

CONCEPT ESSAY

Arabidopsis ~~Thaliana~~, a Model Organism for Molecular Genetic Studies in Plants: How and Why Was *Arabidopsis* Chosen Over Other Plants?

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Introduction

Although millions of species inhabit Earth, only a select few are the subjects of intensive biological research. Have you ever wondered why a small number of species receive most of this scientific attention and how they were selected? Because of the similarities between related organisms, scientists commonly choose a single species to study as a representative for a broader group. This species is called a **model system**. Information obtained from studying the model system can be applied to related organisms as needed. The choice of a representative species is typically driven by how easy it is to obtain, grow, and manipulate, and how well it has been studied. Scientists who use different approaches or techniques normally choose ~~different~~ models that ~~are~~ best suited for the type of experiment. For example, in the past, plant biochemists frequently used spinach as a model because spinach was easy and inexpensive to obtain, and the thin walls of spinach leaf cells could be easily broken open by using a kitchen blender.

~~Scientists employing~~ molecular genetic analysis ~~have~~ different needs ~~in a model system~~. The isolation and characterization of mutants is an integral part of ~~this~~ research ~~approach~~. A **mutation** in a gene normally results in a loss of function of the product (protein) and often has a negative consequence (defect) to the biology of that organism. The observed defect in the mutant (**phenotype**) provides information concerning the function of the protein in vivo and the process in which the protein is involved. For example, mutations in the gene encoding the globin protein can result in anemia, an outcome that connects hemoglobin to its role in carrying oxygen in the blood. Because the genetic analysis of mutants requires dealing with large populations and examining multiple generations of offspring, small organisms with fast life cycles and large numbers of progeny are favoured as a model. Most biology students are familiar with the fruit fly (*Drosophila melanogaster*), adopted as a model system for genetic analysis by Nobel laureate Thomas Hunt Morgan. The plant species most commonly used for molecular genetics at present is the small member of the mustard family (Brassicaceae) *Arabidopsis thaliana* (arabidopsis, Photo A). Unlike the fruit fly adopted as a model at the beginning of the twentieth century, arabidopsis was not widely accepted as a model until relatively recently.

KEY CONCEPTS

- Model organisms are used for biological research.
- Arabidopsis is a model plant for molecular genetic research.
- Genetic analysis requires the study of progeny in multiple generations.

PHOTO A. An arabidopsis plant.

An approximately four-week-old arabidopsis plant with a rosette of leaves close to the soil and an inflorescence bearing flowers and seedpods (siliques; see arrows) is shown.

Source: Photo by Ljerka Kunst.



The Selection of Arabidopsis as a Model System

Before the 1980s the most popular models for plant genetics were crop or horticultural plants, such as maize (*Zea mays*), tomato (*Solanum lycopersicum*), barley (*Hordeum vulgare*), and petunia (*Petunia x hybrida*). Genetic research on these species not only improved our understanding of plant biology but also yielded new traits that could be directly used for breeding better agricultural varieties. Maize played an instrumental role in genetic research during much of the twentieth century. In addition to its status as a major crop, its chromosomes were easily observed ~~by~~ using microscopy, allowing researchers to draw correlations between changes in chromosome structure and genetic inheritance (cytogenetics). Barbara McClintock won a Nobel Prize (1983) for her discovery of transposable elements in maize ~~by~~ using this approach. One problem with most of these early model plant genetic systems, including maize, was that their relatively large size required planting outdoors ~~by~~ using farm machinery, unavailable to the large number of researchers in urban areas. In addition, the long generation times of such species (three to four months) limited the number of successive generations that could be planted in a year, slowing the pace of research in plant genetics.

Arabidopsis was first promoted as a model organism by Friedrich Laibach in 1943. Despite the fact that it had many of the attributes needed for genetic analysis, including a small size and short generation time, arabidopsis did not immediately become popular. Consequently, it lacked the critical number of researchers to develop it as an effective model system (see below). Some of its drawbacks included small chromosomes that were not well suited for cytological analysis, difficulties in regenerating whole plants from cells grown on defined medium, and its lack of commercial value. In the early

1980s three major advances in arabidopsis research caught the attention of others. First, Maarten Koornneef and co-workers at Wageningen Agricultural University identified a large number of genes by mutation and mapped them to chromosomes, establishing the first comprehensive genetic map of the arabidopsis genome. Second, Christopher Somerville working at the University of Illinois and Michigan State University demonstrated the power of genetic analysis in plants by using mutants to characterize important biochemical processes (photorespiration, lipid biosynthesis). Finally, Elliot Meyerowitz (California Institute of Technology) and co-workers determined that the amount of DNA in the arabidopsis genome was smaller than any other seed plant described at that time. These discoveries prompted a large number of other well-established scientists to begin research on arabidopsis, resulting in a rapid increase in information on the species over the next three decades.

Attributes of Arabidopsis as a Model Genetic System

Arabidopsis has a number of natural attributes that collectively make it well suited for molecular genetic studies on flowering plants. First, the arabidopsis plant is very small. Following germination, the arabidopsis seedling produces a series of leaves on a short stem, resulting in a compact rosette close to the soil. On flowering, the stem elongates dramatically and a series of flowers are produced (**inflorescence**), each of which self-fertilizes to produce a seedpod (Photo A). When grown alone in uncrowded conditions (Photo A), the maximum diameter of the rosette is 4 to 6 cm, and the inflorescence reaches 30 to 40 cm in height. However plants grown at high density will be considerably smaller. The small size allows large numbers of arabidopsis plants to be grown indoors in growth chambers and greenhouses, avoiding the need for researchers to have access to field plots. In addition, the small arabidopsis plants are easy to manipulate. For example, thousands of seeds can be sown, and plants grown until flowering, on defined agar medium in containers as small as bacteriological Petri plates (8 cm diameter), which allows for the evaluation of specific nutritional requirements or selection of mutants resistant to specific chemicals (Photo B).

Second, relative to other seed plants, the generation time of arabidopsis is short. Under standard conditions of light and temperature ($100 \mu\text{E}/\text{m}^2/\text{s}$; 20°C), it will flower

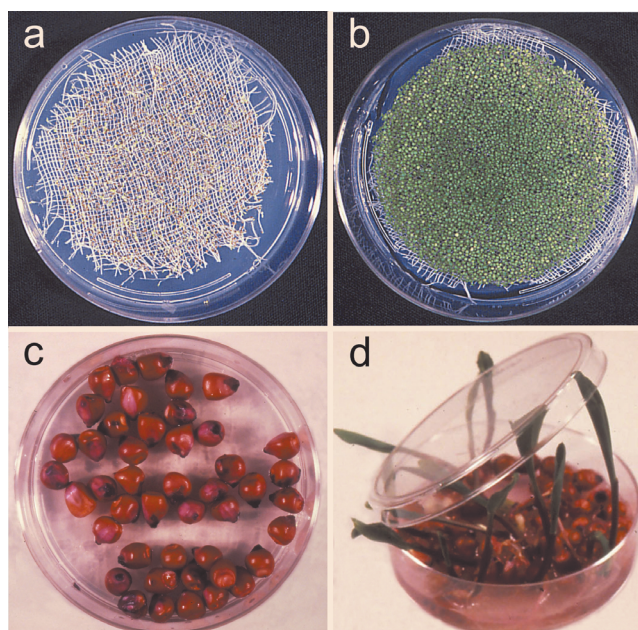


PHOTO B. Arabidopsis seeds and seedlings are very small compared with many other plant species.

Because of their small size, thousands of arabidopsis seeds can be sown in an 8 cm Petri dish, with cheesecloth used to maintain a more even distribution (panel a). These seeds can be grown within the Petri dish until flowering (panel b). Such species as maize that have much larger seeds cannot be grown at high densities (panel c), and even very young seedlings are too big to be grown in the Petri dish (panel d).

Source: Photo by George Haughn.

PHOTO C. Arabidopsis has a shorter generation time than many other seed plants.

A three-week old arabidopsis plant (foreground) that is flowering stands in front of a tobacco (*Nicotiana tabacum*) seedling of the same age that will not flower for many more weeks.

Source: Photo by George Haughn.



within a month (Photo C) and produce mature seeds within two months. The time from seed to seed can be shortened by two weeks if plants are grown under continuous light.

Third, the self-fertility and large numbers of progeny (>1000 seeds/plant) simplify the analyses of inheritance and the maintenance of genetic stocks. Fourth, the small diploid genome (125 megabase pairs) reduces the amount of labour and time needed to clone and manipulate genes. Last, the small number of chromosomes ($n = 5$) simplifies genetic mapping.

The exponential growth in arabidopsis research over the last three decades has made arabidopsis the best-studied species and led to numerous technical advances that have further increased its utility for molecular genetics:

1. In the 1990s, a fast, easy method for introducing engineered genes into the genome (**transformation**) was developed for arabidopsis (Clough and Bent, 1998). To date, this technique does not work efficiently in any other species.
2. The complete sequence of the arabidopsis genome was published in 2000 and was the first seed plant genome to be completed. This information ushered in the era of genomics for arabidopsis and began the drive to determine the function of every one of the approximately 28 000 genes in the genome.
3. **Insertional mutations** (mutations in which a foreign segment of DNA has inserted in the middle of a gene, resulting in the loss of function of the gene product) in virtually all arabidopsis genes have been created and identified. This resource allows for the functional analysis of any gene, providing the material for future generations of molecular geneticists.

The growing knowledge base has been organized and presented in the form of a website: the Arabidopsis Information Resource (TAIR, <http://www.arabidopsis.org>), and seed stocks and DNA clones are distributed by two separate stock centers: the Arabidopsis Biological Resource Center (<http://abrc.osu.edu>) and the European Arabidopsis Stock Center (<http://arabidopsis.info>).

Conclusions

The small size, short generation time, large number of progeny per plant, and small genome of arabidopsis make it attractive for molecular genetic analysis. These attributes influenced a large number of scientists to adopt arabidopsis as a model plant for molecular genetic studies. Thirty years of research have made arabidopsis arguably the best-studied plant species and have resulted in the development of knowledge and resources that further increase its value as an experimental organism. Arabidopsis has much in common with other plant species, including the number, type, and arrangement of genes in the genome. Consequently, the information obtained relatively quickly in arabidopsis can be transferred to other plants, including crops. However, it is important to note that the utility of arabidopsis as a model for studying another species depends on the degree of similarity they share. Arabidopsis is an excellent model for the closely related oilseed rape (*Brassica napus*, Canola) but not always as good a one for more distantly related crops. Legumes, such as beans, can fix nitrogen from the air by interacting with nitrogen-fixing bacteria, while arabidopsis cannot. So to understand the process of nitrogen fixation, a model legume species, *Medicago truncatula*, was developed. Similarly, rice was developed as a model for research questions specific to cereals. Even though arabidopsis is smaller and has a faster life cycle than most seed plants, it cannot serve as a model for biological processes that it does not share with other plants. Thus, the best model organism is determined by the nature of question being asked and the scientific approach being employed. For most questions in seed plants that require molecular genetics, arabidopsis is the model of choice.

Critical Thinking Questions

1. What is important to consider when choosing a model organism for a particular type of research?
2. If a plant were discovered that had a smaller size, smaller genome, or a shorter life cycle than arabidopsis, could it replace arabidopsis as a model system for plant molecular genetics?
3. Explain why small size and short generation time are important features of a model system for molecular genetic research.

Further Research Question

The small roundworm *Caenorhabditis elegans* was developed as a model for genetic analysis in the 1960s despite the fact that several other model species, such as the fruit fly, were already available. For what specialized purpose was it developed and what were the characteristics of *C. elegans* that led to its development as a model?

References

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