Chapter 9
The Embryo Lethal System

Summary Outcrossing, wind-pollinated members of the Pinaceae have high self-pollination rates yet produce few selfed seedlings. Avoiding self-pollen capture is incomplete so how are self-pollinated ovules or seeds selectively eliminated? Barriers to selfing have long been considered to be either competition via simple polyembryony and death to selfed embryos during seed maturation. Experimental results show that simple polyembryony is a weak barrier against selfed embryos. By far, the most effective barrier is the enigmatic mechanism(s) that cause recognition and death to selfed embryos. A survey shows that extreme inbreeding depression occurs in some species but not in others so this is not a feature of conifers as a group. Only five of the 11 genera within the Pinaceae (Abies, Larix, Picea, Pinus and Pseudotsuga) have been well-characterized with respect to self-pollinated embryo deaths. Molecular dissection methods have been used to infer severity and distribution of lethal factors; to date, most are semi-lethal rather than fully lethal. These range from partially dominant to overdominant or perhaps balanced lethals.

Some selfed embryos die at all stages of seed development but a second death pattern has been detected in some Pinus and Picea spp species: a large proportion of selfed embryo deaths peak during early embryogeny. Are these dual death patterns present in other genera and if so, what genetic models might account for them? This chapter is a case study which integrates not only what was introduced in previous chapters but also shows how knowledge of the conifer mating system contributes to the broader understanding of eukaryotic systems.

With a single photograph, Plate III shows the full genetic model. The maternal parent must be a heterozygous carrier for the deleterious albino recessive allele. At least two archegonia were present in the ovule because one germinant is albino and the other is wild type. Each archegonium was pollinated with a different pollen grain so these are polyzygotic embryos. One pollen grain had the deleterious albino recessive allele and the other pollen grain had the wild type allele. But there is another anomaly which cannot be deduced from looking at the photograph. Even though this was a self-pollinated mating, the embryos survived. What is unusual about that? The upcoming chapter addresses this question.
9.1 Moderate Selfing Rates yet Low Selfed Seed Recovery

It is curious that more selfed individuals not found within populations for the Pinaceae and other monoecious conifers. Part of the answer is that 1) male and female strobili are spatially separated on the same tree and 2) that peak pollen shed rarely coincides with female strobilus receptivity. But these are incomplete barriers.

Self-pollination rates can be quite high in the middle of the Pinus taeda crown where female and male strobili often overlap. They are reported to reach as high as 34% yet only 5% of viable seed is recovered as self-fertilized seeds (Franklin 1969). This is also the case for self-pollination rates for Pseudotsuga menziesii which reach as high 40 to 60% without increasing the proportion of selfed seedlings in a population (Sorensen 1982). So how to explain the high proportion of empty selfed seed shown in Fig. 9.1?

Self-pollination (or selfing) occurs at moderate rates yet the selfed seed is not recovered. This means that the selfed embryos must be dying between fertilization and seed maturity. The interval between pollination and fertilization has be ruled out. Self-pollinated ovules do not undergo any morphological changes from pollination to zygote formation, as reported for several members of the Pinaceae: Pseudotsuga menziesii (Orr-Ewing 1957), Pinus peuce (Hagman and Mikkola 1963), Picea glauca (Mergen et al. 1965), Picea abies and Pinus sylvestris (Koski 1971). Pre-fertilization barriers are notably absent (Sarvas 1962) and none have been detected experimentally using molecular markers and viability assays so far (Kuang et al. 1999; Williams et al. 2001; Williams 2008).

Thus it is clear that loss of self-pollinated ovules is occurring between fertilization and seed maturation. Selfed death might be occurring as a consequence of embryo competition among polyzygotic embryos. The more likely barrier is severe inbreeding depression, also known as the embryo lethal system (Koski 1971).

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Fig. 9.1 X-rays are useful for comparing counts of filled Pinus taeda seeds from outcrossed pollinations (left) versus counts of empty seeds from a selfed-pollinated cone, shown on the right. The stage is seed maturity. The species shown here is Pinus taeda. From Williams, C. (2007) Re-thinking the embryo lethal system within the Pinaceae. Canadian Journal of Botany 85: 667–677. Copyright permission granted