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Overview of *Arabidopsis* as a Genetics Model System and Its Limitation, Leading to the Development of Emerging Plant Model Systems

Madhabendra Mohon Kar and Ayan Raichaudhuri

Abstract

Model plant systems make it easier to perform experiments with them. They help to understand and expand our knowledge about the genetic basis behind different plant process. Also, it is easier to design and perform genetic and genomic experiments using a model plant system. *A. thaliana* was initially chosen as the model plant system, and remains to this date, one of the most widely studied plant. With the advent of better molecular biology and sequencing tools and to understand the genetic basis for the unique processes in different plant species, there is emergence of several new model systems.

Keywords: Model plants, emerging model plants, genetic experiments, genomic studies, evolutionary model, legumes, crop plants, *Arabidopsis thaliana*, *Mimulus*, *Medicago truncatula*

1. Introduction

Model organisms are non-human species, which are usually less complex and easier to study to gain a broad understanding about different biological characteristics and phenomena [1]. The results obtained by studying the model organisms, are often used to understand the different biological characteristics and processes of the model of interest, which are usually more complex and difficult to study [1]. The term “model organism”, came into use mostly in the 1990s with the advent of Human Genome Project [1]. The most widely, used model organisms that was recognized for biomedical research by National Institute of Health of USA, includes, thale cress (*A. thaliana*), mouse (*Mus musculus*), rat (*Rattus norvegicus*), zebrafish (*Danio rerio*), fruit fly (*Drosophila melanogaster*), nematode (*Caenorhabditis elegans*) and baker's yeast (*Saccharomyces cerevisiae*) [1].

Model organisms have several advantages that make it convenient to perform experiments with them [1, 2]. Some of those advantages include, being easier to grow and maintain in large numbers in labs, availability of different genetic strains, small genomic size, ease of performing genetic manipulations and ease of standardized isolation of genetic material and availability of thoroughly annotated

genomes [1, 2]. Model organisms serve as useful tools for biological interventions, allowing easier experimental design and interpretation of genetic and genomic experiments. The understanding of the important role of genetics in plant research and the advent of powerful tools for molecular biology, pushed toward the need to focus on a single organism for performing detailed analysis [2, 3]. Use of a single model organism, also promoted interdisciplinary research, and helped in conserving resources required for research [2].

This chapter will provide a brief overview on *Arabidopsis* as a plant model system and its limitation, along with a brief overview of few emerging model plant system that are important in genetics research.

2. *Arabidopsis* as a plant model system

In the 1970s, the search for a model system in plant genetics, lead to interest in *Arabidopsis* research [2]. Several researchers and reviewers have shown interest and documented about the use of *A. thaliana* as a model organism, especially for genetic research [4–6]. *A. thaliana* has been the most used plant model systems for several decades [7]. This has allowed for extensive advances in the understanding of several biological process in plants, like, plant development, biotic and abiotic stress response, hormone biology and signaling [8]. Discoveries made as part of studying *Arabidopsis*, not only have been relevant to other plant species, but have also greatly enhanced the understanding of human biology [8–10].

Arabidopsis develop from a seed into mature plant, in a short period of time as six weeks [11]. Unlike many other plants, they can easily be grown indoors under feeble florescent lighting [11]. Also, the seed and seedlings of *Arabidopsis* is small, allowing the germination of the plant in an adequate number even on a single petri dish [11]. As the growth of this plant, requires no coculture of other species, it increases the possibility of controlling different variables and helps in maintaining aseptic growth conditions [11]. Thus, research using *Arabidopsis* is relatively convenient, fast, and cheap [2, 11]. The small genome size (~132 Mbp), along with the early availability of completed and annotated genome sequence of *Arabidopsis*, further made it central to genetic research [11, 12]. Also, the ability of the plant to undergo self-pollination and tolerate a high degree of homozygosity, makes it advantageous for research [2, 11].

Apart from genetics, *Arabidopsis* is also useful for answering questions about biochemistry, molecular biology, and physiology [13].

3. Limitations of using *Arabidopsis* as a model system

More than 400,000 species of gymnosperms, angiosperms, ferns, hornworts, lycophytes, mosses, liverworts, and algae, are classified as plants [7]. All of them, represents biodiversity in terms of their biochemistry, architecture, reproductive system and ecosystem among other characteristics [7]. *Arabidopsis* is a type of eudicot in the *Brassicaceae* (*Brassicales*) family, which along with monocots, are part of angiosperms (flowering plants) [7, 13]. It is a type of land plant. It is only one species of plant, that is only capable of growing in a certain limited set of environments [7]. So, to understand growth of different crop plants, and the evolutionary history of land plants, necessitates study of additional species [7].

Though many biological processes are common across various species of plant -- especially across flowering plants -- several other processes are species or clade specific [13]. Some of those processes that varies widely across species, families,

genera, and population are response to pathogens and plant secondary chemistry [13]. Also, some cereal crops that comprises as a major source of food, also varies morphologically, physiologically, and developmentally from *Arabidopsis* [13]. *Arabidopsis* does not have much symbiotic relation with soil microorganism as it does not associate with mutualistic arbuscular mycorrhizae [7, 11]. Also, it has an annual lifestyle, dicotyledonous way of development, and performs only C3 photosynthesis [7]. Also, not all genes that are expressed in other plants, are not represented in *Arabidopsis* [7]. Thus, having a single generic model cannot be used for understanding all aspects of plant biology.

4. Emerging plant models for studying genetics

4.1 *Brachypodium distachyon*

The tribe, Triticeae, that includes crops like, wheat, barley, and rye, have large genomes, and are difficult to perform genetic studies on them [13]. *Brachypodium distachyon*, is closely related to wheat and barley (both belong to the tribe Triticeae, which are important crop plants, thus it was chosen as a model plant, to study cereal biology [13, 14]. It also has synteny with major small grains like, wheat, maize, millet, rice, and barley [15]. It is a small annual species, that belongs to the genus *Brachypodium* [13]. It is a C3 plant, that is distributed worldwide [15]. It has some characteristics that make it suitable to be used as a model system, to study genetics. The characteristics include, small genome size (~272 Mb), small size, ease of cultivation in lab and short lifecycle, ability to self-pollinate and ease of genetic crossings [13, 15]. The fully annotated reference genome sequence of *B. distachyon*, is publicly available [15]. Also, a large variety of tools are available to be used with this plant as a model system [13, 16–18]. They include availability of diverse collection of germplasm, microarrays, robust transformation protocol and several T-DNA insertion lines [13].

B. distachyon is an emerging model system that is useful for studying genetics of flowering plants [13]. This model system is particularly useful for understanding and expanding our knowledge about the biology of grasses, including that of small grains [15]. *B. distachyon* can serve as an essential system to study specific processes, like, endosperm development, cell wall biology, flowering control, and inflorescence development [13]. The plant is also useful for studying genetic basis for cold tolerance and genome organization, apart from the studying of floral development, vein patterning, the controls of the perennial versus annual habit [13]. There are several works, that describe the development of this plant as a model system [19–22].

4.2 *Medicago truncatula*

Though legumes are an important source of food apart from playing a major role in nitrogen fixation, most cultivated legumes are poor model systems for genomic research [23]. *Arabidopsis*, the most used plant model system cannot be used to properly understand many of the features uniquely seen in legumes [23, 24]. To study the rhizome legume symbiosis, Barker et al., suggested using *Medicago truncatula* as a model plant system [25, 26]. The plant possesses several features, that make it an ideal candidate for studying legume biology and genetics [24]. Some of them are, its small genome size (~375 Mbp), that is sequenced and fully annotated, diploid genome, autogamous fertilization, relatively short generation time (around 4 months), rapid reproductive cycle, availability of large number of cultivars and presence of a well characterized nitrogen-fixing symbiont, *Sinorhizobium meliloti*

[24, 25, 27–30]. Also, the genus *Medicago* belongs to the phylum Galeoid [31]. So, it is related to several crop legumes like pea, chickpea, faba bean, lentil, chickpea, and clover [31]. Also, as members of this phylum have a similar genetic organization and high level of nucleotide sequence conservation, there is potential for easy transfer of genome sequence between the member species [24].

Several bioinformatics resources are available for *Medicago* like Medicago Gbrowser, LegumeGRN legumeIP, and Legoo [25]. Also, in addition to transcriptomics tools, several libraries for metabolic studies and reference maps for proteomic studies are available for *Medicago truncatula* [25, 32–34]. The capacity of the plant to be transformed efficiently and the generation of different mutants, have enhanced the ability to perform function genetic studies on *Medicago truncatula* [25]. *M. truncatula*, which is a legume related to alfalfa, has emerged as an important model plant, for studying and understanding the molecular biology and genetics of various processes involved in mycorrhizal, rhizobial, and pathogenic plant-microbe interactions [24]. To understand the biological processes like symbiotic nitrogen fixation (involving root nodule formation), the seed development, and the abiotic stress tolerance, genetic studies using *M. truncatula* is ideal [25].

4.3 *Mimulus*

Mimulus (monkeyflower) genus is important not only as a classic ecological and evolutionary model system but is also important for studying the developmental genetics and evolutionary development of certain important plant traits, that are not found in common model plant system like *Arabidopsis* [35]. Genetic studies with *Mimulus* could help to answer a large range of evolutionary and ecological questions [36].

The species within the genus *Mimulus* has become important for understanding the genetics of mating system evolution, speciation, inbreeding depression, ecological adaptations, cytological patterns of evolution and speciation [36–42]. This system is also phylogenetically attractive for broad comparative genomics research across the plant kingdom [36]. Species within *mimulus* has several attributes that facilitate genetic experimentation [36]. Such, attributes include the ability of several species within the genus being self-compatible, many can be clonally propagated using cuttings and short generation time under experimental conditions [36]. The *M. lewisii* complex, is currently best developed to be used as a model system among all the other *Mimulus* species – which includes the bumblebee-pollinated *M. lewisii*, hummingbird pollinated *M. cardinalis* and *M. verbenaceus*, and self-pollinated *M. parishii* -- for studying developmental genetics and evolutionary development [35]. This is owing to their characteristics like, these species being genetically similar enough to allow manual cross pollination to produce fertile offspring. They are also, uniquely suitable for genetic analysis as they have high fecundity (up to 1000 seeds per flower), short generation time (2.5–3 months), and small genome size (c. 500 Mb) [35].

The *M. lewisii* complex is used as a model system, to enhance our understanding in several research areas like, that of, regulation of carotenoid pigmentation, formation of periodic pigmentation patterns, developmental genetics of corolla tube formation and elaboration and molecular basis of floral trait variation underlying pollinator shift [35].

5. Future perspective

Model plant systems are important for studying and understanding the molecular biology and genetics of various plant processes. The definition of model systems

and the list of model systems are changing with the increase in our understanding about plant processes and the advent of newer technologies to study plants [7]. The limitations of classical genetic manipulation that catapulted *A. thaliana* as a model plant system, are being addressed with the development of rapid high throughput genome sequencing and targeted gene editing using tools like TALENs, ZINC-FINGER nucleases, and CRISPR/Cas9 [7, 25]. This enables, a wider variety of plant species to be studied, and that helps to gain insights into unique and varied biological processes. The extensive use of emerging sequencing technologies, along with genomics and systems biology approaches will enhance understanding of the functional aspects of the gene pool of different plant species [25].

The technological advances, leading to the development of emerging model plants, will certainly help in providing more possibilities of choices to plant researchers. This will help in improving our understanding of the underlying genetics that influences the fundamental properties of plants and plant development. The increase in understanding, will increase our ability to genetically modify plants to better suit our needs.

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