

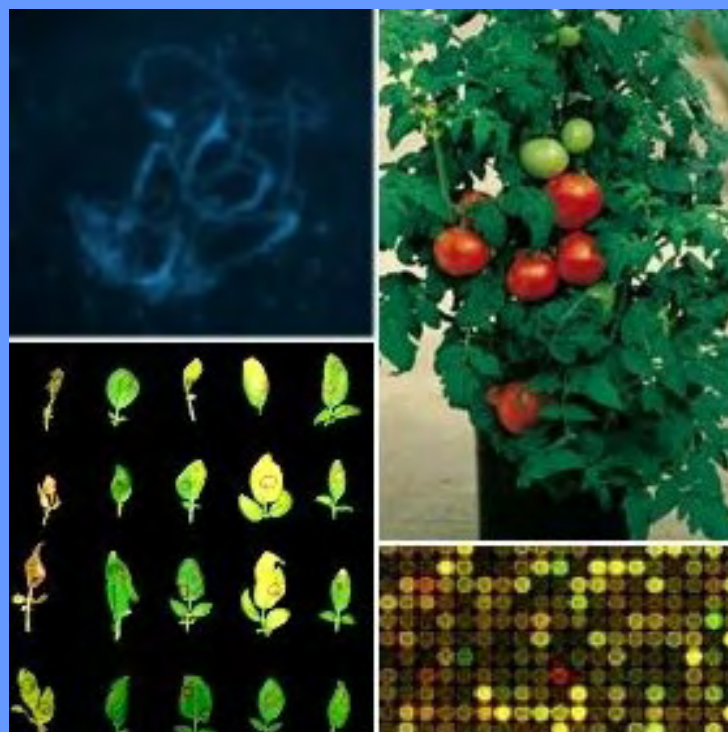
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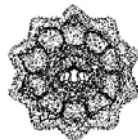
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Arabidopsis thaliana: a highly duplicated genome. How and why?

A. VIGILANTE, M. SANGIOVANNI, M.L. CHIUSANO

The angiosperms are the largest group of plants, with more than 350.000 known species. One of the major challenges of plant biologists is to understand the origin and the evolution of the angiosperms. Charles Darwin called this challenge an “abominable mystery”¹.

Recent analyses of complete genome sequences have revealed that many plant genomes have been duplicated in their evolutionary past. As an example, in 1996, the beginning of the sequencing of the flowering plant *Arabidopsis thaliana* genome² revealed that this model organism with a small genome and a rapid life cycle could be an ancient polyploid organism. Retained whole genome duplications (WGDs) are exceedingly rare, especially in higher animals where WGDs are usually lethal. On the contrary, polyploidy in plants is very common and can, in many circumstances, benefit the plant. So many researchers argue that it plays a significant role in large scale evolution. Polyploidy implies gene duplication. Gene duplication events are considered important mechanisms that facilitate the increasing complexity of organisms because they might have permitted functional diversification of genes. Under the classical model of the evolution, the duplicated genes may have different fate: they go for loss of function, neofunctionalization and subfunctionalization. In the first case, one member of the duplicated pair usually degenerates by accumulating deleterious mutations, while the other copy retains the original function. In the case of neofunctionalization, one duplicate may acquire a new adaptive function and the result is the preservation of both members of the pair, one presenting the new func-

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tion and the other retaining the old one. Functional divergence can occur even by subfunctionalization, that is the two copies act with a complementary effect to accomplish the functionalities of the ancestral gene. Duplicated genes also may interact through inter-locus recombination, gene conversion, or concerted evolution. A better understanding of the complex history which gave place to the organization of the structure of the *Arabidopsis* genome is necessary to consider this organism as a genetic model for other plant species. In fact, nowadays, an increasing number of plant genomes are completely sequenced, so a good knowledge of the model plant organism is an important key for good comparative analyses and to understand the complexity of genome organization, gene function, and regulatory pathways³.

Materials and methods

Identification of paralogs genes within the *Arabidopsis thaliana* genome provides a valuable resource for the comprehension of intragenome similarities. Paralogy between genes means that they are related by duplication within a genome. The most

commonly used procedure for the identification of paralogous genes is based on sequence similarity and the notion of genome-specific best hits. In particular, the first step consists of all-against-all comparison of protein sequences (typically using the BLAST program)⁴. Once paralogous genes are detected using an appropriate threshold, they are clustered with a suitable algorithm. To estimate the relative chronology of duplication events, the age of paralogous genes can be calculated by the number of synonymous substitutions per synonymous site (Ks). Next, it's possible to convert into a graph the putative paralogs, in which the nodes represent genes, and the edges represent their relationships.

Microarray studies in a range of polyploid plant species have confirmed that gene expression is radically altered by polyploidy. In particular, the time since duplication and the function of the genes involved, play important roles in the divergence of gene expression⁴. In this frame, another main topic in the study of duplicated genomes, is focused on the analyses of the functional fate of duplicated genes.

Results and discussion

Recent studies have shown that multiple ancient polyploidy events occurred during angiosperm evolution and most species underwent at least one round of polyploidy. Upfront the completion of the *Arabidopsis* genome sequence, it was clear that a large portion of its genome consists of duplicated segments². In fact, apparently *Arabidopsis thaliana* underwent two WGDs after its separation from the Eurosoid I clade, and some studies had also suggested a possible third duplication event in the distant past of the *Arabidopsis* lineage, probably at the base of the angiosperm radiation³.

Ten years later the release date of *Arabidopsis* ge-

nome, great controversy still exists about the origin of duplicated genes and how duplicated genes evolved new functionalities. Expression studies of duplicated genes revealed outstanding differences in expression profiles among different organ types, developmental stages, and in response to abiotic and biotic stress conditions⁴. The variation in expression patterns could be a clear evidence of functional divergences⁵.

This is in agreement with the 'gene balance' hypothesis, which argues the retention of regulatory genes, such as transcription factors, that have been preferentially maintained in a dosage-sensitive relationship⁵. Moreover, if the duplicated gene's protein product cooperates in a pathway, the retention of all the genes in that particular pathway occurs to avoid gene dosage effects.

Our main aim in this frame is to contribute to the comprehension of *Arabidopsis thaliana* genome organization considering networks of paralogous genes, integrating their functionalities and exploiting comparative approaches to support own observations thanks to related plant species.

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