

Gene wars

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Like in animals, in plants also, resource investment in offspring by parents is asymmetrical; the mother plant invests more resources in the development of seeds (offspring), while the contribution by the pollen parent (the father) is negligible. From the perspective of Darwin's theory of natural selection, selection must be acting on the mother plant for prudence in allocating her limited resources among offspring¹. Indeed, it has recently been shown that plants invest an optimal level of resources in each offspring^{2,3}. However, the interest of the offspring is not similar to that of the mother as long as they are sired by more than one father^{4,5}; selection acts on each offspring favouring increase in the offspring's own fitness by demanding more than the mother is selected to give. Hence it has been argued that, just as in animals⁴, in plants also, there exists a severe conflict between mother and offspring over allocation of resources⁵⁻⁷.

In such a scenario it is easy to visualize that natural selection would favour strategies in the pollen parent that render its offspring able to demand

more resources from the mother; on the other hand, the mother would be selected with strategies that refrain her offspring from drawing more resources. On the basis of this argument, Haig and Westoby^{8,9} and Haig and Graham¹⁰ predicted that parents should manipulate their share of the genes in offspring in such a way as to meet their respective interests. In other words Haig and Westoby predicted that identical alleles at the same locus in offspring should behave differently depending on their parental source; particularly so with respect to the genes involved in garnering resources from the mother.

Haig and Westoby⁹ have offered support for their prediction by drawing evidences from the literature on the genetics of maize. In plants the endosperm (constituted of maternal and paternal genomes in 2:1 proportion) is the major tissue that draws resources from the mother and nourishes the developing embryo¹¹. Development and normal functioning of the endosperm is hence imperative for maturation of seed and the embryo. By a complex set of genetic experiments, Lin¹² had shown

that normal development of endosperm in maize requires certain factors and that these factors are regulated by four loci resident on the long arm of chromosome 10. He also obtained two major types of endosperm tissue with four doses of the long arm of chromosome 10. The first type had all the four doses contributed by the ovule and the second type had two from the ovule and two from the pollen grain. Normal endosperms were formed only in the second type; in the first type, though the tissue contained all the loci in as many doses as the second type, the endosperms were poorly developed. This implies that these endosperm-factor alleles are inactivated when they are passed on through ovules but remain active if passed on through pollen grains.

Such parent-sex-specific activation of genes (PASSAGE) has in fact been reported in a few animals¹⁰, and for other traits such as texture, pigment and morphology of kernels in maize^{13,14}. Though the significance of these genes in the context of resource-drawing ability is not clear, it is interesting that there are pleiotropic effects of hormones regulating pigment formation on protein storage in the endosperm of cereals^{15,16}.

The 'passage' model probably helps in resolving one important problem of parent-offspring conflict. Alexander¹⁷

argued that a female offspring that demands more resources from its mother would eventually become a mother whose offspring in turn demand more from her, thus reducing her own fitness. He therefore argued that such a 'greedy' allele would not spread. But, if as Haig and Westoby predict, 'greedy' alleles are switched off when passed on through mother, the problem raised by Alexander for the spread of such an allele can be resolved. Thus 'passage' appears to be an elegant mechanistic basis of parent-offspring conflict. Recently 'passage' has also been implicated in differential dispersal of the sexes¹⁸.

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