



## Seeds as Products

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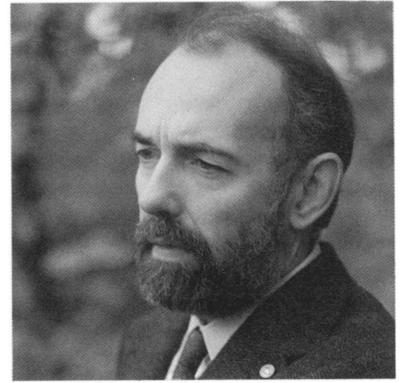
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## Seeds as products

After perhaps 100 years of gestation, wild plant population biology has been delivered unto us and the baby is growing fast. In this area of evolutionary ecology, seeds are often-discussed life forms. Here I suggest that a seed is both much more and less than it seems to be.

First, a seed is more than a bag lunch and spacecraft for the embryo. Every textbook informs us that there is a layer of endosperm around the developing embryo of an angiosperm seed, a layer that sometimes persists into the newly weaned seed. Our summaries of botanical knowledge also tell us that the endosperm is an odd polyploid tissue in which the nuclear DNA is derived from a larger number of maternal than paternal chromosome sets. But much more odd is that inquiry about such a widespread and bizarre trait has invariably been abandoned after offering its description. Seed embryos are begging, nursing offspring in multi-sib broods. It is the maternal parent that gives, not the paternal. The maternal lineage gets something in return for allowing the paternal parasite, but she is paying the resource bill; it is quite reasonable for there to be selection for the presence of a proposal review committee that biases the decision in favor of the maternal side of the parent-offspring mutualism. A maternally-biased mediating board, the endosperm, seems to be a reasonable outcome of such selection. A maternal plant may express its dissatisfaction with an embryo through a response as severe as is abortion. Since it is to the parent's advantage to make such decisions as early in its investment schedule as it can be sure that it is appropriate, it is not startling to find that the endosperm is best developed as a nonstorage tissue early in embryo development, and later either degenerates (disappears) or becomes an obvious nutrient storage tissue for the weaned seed.

Add the above regulatory complication of a seed to the commonplace act of pre-weaning photosynthesis by embryos (familiar to all as green peas and green beans). Not only does the seed participate in a dialogue biased in favor of the maternal parent, but through its own photosynthesis it has own (albeit small) venture capital. To understand why a seed is as it is requires more than a study of lunchbox packing and protection, and of spacecraft launch-orbit engineering.



There is also a strong temptation to denigrate fledgling seeds, since so many of them die. After all, it only takes one to make a new tree. However, plant recruitment is especially stochastic at a variety of steps because plants by-and-large cannot shift location to take advantage of the demise of a sib. The more rolls of the dice, the more chance of a winning number for each of a series of steps. The more seeds that die, the fewer rolls of the dice there are for each successive step. Yes, most seeds (and their immediate resultant seedlings) in the shade of a forest will die following the parental attempt to place  $n$  of them in the next treefall or other high survival microsite that appears. But the tree is like a blind hunter trying to lethally shoot a walking buffalo on an undulating plain. There is a best pattern of shots and a best number of shots into each portion of that pattern. Over a substantial range, the number of bullets he is allowed will have a substantial effect on his success. Likewise, the size of his bullets will determine the number of shots he has and the most lethal pattern over a wide range of possibilities. Finally, he must expend all his ammunition, since he cannot know if he has acutely killed the buffalo. But however it is done, he has to hit the buffalo once and probably many times to put meat on the table. How many tables he fills depends not only on his firing pattern, rifle caliber and bullet size, but on how many buffalo there were in the first place.

But at the same time we have over-estimated the seed. It has become commonplace in evolutionary ecology to place seed production at or near an exact measure of plant fitness. Seeds are deemed to be more important, somehow, in the fitness budget of a plant than are tissues in leaves, stems, flowers, etc. And much of this feeling of relative importance derives from recognition of seeds as whole organisms and as the next generation, rather than just as plant products.

Such a view, for example, leads one to somehow rank paying acorns to squirrels for acorn dispersal as more expensive and wondrous than is paying fruit tissues to birds for seed dispersal. But is it? Consider that the two following behavioral phenotypes for a human family may have exactly the same inclusive fitness. In one, four children are raised and two sent off to war to be killed.

In the other, two children are raised and kept at home and the resources that would have been used to raise two other children are instead donated to the war effort. In like manner, when a squirrel consumes nine acorns and fails to recover one that it buried, the maternal oak has quite simply paid a block of its tissues for the burial service, thereby raising its inclusive fitness higher than would have been the case had all ten acorns been left on the soil surface to be eaten by mice, deer and pigeons. That there happened to be some pieces of paternal tissue tacked onto the nine consumed acorns neither raises nor lowers the fitness gain to the maternal parent of having the squirrel eat the nine acorns. However, it was necessary for there to be paternal tissue tacked onto the maternal tissue of all ten acorns for this particular scenario to be reasonable; the maternal oak cannot know which one of the ten buried acorns will later be missed by the foraging squirrel.

There are many cases in nature where a member of a species indirectly or directly kills a conspecific. For a maternal parent to kill its own tissues through feeding seeds as bait for seed dispersers is no different than is tissue expenditure in the form of nectar, dehiscence leaves, wood production, etc. Likewise, that it is also killing its mate's tissues differs in no fundamental way from a carnivorous animal that would as soon consume a conspecific as some other prey item of the same vulnerability. Obversely, that the pollen grain's sperm nucleus DNA died tacked onto a maternal tissue packet called an acorn is no different than is death through the multitude of other hazards that eliminate pollen grains. It differs only in that this is the only class of lethal hazard that selection cannot lead it away from. Don't complain about your chances, boy. It's the only game in town. Kris Kristopherson said that.



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