P1

Evolutionary Diversification of the Epigenome and Its Functions: a Paragenetic Perspective on the Role of RNA Silencing in the Biology of Plants

Richard Jorgensen, Carolyn Napoli, Karla Gendler

Department of Plant Sciences, University of Arizona, Tucson, Arizona, USA

RNA silencing plays a key role in establishing and maintaining chromatin states in the plant epigenome. Our work on RNA silencing in transgenic petunias reveals that heritable, morphology-based changes in patterns of cosuppression in flowers are induced in plants that carry more than one transgene copy, suggesting that paramutation-like interactions between transgene copies result in changes in transgene epigenetic state that determine cosuppression phenotypes. Changes in plasmodesmal trafficking of the cosuppression state appear to underlie these patterns of cosuppression. Building on the perspectives of Brink and McClintock put forward over 40 years ago, I will discuss the possibility that the mechanisms underlying the two main classes ofhomology-based gene silencing (cosuppression and paramutation), together with plasmodesmal macromolecular trafficking, could comprise a highly sensitive, dynamic regulatory system that transmits (via plasmodesmata) and stores (via chromatin) information that is useful in plant growth, development, and adaptation to the environment. Chromatin (the "epigenome") is comprised of dozens of protein families with diverse molecular functions ranging from histone and DNA modifying enzymes to nucleosome remodeling complexes and RNAi machinery components, which collectively comprise the "epigenome" and which control and integrate patterns of gene expression and mediate chromosomal processes such as genetic recombination, DNA repair and chromosome condensation. Throughmolecular phylogenetic analysis of more than 60 protein families we have estimated the number of clades of chromatin proteins that existed prior to divergence of plants and animals, of monocots and dicots, of fission and budding yeasts, and of insects andvertebrates, and identified new clades representing a variety of ancient gene duplications that arose prior to each divergence event. New proteins have arisen at similar rates in plants and in animals (about 1 new clade per 10My), whereas the yeasts have dispensed with more types of chromatin proteins than have been gained. In plants histone methyltransferases have diversified at 5 times the rate of duplication of histone acetylases/deacetylases, whereas both classes have expanded at similar rates in animals and show a pattern opposite to that of plants. Most strikingly, however, factors responsible for RNA-directed chromatin modification have expanded dramatically in plants as compared to animals, consistent with a much greater role for RNAi-mediated control in plants, possibly involving systemic RNA signals that act on chromatin and transmit epigenetic information throughout the plant. The evolution of new RNAi-mediated functions was often associated with positive selection on branches leading to new clades and seems to have paralleled the evolution in land plants of increasing developmental complexity, including complexity of the vasculature.