buchholz 1946).

The above description illustrates the range of processes that will be discussed in subsequent sections. Brood reduction (broadly defined) occurs at a number of levels. Seed cones may abort, as may individual ovules/seeds within cones, or individual embryos within seeds. The abortion of cones and ovules reduces the number of seeds that a sporophyte is able to mature, whereas embryo abortion does not necessarily reduce seed production

Figure 6.1. The embryonal complex derived from a single fertilized archegonium in *Pinus*. Four embryos are attached to a common suspensor system (after Buchholz 1918).

Rosette tier

Primary suspensor

Secondary suspensor
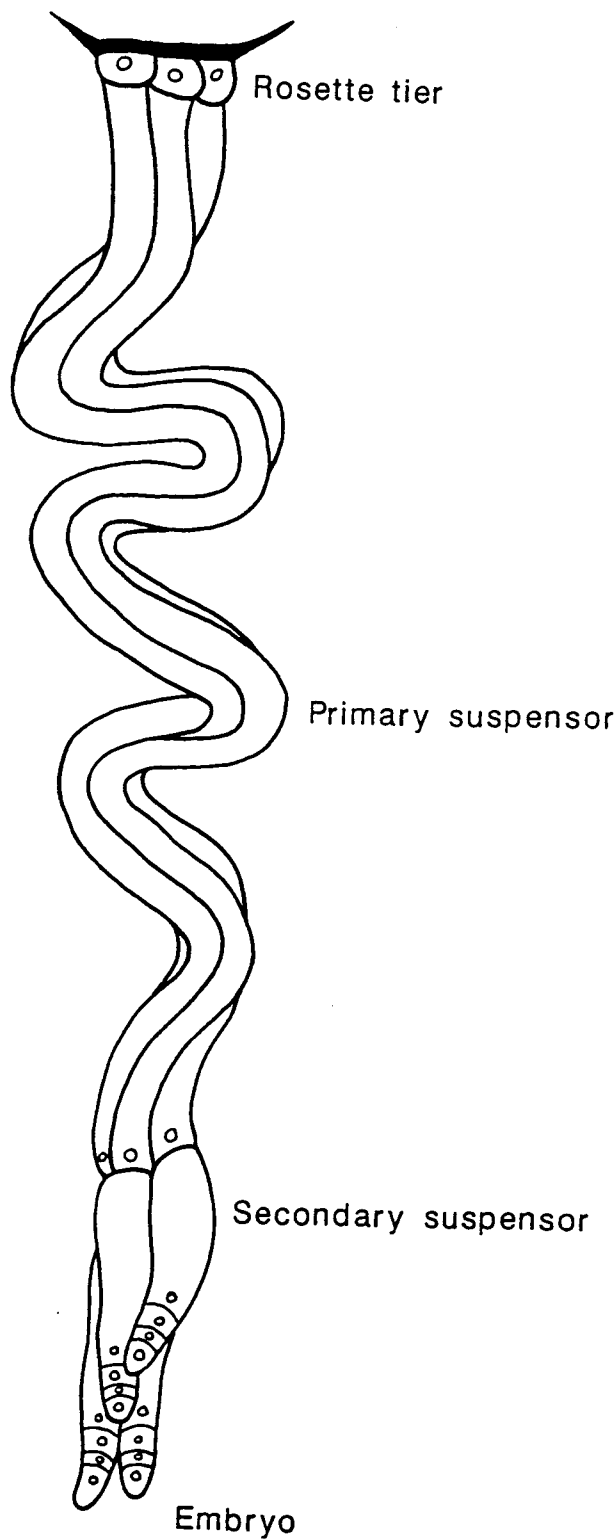
Embryo

because of polyembryony within seeds. Ovule abortion occurs
before fertilization, and seed abortion occurs after
fertilization (by definition of a seed). I classify ovule
abortion as a form of brood reduction because a female
gametophyte within an ovule is a sporophyte's "offspring" in a
similar, though not identical, sense to an embryo within a seed.

II. SEED AND OVULE ABORTION
A. Ovule abortion (before fertilization)

A seed contains food reserves that are supplied by the maternal
sporophyte and stored in the female gametophyte. Resources
committed to an aborted ovule are a cost to the sporophyte. The
magnitude of the cost depends on how much has been committed to
the ovule at the time when it is aborted. A clear distinction
must be made between the size of an ovule and its energy content,
when assessing the costs of abortion. This is because the bulk
of nutrient accumulation usually occurs after expansion is
complete.

Female gametophytes (and ovules) of all modern gymnosperms
are small at the time of pollination. In some species with long
reproductive cycles, the meiotic divisions which initiate the
female gametophyte occur after pollination (*Pinus*: Sarvas 1962;
Lill 1976). The interval between pollination and fertilization
varies greatly. *Ephedra* is atypical, because fertilization may
occur within ten hours of pollination (Land 1907). In *Taxus*
(Dupler 1917; Pennell & Bell 1987, 1988) and *Gnetum* (Vasil 1959),
the delay is about a month. A typical delay for species with one-
year reproductive cycles is 3-4 months. In most species of *Pinus*,
fertilization occurs one year after pollination. A similar delay
occurs in *Agathis* (Kaur & Bhatnagar 1986). In three species of
Pinus, the time lapse is two years (for an overview of time
relations see Singh 1978, chapter 13).

The female gametophyte of many gymnosperms has reached
almost its final size before fertilization (e.g. *Cephalotaxus*,
Ginkgo, cycads: Favre-Duchartre 1958; *Pinus*: Sarvas 1962; *Picea*:
Sarvas 1968). However, scattered cell divisions are a common
feature of post-fertilization gametophytes, and cause some
increase in gametophyte size (Singh 1978, p. 237). In podocarps

and araucarians, there is substantial growth of the ovule and/or
female gametophyte after fertilization (podocarps: Osborn 1960;
Konar & Oberoi 1969; araucarians: Burlingame 1915; Haines 1983;
Kaur & Bhatnagar 1986). In a few other taxa, the greatest part of
the female gametophyte's growth occurs after fertilization
(*Torreya*: Coulter & Land 1905; *Taxus*: Dupler 1917; *Ephedra*: Land
1907; *Gnetum*: Maheshwari & Vasil 1961; *Welwitschia*: Pearson 1929;
Martens 1971). I emphasize this point because I am often told
that gymnosperm ovules have completed their growth before
fertilization.

Ginkgo and cycads differ from other gymnosperms in that
fertilization occurs after nutrient accumulation is complete.
Sterile ovules contain the same food reserves as seeds with an
embryo (Favre-Duchartre 1958). In *Ginkgo*, the interval between
pollination and fertilization is about 5 months. Ovules are very
small at the time of pollination, and unpollinated ovules abscise
(Lee 1955; Favre-Duchartre 1958; Friedman 1987). Pollinated
ovules increase greatly in size, but only accumulate food
reserves in the month before fertilization (Favre-Duchartre
1958). Thus, *Ginkgo* does not provision unpollinated ovules but
does provision pollinated ovules which remain unfertilized and
fertilized ovules in which all embryos die. *Ginkgo* is possibly
unique among modern seed plants in that its female gametophyte is
photosynthetic and can supply some of its own carbon requirements
(Friedman & Goliber 1986).

At least some cycads abort unpollinated ovules (Baird 1939;
Norstog, Stevenson & Niklas 1986; Tang 1987a), though Chamberlain
(1912) reported that ovules of *Ceratozamia* attained full size, in
circumstances where there had been no possibility of pollination.
Ovules of *Cycas* wither away without pollination, but develop to
full size when pollinated by pollen from other cycads. Foreign
pollen provides the necessary stimulus for full growth but there
is no fertilization (de Silva & Tambiah 1952).

Apart from *Ginkgo* and cycads, female gametophytes of other
gymnosperms accumulate the bulk of their food reserves after
fertilization (Schnarf 1933; Favre-Duchartre 1958). This enables
more complex patterns of brood reduction because ovules or seeds
can be aborted after fertilization for less than the full cost of

a seed. In this group, seeds are not provisioned unless they are
fertilized. For some members of the group, ovules develop
independently of pollination until the archegonial stage.
Unpollinated and pollinated (but unfertilized) ovules are aborted
together. Other members abort unpollinated ovules before the
archegonial stage.

Pinus aborts unpollinated ovules shortly after the expected
time of pollination. At this stage ovules are little-developed
(Sarvas 1962; Owens et al. 1981a). Juniperus also has a two-year
cycle and, like Pinus, aborts unpollinated ovules in the first
growing season (Sarvas 1962). Podocarpus has a one-year cycle
(12-13 months from pollination to ripe seeds), and abscises
unpollinated ovules before fertilization. A different pattern is
found in members of the Pinaceae with a one-year reproductive
cycle. The integuments develop into a hard seed-coat whether or
not ovules are pollinated. Unpollinated ovules form full-sized
empty seeds which contain the degenerate remains of the nucellus
and female gametophyte (e.g. Picea: Owens & Molder 1979a, 1980;
Larix: Owens & Molder 1979b; Pseudotsuga: Owens et al. 1981b).
Female gametophytes of unpollinated Picea ovules begin to
degenerate before fertilization (Sarvas 1968; Mikkola 1969),
though occasional ovules will develop to the archegonial phase
without pollen (Mikkola 1969; Koski 1973).

Female gametophytes of Metasequoia (Engels & Gianordoli
1983), Araucaria (Haines 1983) and Agathis (Kaur & Bhatnagar
1986) develop archegonia independently of pollination, but do not
accumulate nutrients unless fertilized. I do not know whether
Metasequoia ovules are full-sized at fertilization. However, the
female gametophyte of Araucaria and Agathis increases in size
after fertilization. Abortion of unpollinated ovules at the
archegonial stage would be relatively more expensive in other
species which complete growth before fertilization.

The frequency of pollination varies from year to year at a
single site. Two Finnish examples are illustrative. At the
Tuusula XXIII stand of Pinus sylvestris, 4% of ovules were
unpollinated in 1958 but 32% were unpollinated in 1959 (Sarvas
1962). Over a period of 13 years at the Tuusula XXX stand of
Picea abies, the proportion of empty seeds ranged from 22% to

100%, mainly because of differences in pollination (Sarvas 1968).

Some pre-fertilization ovules abort for reasons other than non-pollination. *Juniperus monosperma* preferentially abscises "fruits" that are parasitized by insects (Fernandez & Whitham 1989). Unseasonal frosts cause increased proportions of empty pine seed (Sarvas 1962) and pollinated ovules sometimes abort for unknown reasons (Saxton 1913; Lyons 1956; Owens & Molder 1977b). In some experimental crosses between *Pinus* species, pollination initiates normal development but ovules abort before fertilization (McWilliam 1959; Mikkola 1969; Kormutak 1984).

B. Seed abortion (after fertilization)

Not all fertilized ovules develop into filled seeds. In years of abundant pollination, the major cause of empty *Picea* seeds is the abortion of all embryos within a seed. In two stands of *Picea abies*, 8% and 6% of seeds were empty because of abortion before fertilization, but 30% and 16% of seeds were empty because of abortion after fertilization. Most seed abortion occurred during early embryo stages before there had been substantial accumulation of nutrients in the female gametophyte (Sarvas 1968). *Picea glauca* appears to be similar. At one site, one in two ovules aborted at an early embryo stage. In the next year, two out of every three ovules aborted (Owens & Molder 1979a).

The formation of empty seeds from fertilized ovules is often tacitly assumed to be an adaptive response to the death of all embryos within a seed. (The alternative hypothesis would be that embryos die as a result of the abortion process.) Embryos are assumed to die because they are homozygous for deleterious recessive alleles that were heterozygous in their parents. This hypothesis is supported by the high incidence of empty seed after selfing. Typically, many more empty seeds are formed after self-pollination than after cross-pollination (Sarvas 1962, 1968; Koski 1973; Franklin 1970; Plym Forshell 1974; Griffin & Lindgren 1985; Smith, Hamrick & Kramer 1988). There is no evidence of prezygotic incompatibility. Self-pollen is able to fertilize archegonia, but many of the resulting embryos abort during early development. Some sporophytes are less self-sterile than other sporophytes within the same species (Plym Forshell 1974; Johnsson

1976) as would be expected if some sporophytes carried more recessive lethals than others.

Under open-pollination, monoecious sporophytes are likely to receive a mixture of own pollen and cross-pollen. Koski (1973) inferred that the proportion of selfed seedlings in stands of a variety of conifers was about 10% on average. Significantly, this was considerably less than the proportion of own pollen in total pollination. Many natural products of selfing are probably eliminated as empty seeds before the seedling stage or are eliminated in filled seeds that also contain an outcrossed embryo. Rudin, Muona & Yazdani (1986) found 12% selfing among embryos in mature seeds from a *Pinus sylvestris* stand. The proportion of self-pollination is likely to be greater for isolated trees than for trees in monospecific stands.

Selfing is not the only cause of empty seeds. Sarvas (1962) and Johnsson (1976) recorded 10% and 19% empty seeds following cross-pollination of *Pinus sylvestris*. Either there is a relatively high frequency of homozygosity for recessive lethals among outcrossed progeny, or some empty seeds are produced for reasons other than embryo lethality. Burdon & Low (1973) reported a higher proportion of empty pine seed on a phosphorus-deficient site. This suggests that resource-limitation could be one possible explanation of background levels of empty seeds.

C. Conelet abscission

So far this section has discussed the abortion of individual seeds or ovules. *Pinus* spp. regularly abscise cones with many aborted ovules. Abscission takes place during the first year of the reproductive cycle, after pollination but before cones enlarge. Roughly speaking, *P. sylvestris* abscises conelets if more than 60% of ovules are aborted. In this species, conelet abscission approaches 100% when pollination is poor, but never falls much below 20%, even when pollen is superabundant (Sarvas 1962). Hagman (reported in Sweet 1973) observed about 30% conelet abortion in three other pine species, despite adequate pollination. Conelet abortion is a problem in pine-seed orchards even when there is no evidence that pollen is limiting (Sweet & Thulin 1967; Sweet 1973; White, Harris & Kellison 1977). Sweet

(1973) proposed that *P. radiata* conelets abort because of competition for carbohydrates.

Juniperus, like *Pinus*, abscises poorly-pollinated conelets during their first growing season. Thus, conelet abortion appears to be associated with two-year reproductive cycles (Sarvas 1962). By contrast, *Picea* (which matures seeds in the same year as pollination) does not abort poorly-pollinated cones, even if the cones have 100% empty seeds (Sarvas 1968).

D. Functions of seed and ovule abortion

At first sight, brood reduction appears paradoxical. Natural selection should promote the efficient use of limited reproductive resources, but resources committed to abortive offspring are non-productive. Why should a parent go to the expense of initiating an ovule, only to abort it at a later stage?

The paradox is easily resolved. An ovule's fate is uncertain at the time when it is initiated. Some ovules will outcross, some will self, and others will remain unpollinated. Moreover, each ovule is subject to the vagaries of parasitism, frost-damage, drought, and the other slings and arrows of outrageous fortune. As a consequence, sporophytes can gain higher fitness returns from some ovules than from others. Brood reduction will be adaptive if resources can be redirected from low-yielding to high-yielding ovules. This is best illustrated by the abortion of ovules that cannot produce a seedling because of non-pollination, embryo death or some other factor. However, if a sporophyte benefits by aborting ovules which give no return on investment, it should also benefit by aborting ovules which give a very low return. For example, some viable ovules may be aborted when poorly-pollinated conelets abscise, but these ovules would give a low return on investment if matured because the cost of maturation would include the protective structures of the cone. Therefore, the cost per seed should be greater for cones with many aborted ovules, and abscising few-seeded cones may be adaptive if the resources so liberated can be used more efficiently elsewhere.

Any benefit of brood reduction will become more economical

as the cost of an aborted ovule is reduced. At least in theory, resources should be supplied to ovules as late as possible relative to significant events (pollination, fertilization) that determine an ovule's probability of producing a successful seedling. Among gymnosperms, ovules do not accumulate food reserves until after pollination (*Ginkgo* and cycads) or until after fertilization (other gymnosperms). Therefore, unpollinated or unfertilized ovules can usually be aborted for much less than the cost of a mature seed. The costs of abortion would be further reduced if nutrients can be recovered from aborting ovules. Sarvas (1962) and Sweet (1973) both refer to the transfer of accumulated nutrients from aborting pine ovules, but I know of no experimental evidence for nutrient transfer.

Some gymnosperms appear to be less efficient than others at eliminating low-yielding ovules for minimal cost. Unlike other gymnosperms, *Ginkgo* and cycads provision pollinated ovules that remain unfertilized. Within the Pinaceae, *Pinus* aborts unpollinated ovules before substantial growth of the female gametophyte, whereas unpollinated *Picea* ovules grow to full size and form a hard seed coat. Moreover, *Pinus* abscises poorly-pollinated conelets but *Picea* does not. *Picea* seeds reach maturity in the same growing season as pollination, and the shorter reproductive cycle probably imposes stricter limits on flexible resource allocation.

An ovule's fate can be uncertain at two levels that will be illustrated using the example of pollinated and unpollinated ovules. (1) The proportion of pollinated ovules is predictable but which ovules will be pollinated is uncertain. Such uncertainty is necessary for brood reduction to be adaptive because, if the fate of individual ovules was known beforehand, the sporophyte should initiate only those ovules which would be pollinated. (2) Which ovules are to be pollinated and the proportion of pollinated ovules are both uncertain at the time of ovule initiation. This second kind of uncertainty provides an adaptive reason why sporophytes might occasionally abort ovules with high expected fitness, as discussed below.

An ovule can be produced for less than the cost of a seed. Therefore, a sporophyte may initiate more ovules than it is

physiologically capable of maturing into seeds. The sporophyte can then abort unpollinated ovules, and provision the remainder. If the proportion of pollinated ovules is predictable in advance, the number of ovules should be adjusted so that there are sufficient resources remaining to provision all pollinated ovules. However, if the proportion of pollinated ovules is uncertain, some pollinated ovules may abort in years of abundant pollination because the sporophyte has insufficient resources. In such years, the sporophyte could have matured more seeds if it had produced fewer ovules. If the sporophyte produced the same number of ovules but pollination had been poor, resources might have remained after all pollinated ovules had been provisioned. In such years, the sporophyte could have matured more seeds if it had produced more ovules. The abortion of "excess" ovules when pollination is good is the price that is paid for a buffer against low seed production when pollination is poor.

There is circumstantial evidence that resources may be limiting when pollen is abundant. Conelet drop in *Pinus* is reduced but never eliminated in years of high pollen density (Sarvas 1962; Sweet 1973), and repeated hand-pollination of *Picea* does not reduce the proportion of empty seeds below 50% (Ho 1985). The evidence for resource-limitation is circumstantial because it is not known whether aborted ovules would develop if other ovules were removed.

The argument developed here for pollinated and unpollinated ovules applies generally to other unpredictable causes of ovule loss. The number of ovules initiated should be such that some viable ovules are aborted because of resource-limitation in the best years but available reproductive resources are not fully utilized in the worst years. Such resources can, of course, be redeployed for vegetative growth and future reproduction. Other things being equal, the cheaper an aborted ovule is relative to a seed, the greater the number of ovules that should be initiated and the higher the proportion of years in which seed production will be resource-limited (see Chapter 7).

III. POLYEMBRYONY

Two causes of polyembryony should be distinguished. Cleavage polyembryony (CPE) is the subdivision of the embryonal mass derived from a single zygote into multiple embryos. Simple polyembryony (SPE) is the development of embryos from more than one zygote within a seed. Cleavage polyembryony has a sporadic distribution among gymnosperms (see Doyle & Brennan 1971, 1972; Singh 1978; Willson & Burley 1983) whereas simple polyembryony is almost universal among gymnosperms. This section deals with simple polyembryony unless otherwise stated.

Although polyembryony is a common feature of gymnosperms, it is rare for more than one seedling to germinate from a seed. Johnstone (1940) summarized data from 11 species of *Pinus*. The proportion of twin seedlings varied from 2.2% to much less than 1%. Burdon & Zabkiewicz (1973) found that some twins were the genetically-identical cleavage products of a single zygote whereas others were the products of separate fertilizations. The proportion of mature pine seeds that contain multiple embryos is considerably higher than the proportion of twin seedlings (Berlyn 1962). The additional embryos do not emerge from the seed coat and possibly are consumed by the germinating embryo as it digests the food reserves of the female gametophyte. Mature seeds with a single embryo probably once contained other embryos that were suppressed earlier in development.

A. Number of archegonia

The ubiquity of simple polyembryony is inferred from the widespread occurrence of female gametophytes with more than one archegonium (see Figure 20 of Favre-Duchartre 1970 and the Appendix to Willson & Burley 1983 for useful reviews). Exceptions are rare. Female gametophytes of *Torreya taxifolia* only ever produce a single archegonium (Land 1907). Some other species produce a significant proportion of female gametophytes with only one archegonium (e.g. *Abies balsamea* (15%): Favre-Duchartre *loc cit*). I will discuss variation in the number of archegonia per female gametophyte in relation to different modes of fertilization and different spatial arrangements of archegonia.

Two modes of fertilization can be distinguished in living

gymnosperms. In *Ginkgo* and cycads, archegonia are fertilized by free-swimming sperm (zooidogamy). In all other gymnosperms, male gametes are delivered directly to archegonia by pollen tubes (siphonogamy). This dichotomy also corresponds to the distinction between species in which female gametophytes accumulate all their food reserves before fertilization and species in which female gametophytes accumulate most of their food reserves after fertilization.

Most gymnosperms with free-swimming sperm do not produce large numbers of archegonia. Female gametophytes of *Ginkgo* usually produce two archegonia (Lee 1955; Favre-Duchartre 1958). *Macrozamia* spp. produce up to 15 archegonia but the usual number is 4-7 (Chamberlain 1913; Baird 1939; Brough & Taylor 1940). *Microcycas* stands out. According to Caldwell (1907), female gametophytes of *Microcycas* produce more than 200 archegonia. Reynolds (1924) did not comment on Caldwell's claim but gave the more cautious estimate of more than 64 archegonia.

Most siphonogamous gymnosperms have archegonia that occur singly, rather than grouped into complexes. Female gametophytes typically produce 4-7 archegonia, though lower and higher numbers also occur (Singh 1978). Archegonia are grouped into complexes in the traditional families Cupressaceae and Taxodiaceae. Female gametophytes of this group usually produce greater numbers of archegonia than occur in other families (Favre-Duchartre 1970; Singh 1978; Willson & Burley 1983). For example, *Biota* has an apical complex with 15-28 archegonia (Singh & Oberoi 1962). Cladistic analyses suggest that the traditional Cupressaceae is a monophyletic lineage nested within the Taxodiaceae (Hart 1987; Price & Lowenstein 1989). Price & Lowenstein have proposed that both families be subsumed within an expanded Cupressaceae, and I adopt this proposal in the rest of this chapter.

Members of the Cupressaceae can be divided into those species (like *Biota*) that have a single apical complex, and those that produce lateral complexes. Lateral complexes are produced by female gametophytes of *Widdringtonia* (Saxton 1909), *Actinostrobus* (Saxton 1913), *Callitris* (Baird 1953), *Sequoia* and *Sequoiadendron* (Buchholz 1939a, 1939b). Female gametophytes of these genera may produce two or more lateral complexes each associated with a

pollen tube. In *Actinostrobus*, the location of "archegonial initials" is not determined by proximity to a pollen tube, but pollen tubes do determine which of the very numerous initials become functional archegonia (Saxton 1913). Neither species with apical complexes nor species with lateral complexes form a monophyletic group in Hart's (1987) cladistic analysis.

Very large numbers of archegonia are sometimes reported for species with lateral archegonia, but these numbers appear to be counts of archegonial initials rather than numbers of functional archegonia. Thus, Saxton (1934) reported 200 archegonia from *Widdringtonia juniperoides* and Moseley (1943) reported 100 archegonia from *W. cupressoides*. However, Moseley noted that many archegonia did not mature and disintegrated soon after fertilization. In *Sequoia* and *Sequoiadendron*, archegonial initials are numerous but many do not form functional archegonia. Some archegonial initials may divide to form ordinary cells of the female gametophyte (Buchholz 1939a, 1939b; Looby & Doyle 1942).

B. Three examples from the Pinaceae

The number of archegonia sets an upper limit on the number of zygotes within an ovule, but it is not the only determinant of the degree of simple polyembryony. Other important factors are the quantity of pollen received by an ovule, the capacity of the pollen chamber, and how many pollen tubes achieve fertilization. Three members of the Pinaceae will illustrate the interplay of factors.

The first example is *Pinus sylvestris* (Sarvas 1962). Simple polyembryony is common but a proportion of ovules produce only one zygote because the female gametophyte produces only one archegonium or because the pollen chamber contains only one pollen grain. If pollinated ovules are examined, about 30% of pollen chambers contain only one pollen grain, roughly 50% contain two grains, and the rest contain three or more grains. Pollen chambers contain a single pollen grain either because this is the maximum capacity of the chamber or because the ovule has received insufficient pollen. Most pollen chambers have a maximum capacity of 2-3 pollen grains, but about 18% of pollen chambers

have room for only one grain. When pollination is abundant, most ovules receive more pollen at the micropyle than can be accommodated within the pollen chamber. Almost all pollen grains that reach the pollen chamber will fertilize an archegonium if there is one available. The most common number of archegonia is two (about 70% of ovules), but some trees produce up to 30% of ovules with only one archegonium.

The second example is *Picea abies* (Sarvas 1968). About 30% of ovules with embryos contain only one embryo. This figure overestimates the frequency of single fertilizations because it does not take account of the frequent abortion of embryos before the third division of the zygote. Pollen chambers have an average capacity of 5 pollen grains, and female gametophytes produce an average of 3 archegonia. Therefore, some pollen tubes may be unable to fertilize an egg. About 6% of pollen chambers have room for only one grain and less than 1% of ovules contain only one archegonium.

The final example is *Pinus monticola* (Owens & Molder 1977a). Female gametophytes produce 3-5 archegonia but it is unusual for more than one egg to be fertilized, even though the nucellus contains abundant pollen grains and pollen tubes. Fertilization of one egg appears to inhibit the fertilization of adjacent eggs.

C. Functions of polyembryony

Buchholz (1922) suggested that polyembryony is a mechanism of "developmental selection". He proposed that competition among embryos within a seed results in the elimination of less vigorous embryos. Because the unfit are eliminated early in development, this is "doubtless a most valuable form of biological economy". Buchholz's proposal remains the most plausible function of simple polyembryony. At the time of fertilization, most gymnosperms have already made a substantial investment in each ovule. By this stage, ovules have already grown to considerable size, even though food reserves do not accumulate until after fertilization. The death of all embryos within a seed, therefore, entails a significant loss of reproductive resources. Simple polyembryony increases the probability that each ovule will contain a viable embryo. Suppose that 50% of zygotic genotypes are inviable, then

the proportion of seeds without a viable embryo would be 25% for two zygotes per ovule, 12.5% for three zygotes per ovule, and so on. The benefits of simple polyembryony are subject to diminishing returns.

Buchholz's proposal assumed competition between viable embryos. If most seeds produce two or more zygotes, some seeds will contain more than one viable embryo, and embryos will compete to become the successful embryo of their seed. Such competition will be adaptive if the average fitness of surviving embryos is greater than would have been the case if there had been no selection.

The "selection arena hypothesis" (Stearns 1987) is a modern version of Buchholz's hypothesis. Buchholz and Stearns have emphasized the importance of embryos competing on even terms. However, fertilizations are not always synchronous within an ovule (Kozinski 1986). Mikkola (1969) has questioned the evidence for effective competition between embryos in Picea, because one embryo always seemed to have a favored position within the corrosion cavity. The process of developmental selection is somewhat analogous to choosing a candidate to fill a job. A "competitive audition" is not the only possible approach. An embryo can be given a "probationary appointment" and be replaced if found to be unsuitable. A mechanism in which the first embryo was always successful, unless it was inviable, might be more efficient than embryonic competition if there was little correlation between competitive success and seedling fitness.

Developmental selection appears to be an unsatisfactory explanation for cleavage polyembryony. Cleavage produces embryos that share a common genotype. Therefore, it is difficult to see how competition among these embryos could be adaptive. Sarvas (1962) and Willson & Burley (1983) proposed that cleavage may increase a genotype's competitiveness in the conflict with other embryo genotypes within the same seed. Sorensen (1982) suggested that monozygotic polyembryony (i.e. CPE) had the potential to reduce the effects of climatic disturbance. For example, the development of cleavage embryos could be non-synchronous and different stages could differ in their sensitivity to environmental stress. Hurst (in press) suggested that selection

among cleavage products may be adaptive because embryos differ in their cytoplasmic parasites. In summary, the function of cleavage polyembryony remains obscure.

For developmental selection to be effective, some pollen grains must be more likely than others to father successful embryos. Genetic markers can be used to test whether pollen of different genotypes is equally effective in mixed pollinations. Matheson (1980) and Smith et al. (1988) found that mixtures of self and outcross pollen produced fewer than expected inbred seedlings. Apsit, Nakamura & Wheeler (1989) showed differential male reproductive success in mixtures of outcross pollen. A pollen parent that was relatively successful in one cross was sometimes relatively unsuccessful in other crosses. This suggested that some form of complementarity between male and female genomes was a factor in differential success. Fowler (1964) observed non-Mendelian ratios among the selfed progeny of a sporophyte heterozygous for a morphological mutant. These studies do not identify the stage at which differential success is determined, and competition between embryos within seeds is only one possibility.

Sarvas (1962, 1968) distinguished two processes at work during embryonic selection in Pinus and Picea. The first was the death of embryos that would have died whether or not they were the only embryo within the seed. Most of these deaths occurred before the third division of the zygote. Because of simple polyembryony, aborted embryos sometimes occurred in seeds with a viable embryo and the proportion of aborted embryos was considerably greater than the percentage of empty seed. The second process was the death of embryos that would have been viable if there had been no other embryos in the seed. This death by competition had the potential to increase the average vigor of surviving embryos.

As Sarvas and others have pointed out, these processes have the potential to reduce the deleterious effects of selfing. Self-pollination of gymnosperms usually results in an increased proportion of empty seeds and a reduced growth rate of seedlings from filled seeds (Franklin 1970; Koski 1973; Matheson 1980). The undesirable effects of selfing are almost certainly caused by

increased homozygosity for deleterious alleles. Therefore, if ovules receive a mixture of self and cross pollen, simple polyembryony will result in the disproportionate production of outcrossed progeny and a reduction in the proportion of empty seeds (Sorensen 1982).

Simple polyembryony can also be advantageous if ovules only receive self pollen. At any locus heterozygous in the parent, only some selfed zygotes will be homozygous for the deleterious allele. Sarvas (1962) observed a negative correlation between the proportion of unpollinated ovules in a cone and the proportion of pollinated ovules that formed filled seeds in naturally self-pollinated *Pinus*. In other words, the proportion of filled seeds increased as a cone received more self pollen, probably because on average more zygotes were formed in pollinated ovules. Simple polyembryony and developmental selection must have advantages after pure out-crossing because they occur in dioecious gymnosperms that cannot self.

A number of authors have used the percentage of empty seeds formed after selfing to estimate the frequency of embryonic lethals in members of the Pinaceae (Sorensen 1969; Franklin 1972; Koski 1973; Park & Fowler 1982, 1984; Fowler & Park 1983). Such studies have revealed higher genetic loads than similar estimates from animals. An average sporophyte is estimated to be heterozygous for several recessive lethals. The frequency of deleterious alleles is determined by the opposing forces of mutation and selection. Klekowski (1982) argued that simple polyembryony reduces the expressed genetic load for a given frequency of lethal alleles. Thus, natural selection is relaxed and recessive lethals are maintained at a high equilibrium frequency.

Estimates of the average number of lethals per sporophyte usually assume that embryo death is caused by homozygosity for independent recessive lethals. Griffin & Lindgren (1985) obtained a better fit to data when they assumed that embryo death is caused by homozygosity for recessive alleles at two or more loci which are individually non-lethal. These models all tacitly assume that the female gametophyte and parental sporophyte are passive participants in an embryo's death. Alternative

assumptions may allow different interpretations. For example, seeds could be aborted if the vigor of the 'best' embryo falls below some threshold. In this case, vigor (and embryo death) could be a quantitative character determined by the segregation of alleles at many loci (see Chapter 3 for a detailed discussion of "genetic load" in homosporous ferns). Bishir & Namkoong (1987) concluded that 5% to 30% of empty seed was caused by "maternal effects" rather than embryonic lethals. If a model allows sufficient flexibility in the choice of its parameters, agreement with observation is not strong confirmation of the model. Moreover, embryo deaths need not have a single cause. Some deaths are undoubtedly caused by independent lethals, but this does not negate other factors.

D. Reproductive strategies of female gametophytes

Embryos are the progeny of gametophytes. They are only indirectly the progeny of sporophytes. From our human perspective, it is easy to view polyembryony in terms of costs and benefits to diploid sporophytes. However, gametophytes are genetic individuals in their own right and it is probably more informative to consider polyembryony in terms of the genetic interests of haploid gametophytes. A gametophyte passes on its genes when it contributes a gamete to the zygote which becomes the successful embryo in a seed. A gametophyte can only contribute one gamete to the next (sporophyte) generation because only one embryo germinates from a seed. Despite this fact, most female gametophytes and many male gametophytes contribute gametes to more than one zygote.

All zygotes within an ovule carry a copy of the female gametophyte's genome. From the perspective of a gene in the female gametophyte, the important issue is not whether it will be present in the successful zygote, but with what other genes it will be associated. As a result of simple polyembryony, the female gametophyte's genome is combined with different sets of paternal genes. Natural selection will favour any process in the female gametophyte that ensures the most compatible combination becomes the successful embryo. Selection among embryos acts on the paternal genetic contribution because the maternal genetic

contributions are identical. Plastids are paternally-inherited in some gymnosperms, and male gametophytes may contribute organellar as well as nuclear genes (Whatley 1982; Neale & Sederoff 1989).

Generally speaking, the greater the number of embryo genotypes sampled, the greater the expected fitness of the best genotype. The increase in expected fitness is greatest when the number of genotypes is increased from one to two. Thereafter, the increase in expected fitness decreases for each additional genotype. These statements do not take account of the costs of an additional embryo. Simple polyembryony has costs as well as benefits, because organic molecules respired in the course of embryonic competition are not available for the successful embryo when it germinates. Put another way, a female gametophyte receives a limited amount of resources from the maternal sporophyte and there is a trade-off between allocating more resources to additional embryos and having less resources available for germination. There must be some finite number of embryos which maximizes the gametophyte's expected fitness. This is because the increase in quality of the best embryo is subject to diminishing returns and there is no reason to believe that the cost of additional embryos will decrease in proportion to the decrease in benefit.

The relative costs and benefits of producing $n + 1$ rather than n embryos will differ for female gametophytes in seeds of different sizes. Presumably, the energetic cost of an additional embryo will be similar for small and large seeds, as will be the increase in expected seedling quality (where "quality" is an abstract property that measures the relative fitness of different genotypes under uniform conditions, including identical food reserves). Therefore, the energetic cost of the additional embryo will account for a smaller proportion of total food reserves in larger seeds, for the same increase in seedling quality. Other things being equal, one would expect higher levels of simple polyembryony in species with larger seeds. I have been unable to test this prediction.

The benefits of simple polyembryony are influenced by the variation in quality among embryos within an ovule. Ovules of monoecious species may receive a mixture of self and cross

pollen, but ovules of dioecious species never receive self
pollen. One might predict that dioecious species would have a
lesser degree of simple polyembryony than related monoecious
species. I have been unable to test this hypothesis because
monoecy versus dioecy is usually a constant character within a
genus, and is often constant within families (see Figure 1 of
Favre-Duchartre 1970). Comparisons between monoecious and
dioecious families are confounded with other factors. For
example, the dioecious cycads and the monoecious Pinaceae produce
similar numbers of archegonia (*Microcycas* excluded from
comparison), but the two groups have different modes of
fertilization which affect the likelihood that a single male
gametophyte will fertilize more than one archegonium. A possible
test would be to compare numbers of archegonia for monoecious and
dioecious species of *Juniperus*, but I have been unable to find
relevant data.

All sperm produced by a male gametophyte are genetically
identical, as are the eggs of a female gametophyte. Therefore, if
a male gametophyte fertilizes more than one archegonium this is
genetically equivalent to cleavage polyembryony. The female
gametophyte would have to produce more zygotes to get the same
benefits from developmental selection. Therefore, female
gametophytes should produce more archegonia in those species in
which individual male gametophytes can fertilize more than one
archegonium.

Among gymnosperms with free-swimming sperm, *Microcycas*
stands out because of its large number of archegonia and because
its male gametophytes each produce several sperm (see below).
Female gametophytes of this species probably evolved additional
archegonia to maintain the effectiveness of simple polyembryony
given multiple fertilizations by individual male gametophytes.
All zooidogamous gymnosperms are dioecious.

Among siphonogamous gymnosperms, female gametophytes with
archegonial complexes tend to produce more archegonia than female
gametophytes with scattered archegonia. This may be related to
the behavior of male gametophytes. When archegonia are grouped in
complexes, a single pollen tube can fertilize more than one
archegonium, thus decreasing the efficiency of simple

polyembryony. The Pinaceae (scattered archegonia) generally have fewer archegonia than the Cupressaceae (archegonial complexes). Both families are predominantly monoecious.

Gnetum and Welwitschia are unique among gymnosperms in having tetrasporic development of the female gametophyte (Martens 1971). No cell walls are formed after the meiotic divisions and all four megaspore nuclei divide to produce the female gametophyte. Both alleles at a locus in the sporophyte are present in different haploid nuclei of the female gametophyte. Therefore, the two alleles are competitors to be present in the successful embryo. A number of unusual gametophyte characters can be understood in terms of competition among nuclei to be fertilized. For example, egg nuclei of Welwitschia form "prothallial tubes" that grow upwards to meet pollen tubes growing down from the micropyle. After fertilization, the embryos race back into the nutritive tissue of the female gametophyte (Pearson 1929; Martens 1971; Haig 1987).

E. Reproductive strategies of male gametophytes

An ovule may contain two or more male gametophytes (pollen tubes), but only one will contribute its genome to the successful embryo. Therefore, the male gametophytes within an ovule are strict competitors for reproductive success. Agonistic interactions between pollen tubes are possible during the period between pollination and fertilization, but I know of no studies. In theory, male gametophytes could compete by fertilizing as many archegonia as possible, thus preempting fertilization by other gametophytes. All zygotes fathered by a pollen tube would be genetically identical because there is (usually) only one female gametophyte in the ovule. The interests of male and female gametophytes conflict because multiple fertilizations by a pollen tube decrease the efficiency of simple polyembryony.

The motile sperm of Ginkgo and cycads are enormous. Zamia spermatozoids can reach 400 μm in diameter and may have over 10,000 flagella (Norstog 1975). Spermatozoids have probably been subject to intense selection for speed and power because of intense competition within ovules for fertilization (see Chapter 5; Haig & Westoby 1989b). For example, a Macrozamia ovule may

contain twenty male gametophytes, but only five archegonia. Each
male gametophyte produces two sperm cells, giving a ratio of
eight sperm to each egg (Brough & Taylor 1940). Frequently,
several sperm are found within an archegonium though only one can
fertilize the egg (*Macrozamia*: Brough & Taylor 1940; *Ginkgo*: Lee
1955; *Ceratozamia*: Chamberlain 1912; *Cycas*: de Silva & Tambiah
1952).

Male gametophytes of most zooidogamous gymnosperms produce
two functional sperm (*Ginkgo*: Friedman 1987; *Stangeria*:
Chamberlain 1916; *Macrozamia*: Baird 1939; Brough & Taylor 1940;
Bowenia: Lawson 1926). *Ceratozamia* usually produces two
functional sperm per pollen tube but occasionally produces four
(Chamberlain 1912). Male gametophytes of *Microcycas* produce up to
16 sperm cells (Caldwell 1907). Male gametophytes often produce
fewer sperm than there are archegonia to fertilize. Why have
these species not evolved larger numbers of sperm cells? The
probable answer is that there is a trade-off between sperm size
and number. If a male gametophyte produced more sperm, each sperm
would be smaller and less competitive in the race for
fertilizations.

The pollen tubes of siphonogamous gymnosperms deliver their
gametes directly to archegonia. An important difference exists
between species in which archegonia occur singly and species in
which archegonia are grouped into complexes. When archegonia
occur singly, a pollen tube can only deliver gametes to one
archegonium (Lawson 1907). Pollen tubes produce two male gametes,
but only one can fertilize an egg. Several authors have reported
morphological differences between the functional and non-
functional sperm cells but the evidence is not compelling. Modern
ultrastructural techniques failed to find differences between the
two sperm present in *Taxus* pollen tubes (Pennell & Bell 1986,
1988), despite several earlier reports to the contrary.

When archegonia are grouped into complexes, a pollen tube
can fertilize more than one archegonium. Both male gametes of a
pollen tube have been observed to fertilize an archegonium in
Libocedrus (Lawson 1907), *Widdringtonia* (Saxton 1909),
Sequoiadendron (Buchholz 1939a), *Sequoia* (Buchholz 1939b) and
Callitris (Baird 1953). Male gametophytes of some species produce

more than two sperm. Up to 14 sperm have been reported from
pollen tubes of *Cupressus* (Doak 1932, 1937; Mehra & Malhotra
1947). Nichols (1910) reported the occasional production of four
sperm by male gametophytes of *Juniperus*.

F. An embryo's perspective on polyembryony

Within a seed, embryos fathered by different male gametophytes
are identical with respect to maternally-derived genes but have
different paternally-derived genes. Such pairs of embryos do not
correspond to any of the conventional categories of full-sibs,
half-sibs, or selfed-sibs. The two male gametophytes that are the
'fathers' of a pair of embryos have a number of possible
relationships. These gametophytes may be the progeny of the same
or different sporophytes, and either male gametophyte may be
derived from the same sporophyte as the female gametophyte that
is fertilized. Embryos fathered by a single male gametophyte are
equivalent to monozygotic twins. Such twins are produced when a
male gametophyte fertilizes two or more archegonia, or when the
products of a single zygote cleave to form multiple embryos.

At any locus in an embryo there are two alleles, one
maternally-derived and the other paternally-derived. Clearly, the
genetic interests of the alleles are different with respect to
polyembryony. The maternally-derived allele is present in every
other embryo within the seed. Therefore, this allele's genetic
interests are the same as those of the female gametophyte, and
the allele's inclusive fitness is maximized if the fittest embryo
within the seed is successful in embryonic competition. On the
other hand, the paternally-derived allele may be absent from the
other embryos within the seed. Therefore, this allele's inclusive
fitness will usually be maximized by the victory of its own
embryo, rather than by the success of another embryo.

A conventional assumption of evolutionary models has been
that an allele has the same phenotypic effect whether it is
maternally or paternally-derived. Therefore, gene expression in
the embryo would be expected to be a compromise between the
different interests of maternal and paternal alleles. However,
gene expression is not always independent of parental origin
(Solter 1988). Differential expression of maternal and paternal

alleles at a locus is predicted, and observed, when the alleles have different genetic interests and when gene expression at the locus can influence these interests (see Chapter 9; Haig & Westoby 1989a).

Loci that are involved in embryonic competition satisfy the conditions for differential gene expression. Therefore, one might predict paternal genes in embryos would be particularly active in embryonic selection and maternal genes would have a more passive role. There is only indirect evidence to support this prediction. Parthenogenesis is unknown among mammals, and its absence is explained by 'chromosomal imprinting' and the requirement for both a maternal and a paternal genome during normal development (Solter 1988). Parthenogenetic gymnosperms are also unknown, and this could be explained in the same manner if paternal and maternal genes have different roles during embryogenesis. If these speculations are well-founded, there is no such thing as an embryo's perspective on polyembryony. Rather, maternal and paternal alleles in an embryo have separate interests which correspond to the different interests of the embryo's maternal and paternal gametophyte.

IV. DEVELOPMENTAL SELECTION AND SEED ABORTION

Embryonic selection within seeds can enhance the average quality of seedlings, provided that the surviving embryos are an improved subset of all embryos. However, there will be residual variation in quality among the embryos that survive in different seeds. This section discusses whether seed abortion could have a role in further enhancing seedling quality.

In the appendix to Chapter 2, I described the optimal allocation of a sporophyte's resources among seeds that differ in expected fitness. The return in seedling fitness per unit investment is maximized when the sporophyte aborts all ovules whose expected fitness falls below some threshold and provisions the rest. The allocation pattern is an ESS (evolutionarily-stable strategy) if the decision to abort or not to abort is determined by genes expressed in the sporophyte. This is because a gene in the sporophyte has an equal likelihood of being present in the female gametophyte of each ovule, and because the distribution of

resources which maximizes the number of successful seedlings also maximizes the number of seedlings which carry the gene.

At the ESS, whether a seed is aborted depends on the sporophyte's expected return on investment if the seed was provisioned. The expected return depends on the information available to the sporophyte. A sporophyte can probably detect whether a seed contains a living embryo. If this was the only information available to the sporophyte, seeds could be classified as inviable or potentially viable, and the sporophyte should abort the first category but provision the second. If the sporophyte has additional information that is correlated with the relative viability of living embryos, more sophisticated strategies could be possible.

In gymnosperms, a sporophyte probably has very limited information about embryo quality. Embryos are enclosed by female gametophyte tissues which solicit food reserves from the sporophyte. The sporophyte probably must rely on the relative vigor of female gametophytes to assess the relative quality of embryos. There should be only limited variation in vigor among female gametophytes because grossly defective gametophytes would be eliminated before fertilization. Moreover, the remaining variation should be only weakly correlated with differences in embryo quality. On the other hand, the female gametophyte should have much better information about embryo vigor but should be less likely to abort the ovule if the embryo has low vigor (see below).

If all zygotes produced by a female gametophyte are inviable, a gene present in the female gametophyte can benefit from its own ovule's abortion. This is because resources may be redeployed to other ovules on the same sporophyte, and these ovules will contain female gametophytes with a 50% chance of carrying the gene. Since a gene benefits from the abortion of its own ovule when all embryos are inviable, the gene could also benefit from abortion if the best embryo has very low viability. A threshold viability must exist below which a gene in the female gametophyte would gain from abortion of its ovule.

Suppose that a gene expressed in the female gametophyte determines whether or not an ovule will be aborted. The

gametophytic ESS is to abort all ovules whose expected fitness falls below some threshold t_g, where t_g is less than t_s (the threshold for the sporophytic ESS, given that gametophyte and sporophyte have equivalent information). The distribution of resources at the gametophytic ESS does not maximize the number of successful seedlings, because genes expressed in gametophytes are subject to a Prisoner's Dilemma (Axelrod 1984). There are two alleles at each locus in a sporophyte. Half the female gametophytes produced by the sporophyte will carry one allele and half will carry the other. If one allele aborts ovules that fall below t_s, the other allele can benefit by provisioning ovules that fall below t_s but above t_g because, by so doing, its ovules obtain more than 50% of the sporophyte's total reproductive resources. If both alleles adopt t_g, both receive 50% of reproductive resources, but these resources are not optimally allocated (see Queller 1984 for a more formal development of ESS models).

A similar conclusion is reached by consideration of kinship coefficients. A sporophyte is equally related to the embryos in all ovules but the female gametophyte is more closely related to the embryo in its own ovule. A sporophyte is predicted to abort an ovule and redistribute resources, whenever the benefit to embryos in other ovules is greater than the cost to the embryo in the aborted ovule. By contrast, a gametophyte should only abort an ovule when the benefit to embryos in other ovules is greater than twice the cost to the embryo in the aborted ovule (Westoby & Rice 1982; Queller 1983; for the applicability of relatedness arguments, see Queller 1984).

In summary, the female gametophyte of gymnosperms controls access to information about embryo quality. Therefore, selective seed abortion is probably controlled by genes expressed in female gametophytes and resources will not be optimally allocated among ovules because of competition between the maternal alleles in different female gametophytes.

V. BROOD REDUCTION IN ANGIOSPERMS

Fruit and ovule abortion are common among angiosperms (Stephenson 1981; Lee 1988). Some of the hypotheses that have been proposed to explain low seed set in angiosperms are similar to those discussed above for seed and ovule abortion in gymnosperms. Angiosperms differ from gymnosperms in a number of important respects, and these will be discussed below before considering brood reduction in angiosperms.

In angiosperms, the mature female gametophyte usually contains no more than eight nuclei, only one of which is an egg nucleus. By contrast, female gametophytes of gymnosperms have from 512 to several thousand nuclei at cell formation, and usually produce two or more archegonia (Favre-Duchartre 1970). In most angiosperms, the interval between pollination and fertilization is 24 to 48 hours, though the period can be as brief as 15 minutes (*Taraxacum*) or as long as 14 months (*Quercus*) (Maheshwari 1950, p. 190). This compares with periods of one month to two years for the majority of gymnosperms (see Section II.A above). In angiosperms, the female gametophyte usually disappears soon after fertilization, whereas the female gametophyte of gymnosperms persists in the mature seed as a food storage tissue. In angiosperm seeds, this storage function is assumed by a novel tissue called endosperm or by the embryo itself.

Endosperm is arguably the most distinctive feature of angiosperms. At fertilization, a male gametophyte releases two sperm. One fuses with the egg nucleus to form the zygote and the other fuses with two other nuclei of the female gametophyte to form a triploid nucleus. The zygote gives rise to the embryo, whereas the triploid nucleus divides to form a tissue called endosperm. Endosperm often persists in the mature seed as a storage tissue, but in other species the endosperm is obliterated in the mature seed and all nutrients are stored in the embryo (Martin 1946).

Angiosperms differ from gymnosperms in two other important respects. First, gymnosperms have separate male and female reproductive structures, whereas most angiosperms are hermaphroditic and produce pollen and ovules from the same

flowers. Second, gymnosperms have no mechanism to prevent fertilization once self-pollen is received by an ovule, whereas many angiosperms are self-incompatible and have prezygotic mechanisms that prevent self-fertilization.

Five kinds of hypotheses have been proposed to explain why angiosperms often produce many fewer seeds than ovules. The hypotheses are not mutually exclusive and no single hypothesis can explain all observations.

(1) Pollen limitation: seed set can sometimes be increased by pollen supplementation (e.g., Bierzychudek 1981). There are exceptions because, in other cases, additional pollen has little effect (Stephenson 1981).

(2) A buffer against uncertainty: "overproduction" of flowers could act as a buffer against years of poor pollination or against fluctuations in the availability of resources (e.g., Stephenson 1979). However, in *Lotus corniculatus*, seed/ovule ratios were not increased despite addition of both pollen and nutrients (Stephenson 1984).

(3) Genetic load: seeds may abort because their embryos possess lethal genotypes (Wiens 1984; Wiens et al. 1987, 1989). Genetic load is undoubtedly the cause of some seed abortion. However, many seeds must abort for reasons other than genetic load, because seeds that would normally be aborted will sometimes develop if other ovules/seeds are experimentally removed (e.g., Casper 1984; Stephenson, Johnson & Winsor 1988).

(4) Male function: hermaphroditic flowers produce both pollen and ovules. Sutherland & Delph (1984) proposed that the number of flowers produced by a sporophyte is determined by natural selection for increased reproductive success through male function. As a result, the sporophyte produces more ovules than can be matured into seeds. Consistent with this hypothesis is the observation that hermaphrodite flowers are less likely to set fruit than the female flowers of monoecious and dioecious angiosperms (Sutherland & Delph 1984). However, fruit-set was not 100% for species without hermaphrodite flowers. Therefore, the male function hypothesis cannot be the only explanation of fruit abortion (also see Campbell 1989).

(5) Selective abortion: embryos of low expected fitness are
aborted, thus increasing the efficiency with which reproductive
resources are converted into successful seedlings (Stephenson
1981; Stephenson et al. 1988).

Pollen-limitation, environmental uncertainty and genetic
load are all factors that could contribute to seed and ovule
abortion in gymnosperms as well as angiosperms. The male-function
hypothesis is specific to angiosperms, because gymnosperms
produce pollen and ovules in separate structures and can adjust
resource allocation to pollen independently of resource
allocation to ovules. If fruit abortion is a non-adaptive
consequence of hermaphroditism, it is difficult to understand why
more angiosperms do not reduce female costs by producing some
flowers without ovules. The advantage of hermaphrodite flowers
in insect-pollinated species is that the same attractive
structures (petals etc.) can function for pollen donation and
pollen capture. These structures are a fixed cost per flower,
whether or not the flower contains ovules. The marginal cost of
an ovule may be small. Therefore, other functions of "surplus"
ovules, such as a buffer against uncertain pollination or
selective abortion, may become more economical.

Selective seed abortion may occur in gymnosperms, but the
major form of developmental selection in gymnosperms is simple
polyembryony. Angiosperms lack simple polyembryony, and embryonic
selection must occur among ovules rather than within ovules. A
number of factors may have contributed to this change. First,
most growth of the angiosperm ovule occurs after fertilization.
Therefore, it is probably less expensive to abort an ovule at
fertilization or shortly afterwards than is the case in
gymnosperms. Put another way, angiosperm ovules are cheaper to
produce than gymnosperm ovules and this increases the merits of
developmental selection among ovules relative to developmental
selection within ovules. An interesting comparison can be made to
Torreya taxifolia, which is a gymnosperm that has one egg per
ovule like angiosperms and which also resembles angiosperms in
that the major increase in ovule size occurs after fertilization
(Land 1907). Second, many angiosperms are self-incompatible and

do not self-fertilize. Therefore, simple polyembryony is not required to eliminate selfed embryos. Third, the maternal sporophyte of angiosperms probably has better information than its gymnosperm counterpart about the relative quality of embryos in different seeds.

In gymnosperms, the maternal sporophyte appears to be shielded from direct access to information about the quality of embryos within seeds, and selective seed abortion is probably controlled by genes in the female gametophyte (see previous section). However, the maternal sporophyte of angiosperms probably has better information about embryo quality because the female gametophyte's role is taken by the endosperm, which is a tissue genotypically identical to its associated embryo, except for the second copy of the maternal genome. Thus, an angiosperm sporophyte can probably assess embryo fitness from properties of the endosperm and can use this information in choosing which seeds to abort. The evolutionary reasons for the second maternal genome in endosperm are discussed in Chapter 9.