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Unorthodox Defense in a Model Plant

Thale cress (*Arabidopsis thaliana*) may be a small weed, but it's a big deal in the world of plant genetics. Its compact size, short life cycle, relatively small genome, and supposed dearth of genetic redundancy made *Arabidopsis* the model organism of flowering plants and the first plant chosen for genome sequencing. The sequence was completed in 2000.

Through the work of geneticists at Purdue University, the tiny plant is in the spotlight again thanks to a mutant with a mysterious mechanism for reverting to wild type. Susan Lolle, Robert Pruitt, and colleagues have isolated and studied a mutation, "*hothead*," that causes tissues of the developing plant to fuse. They have discovered that selfed homozygous *hothead* mutants produce heterozygous wild-type offspring at a low but significant rate (4 to 8 percent). In the 24 March *Nature*, the authors show that, somehow, the revertants restored the gene missing from their parents but present in their grandparents or great-grandparents.

Genotyping of tissues from parents and offspring ruled out seed contamination and out-crossing as possible explanations; mutant adults are indeed responsible for producing wild-type offspring. Sequence analysis of the wild-type *HOTHEAD* gene in revertants ruled out other explanations, such as random mutation to wild type; the nucleotide changes are specific and nonrandom. Genome blotting experiments did not uncover another, hidden version of the wild-type gene, ruling out gene conversion by means of DNA elsewhere in the genome.

A likely source of the wild-type gene in revertants may well be a form of stored or double-stranded RNA, but mature messenger RNA is not a likely candidate because the sequence of the revertant allele is the same as the original DNA sequence, including introns and untranslated regions of the gene. The authors postulate that this extragenomic inheritance, though as yet unspecified, may be an adaptation of self-fertilizing plants to inbreeding.

BACKUP GENES IN YEAST

"A key question in molecular genetics is why severe mutations often do not result in a detectably abnormal phenotype," begins an article by Weizmann Institute of Science geneticists Ran Kafri, Arren Bar-Even, and Yitzhak Pilpel in the March issue of *Nature Genetics*. They then proceed to show how 40 different knockout mutations in yeast (*Saccharomyces cerevisiae*) are rescued by activation of functionally similar duplicate genes.

Gene duplication, long considered to be a key evolutionary mechanism, has been found to be a common phenomenon through genome sequencing. Large proportions of the genomes that have been sequenced (30 percent in *S. cerevisiae*; 65 percent in *A. thaliana*) have been found to contain duplicated, or paralogous, genes. Many duplicates are lost; yeast, for example, appears to have undergone duplication of the whole genome, with subsequent loss of most of the genetic redundancy. One way it is supposed that duplicates are stably maintained in the genome is that they undergo a division of labor, or subfunctionalization, often involving differential expression, soon after duplication.

Pilpel and colleagues mined the wealth of available yeast data for viable mutants lacking one of the members of duplicate gene pairs and examined the expression profiles of the paralogs. The more dispensable genes, that is, those with better backup, differ from their paralogs in their expression. When both are present, they tend not to be coexpressed. When one is absent, the other is up-regulated to back up the missing gene.

What paralogs have in common are regulatory sequence motifs, although in pairs with better backup, these motifs only partially overlap. In fact, partial coregulation of pairs in wild-type conditions is the best predictor of backup by a duplicate gene. And the more regulatory motifs a paralog has, the less dispensable it tends to be. Clearly, the expression of paralogs diverges after gene duplication, and the backup system, if not selected for itself, may be a fortuitous consequence.

METAL FOR DEFENSE

Over 400 plant species are known to accumulate trace metals such as nickel and zinc. Plant physiologist David Salt and his colleagues at Purdue University have been studying metal accumulation in several *Thlaspi* species, with the aim of isolating genes that could be transferred to crops to remediate polluted water or soils or add micronutrients to food. Their recent findings, reported in the March issue of *Plant Physiology*, indicate that metal hyperaccumulation may have evolved as a defense against pathogens.

Plants typically respond to fungal or bacterial pathogens by producing salicylic acid, the compound from which aspirin is made. Salt and colleagues have linked salicylic acid production with metal hyperaccumulation in *Thlaspi*, as well as with metal tolerance in nonaccumulators. Healthy plants normally produce very little salicylic acid, but those with elevated levels in the absence of a pathogen tend to be hyperaccumulators of trace metals.

One species, a small wild mustard (*Thlaspi goesingense*), can tolerate 100 to 1000 times the amount of nickel that normal plants can. Though *T. goesingense* produces salicylic acid, it lacks the normal pathogen response. When grown in soil without metal, it is susceptible to fungal infection. When grown in their native nickel-rich soil, however, the metal-heavy plants resist infection.

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