

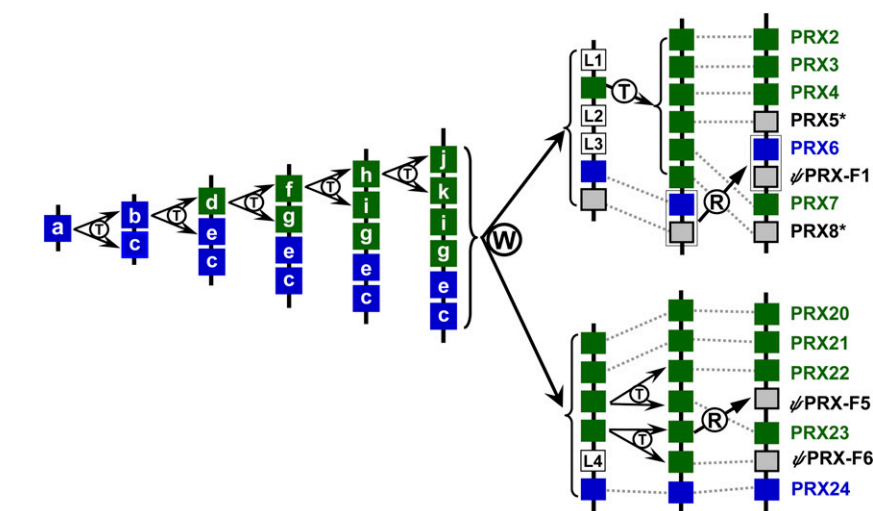
## IN BRIEF

# When to Hold Them: Retention of Duplicate Genes in Poplar

In some ways, your genes resemble playing cards: you work with the hand you're dealt. Sometimes, during the course of evolution, the dealer throws a species an unusual hand that includes duplicates of a few, or all, of its genes. Indeed, in plants, single-gene and whole-genome duplications have played a major role in evolution. For cards and genes, holding too many can prove a burden, and genes can be discarded over evolutionary time by deletion or inactivation through the accumulation of mutations. The mechanisms that retain genes in the genome remain a subject of ongoing study (reviewed in Conant and Wolfe, 2008). Duplicate genes can diverge in function, as if you could turn one of your two copies of the queen of hearts into a queen of diamonds, or even into a novel card—say the princess of stars—that could be a game-changer. However, such neofunctionalization occurs as a race against the accumulation of deleterious mutations, which inactivate the gene.

Unlike a card player, the genome does not choose to retain a gene; chance and evolutionary forces affect whether the gene ends up in the evolutionary discard pile. To examine the factors that shape the retention and divergence of duplicate genes, **Ren et al. (pages 2404–2419)** reconstructed the evolutionary history of a class of peroxidase (*PRX*) genes in *Populus trichocarpa*. The authors identified 93 full-length *PRX* genes in the *P. trichocarpa* genome; 10 *PRX*s with a frameshift or premature stop codon and 43 fragmentary *PRX*s indicate that this gene family has lost many members. Roughly half of the *PRX* genes showed ubiquitous expression and half showed tissue- or stage-specific expression. Some *PRX* enzymes localize to the cell wall and function in processes such as lignin polymerization; others localize to the vacuole and function in the responses to biotic and abiotic stress.

Mapping the *PRX*s to the genome showed that 37 of the 93 *PRX* genes occurred in clusters, indicating that many copies were



Hypothetical evolutionary history of two *PRX* clusters. Rearrangements (R) and tandem (T) or whole-genome (W) duplications produce clusters of *PRX* genes, including fragments (ψ) and putative pseudogenes (\*). Green indicates a vacuole-localized *PRX*, blue indicates a cell wall-localized *PRX*, gray boxes indicate pseudogenes, and white boxes indicate lost genes. (Reprinted from Ren et al. [2014], Figure 2C.)

produced by tandem duplication. The authors further examined two clusters that occur in paralogous blocks. Fusions to green fluorescent protein showed that these clusters include both cell wall and vacuolar *PRX*s. Comparison of sequence substitutions allowed the authors to infer their evolutionary history, which indicated that both types of *PRX*s evolved from a cell wall *PRX* (see figure). Functional assays on recombinant proteins, including reconstructed ancestral enzymes, showed that the *PRX*s have different activities on different substrates. Further, maximum likelihood codon models indicated that several vacuolar *PRX*s were under strong positive selection and mutants of the sites under selection altered the substrate preferences of the *PRX*s. Thus, changes in protein localization and positive selection affected the retention of *PRX*s in poplar.

Meiosis and fertilization deal the hand for a plant's genetic composition. This study indicates that, at least for *PRX* genes, keeping a few extra cards in the deck can

involve positive selection and changes in subcellular location. Exploring how this plays out for other duplicated genes, which likely have different selective constraints, will prove an interesting subject for future research.

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