

Genetic Piracy: A Newly Discovered Marvel of the Plant World

Richard B. Primack

Plants have evolved a variety of reproductive systems. The trees of some species, such as ash and ginkgo, are differentiated by gender, with both a female and a male individual required for seed production. Other species, such as cherries and almonds, ensure cross-pollination without separating individuals by gender: each plant is self-incompatible, so that stigmas cannot be fertilized by pollen produced on the same plant. And then there are species that don't require cross-pollination, including the many weedy species and annuals that can produce seeds even when stigmas and pollen are from the same plant.

Yet another reproduction system, called apomixis, involves seed production with no fertilization at all. Apomixis occurs inside the ovary of the flower when a cell divides to become an embryonic seed. The resulting seed looks quite normal but is in fact a clone that is genetically identical to the parent plant, with slight differences arising from the peculiarities of cell division. Apomixis occurs in many plant families and is especially common in the raspberries of the genus *Rubus*. It is thought to confer certain advantages: no other plant is required for fertilization, and the seeds produced belong to a genotype of proven success.



*The cypress *Cupressus dupreziana* is found only in the desert of Algeria. Just 231 individuals of this endangered species remain alive in the world.*



Cupressus dupreziana.

Until recently, all known examples of apomixis involved the production of seeds from cells of the female plant, that is, the plant that actually makes the seeds, although male (pollen-producing) plants existed, they made no genetic contribution to the embryo. Now, however, a group of French scientists headed by C. Pichot and M. El Maâtaoui have found an example of apomixis in which the seeds are identical to the pollen-producing plant, rather than the female plant. The species involved is a rare cypress, *Cupressus dupreziana*, that occurs only in the Tassili N'Ajjer desert of Algeria, in extremely hot, arid conditions. Because of its small population size and poor regeneration rate, it has been classified as endangered and studied intensively. Field research has shown that only around ten percent of wild seeds have a viable embryo; and since the same low rate has been observed in trees being cultivated in France, the problem was assumed to result from the intrinsic nature of the species, rather than simply from inadequate pollination.

But further study showed that the low rate of seed viability was related to *Cupressus dupreziana*'s atypical meiosis process. In most diploid plant species (those with two sets of chromosomes), meiosis of the male reproductive cell results in the cell splitting to form haploid pollen grains—that is, grains with only one set of chromosomes, half the number of the parent plant. Seeds result from the merger of the haploid pollen grains with haploid egg cells produced in the ovule. In *C. dupreziana*, however, chromosome behavior and cell division are erratic: sometimes a nucleus divides, but the two resulting nuclei fuse together again; and instead of producing a uniform mass of haploid pollen, the male cones produce pollen of widely varying sizes, many with no chromosomes at all and some with one, two, or four sets of chromosomes. Laboratory studies have shown that only the diploid pollen is capable of germinating. This pollen is almost identical genetically to that of the pollen-producing tree itself, with slight variations arising during meiosis. And it plays a role in seed formation that is unique among known plants—male apomixis.

Analysis of seeds from a plantation of *Cupressus dupreziana* trees showed that the



The pollen of *Cupressus dupreziana* is variable in size and shape, as shown in this section taken through a microsporangium before the pollen is shed. Only the larger, round pollen would be viable; the other pollen grains will not germinate. The epidermal wall of the pollen sac is shown on the right side.

identifying DNA markers of the seeds did not match those of the mother tree—that is, the female tree on which the embryonic seeds developed. In typical diploid species, each seed contains half of the identifying DNA markers of the mother and half of those of the pollen-producing parent. The fact that the DNA markers of *C. dupreziana*'s seeds match those of only one parent—the father tree—shows clearly that this species uses apomixis to produce seeds. Presumably, a diploid nucleus in the pollen tube enters the ovule within the young cypress cone and, instead of combining with a female nucleus, begins to divide on its own, taking on the appearance of an embryo. If there is a female nucleus present, it simply deteriorates.

The ability of the pollen of *Cupressus dupreziana* to produce new offspring via apomixis was further examined in a special plantation of hybrid trees that had been created by dusting pollen of *C. dupreziana* onto the receptive female cones of *C. sempervirens*, the com-

mon, or Mediterranean, cypress. The seeds produced by these crosses were germinated and then grown for fifteen years. The resulting "hybrids" were identical to *C. dupreziana* in twig orientation, female cone size, and pollen diameter; they bore no visible resemblance to *C. sempervirens*, suggesting that no genetic material had come from *C. sempervirens*. And in fact, the DNA markers of the hybrids were identical to those of *C. dupreziana*, but completely unlike *C. sempervirens*. These surprising results demonstrated conclusively that *C. dupreziana* pollen is able to produce seeds with no genetic contribution from the female plant, not only within its own species but also when "crossed" with other species.

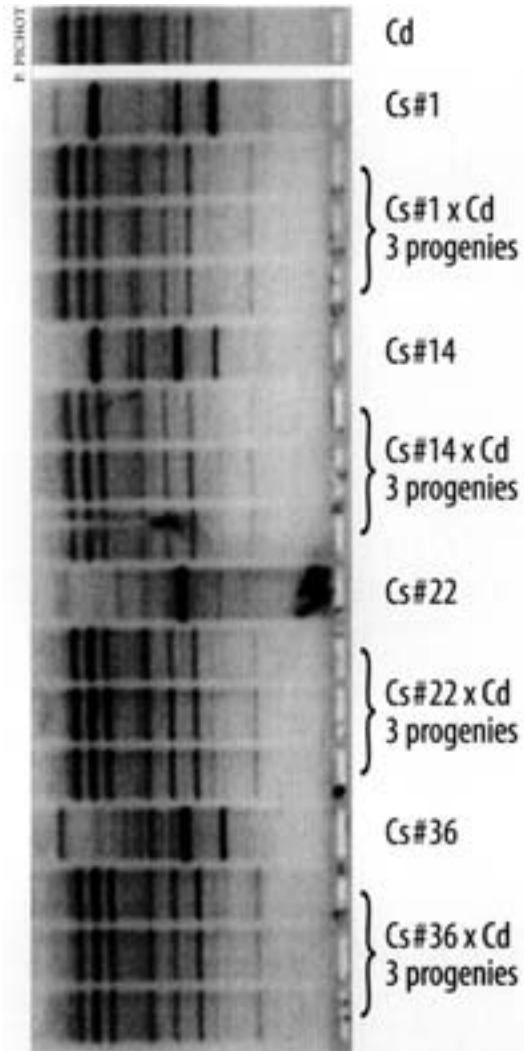
This is the only known example of apomixis involving the pollen parent. In human terms, this is equivalent to a human mother giving birth to a baby that is genetically unrelated to herself, but genetically identical to the father. The evolutionary advantages of this method of reproduction are not evident. One possibility is that isolated trees of this rare species can use the female cones of other cypress species growing in the vicinity as vessels for producing copies of its own genotype. This "genetic piracy" might allow the species to survive at low densities; however, at present no other cypress species grows nearby in *C. dupreziana*'s wild habitat. But even if genetic piracy were feasible, this unusual reproductive system has its shortcomings: it cannot generate the genetic variations that allow sexually reproducing organisms to adapt as environmental conditions change.

References

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This is a gel showing DNA markers of tissue taken from trees of *Cupressus dupreziana* (Cd) and *C. sempervirens* (Cs), as well as from trees produced by cross-pollinating them. Pollen from one tree of *C. dupreziana* was used to fertilize four trees of *C. sempervirens*. Seeds from each of these hybridizations were used to grow three progeny trees from each mother tree. For each of the four crosses, tissue taken from the offspring is genetically identical to *C. dupreziana*, as shown by their DNA bands being exactly like *C. dupreziana* but unlike the DNA bands of *C. sempervirens*. These results clearly demonstrate that the inheritance of genetic material is strictly from the pollen-producing parent.

Richard Primack is professor of biology at Boston University. He is currently conducting research at the Arnold Arboretum and in Concord, Massachusetts, on how climate change affects the flowering time of plants.