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ARABIDOPSIS THALIANA: A MODEL PLANT FOR BIOINFORMATICS

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ABSTRACT

Arabidopsis thaliana (thale cress, mouse-ear cress or arabidopsis) is a small flowering plant native to Europe, Asia, and north-western Africa. *Arabidopsis* was the first plant genome to be sequenced, and is a popular tool for understanding the molecular biology of many plant traits, including flower development, light sensing, transport mechanisms and the effect of seed and rosette cold treatment on germination and flowering time in plants.

KEYWORDS:- *Arabidopsis thaliana*, model organism, Bioinformatics, plant biology, plant genome etc..

INTRODUCTION

Arabidopsis thaliana (thale cress, mouse-ear cress or arabidopsis) is a small flowering plant native to Europe, Asia, and northwestern Africa ^[1]. A spring annual with a relatively short life cycle, *Arabidopsis* is popular as a model organism in plant biology and genetics. *Arabidopsis thaliana* has a rather small genome, only 157 megabase pairs (Mbp), and was thought for a long time to have the smallest genome of all flowering plants, but the smallest flowering plants' genomes are now known to belong to plants in the genus *Genlisea*, order Lamiales, with *Genlisea margaretae*, a carnivorous plant, shows a genome size of 63.4 Mbp ^[2].

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Figure 1: *Arabidopsis thaliana* plant





DISCOVERY AND NAME ORIGIN

The plant was first discovered in 1577 in the Harz Mountains by Johannes Thal (1542–1583), a physician from Nordhausen, Thüringen, Germany, who called it *Pilosella siliquosa*. In 1841 the plant was renamed *Arabidopsis thaliana* by German botanist Gustav Heynhold in honor of Thal. The genus name, *Arabidopsis* comes from Greek, meaning "resembling *Arabis*".

MORPHOLOGY

It is an annual (rarely biennial) plant, usually growing to 20–25 cm tall. The leaves form a rosette at the base of the plant, with a few leaves also on the flowering stem. The basal leaves are green to slightly purplish in color, 1.5–5 cm long and 2–10 mm broad, with an entire to coarsely serrated margin; the stem leaves are smaller and unstalked, usually with an entire margin. Leaves are covered with small, unicellular hairs (called trichomes). The flowers are 3 mm in diameter, arranged in a corymb; their structure is that of the typical Brassicaceae. The fruit is a silique 5–20 mm long, containing 20–30 seeds^[3]^[4]. Roots are simple in structure, with a single primary root that grows vertically downwards, later producing smaller lateral roots. These roots form interactions with

rhizosphere bacteria such as *Bacillus megaterium*^[5].

LIFE CYCLE

Arabidopsis can complete its entire life cycle in six weeks. The central stem that produces flowers grows after about three weeks, and the flowers naturally self-pollinate. In the lab, *Arabidopsis* may be grown in Petri plates or pots, under fluorescent lights or in a greenhouse^[6].

ARABIDOPSIS THALIANA – ADVANTAGE AS A MODEL ORGANISM

During the last 8 to 10 years, *Arabidopsis thaliana* has become universally recognised as a model plant for study. It is a small flowering plant that belongs to the *Brassica* family, which includes species such as broccoli, cauliflower, cabbage, and radish. Although it is a non-commercial plant, it is favoured among basic scientists because it develops, reproduces, and responds to stress and disease in much the same way as many crop plants. Scientists expect that systematic studies of *Arabidopsis* will offer important advantages for basic research in genetics and molecular biology and will illuminate numerous features of plant biology, including those of significant value to agriculture, energy, environment, and human health. Because of several reasons *Arabidopsis* has become the organism of choice for basic studies of the molecular genetics of flowering plants.

- It has a small genome (125 Mb total), which already has been sequenced in the year 2000, and it lacks the repeated, less-informative DNA sequences that complicate genome analysis.
- It has extensive genetic and physical maps of all 5 chromosomes.
- A rapid life cycle (about 6 weeks from germination to mature seed).
- Prolific seed production and easy cultivation in restricted space.
- Efficient transformation methods utilising *Agrobacterium tumefaciens*.

- A large number of mutant lines and genomic resources (Stock Centres).
- Multinational research community of academic, government and industry laboratories.

But how can discoveries with *Arabidopsis* contribute to the development of improved crops? Simply, once a gene has been discovered in *Arabidopsis*, the equivalent gene may be found more easily in other plants. Thus, the function of many genes isolated from crop plants can be better understood via study of their *Arabidopsis* homologues. So knowledge gained from *Arabidopsis* on the defence mechanisms against pathogens, for example, can be used directly to develop disease-resistant plants in other species.

USES AS A MODEL ORGANISM

By the beginning of 1900s, *A. thaliana* had begun to be used in some developmental studies. The first collection of its mutants was made around 1945. It is now widely used for studying plant sciences, including genetics, evolution, population genetics, and plant development^{[7][8][9]}. It plays the role in plant biology that mice and fruit flies (*Drosophila*) play in animal biology. Although *A. thaliana* has little direct significance for agriculture, it has several traits that make it a useful model for understanding the genetic, cellular, and molecular biology of flowering plants.

The small size of its genome makes *Arabidopsis thaliana* useful for genetic mapping and sequencing — with about 157 megabase pairs^[10] and five chromosomes, *Arabidopsis* has one of the smallest genomes among plants. It was the first plant genome to be sequenced, completed in 2000 by the *Arabidopsis* Genome Initiative^[11]. The most up-to-date version of the *A. thaliana* genome is maintained by the *Arabidopsis* Information Resource (TAIR). Much work has been done to assign functions to its 27,000 genes and the 35,000 proteins they encode.

The plant's small size and rapid life cycle are also advantageous for research. Having specialized as a

spring ephemeral, it has been used to found several laboratory strains that take about six weeks from germination to mature seed. The small size of the plant is convenient for cultivation in a small space, and it produces many seeds. Further, the selfing nature of this plant assists genetic experiments. Also, as an individual plant can produce several thousand seeds, each of the above criteria leads to *A. thaliana* being valued as a genetic model organism.

Plant transformation in *Arabidopsis* is routine, using *Agrobacterium tumefaciens* to transfer DNA to the plant genome. The current protocol, termed "floral-dip", involves simply dipping a flower into a solution containing *Agrobacterium*, the DNA of interest, and a detergent^{[12] [13]}. This method avoids the need for tissue culture or plant regeneration.

The *Arabidopsis* gene knockout collections are a unique resource for plant biology made possible by the availability of high-throughput transformation and funding for genomics resources. The site of T-DNA insertions has been determined for over 300,000 independent transgenic lines, with the information and seeds accessible through online T-DNA databases. Through these collections, insertional mutants are available for most genes in *Arabidopsis*.

Finally, the plant is well suited for light microscopy analysis. Young seedlings on the whole and their roots in particular, are relatively translucent. This, together with their small size, facilitates live cell imaging using both fluorescence and confocal laser scanning microscopy^[14]. By wet mounting seedlings in water or in culture media, plants may be imaged uninvasively, obviating the need for fixation and sectioning and allowing time-lapse measurements^[15]. Fluorescent protein constructs can be introduced through transformation. The developmental stage of each cell can be inferred from its location in the plant or by using fluorescent protein markers, allowing detailed developmental analysis.

TAIR and NASC are curated sources for diverse *Arabidopsis* genetic and molecular biology

information, and also provide numerous links, for example, to databases that store the results of hundreds of genome-wide gene expression profile experiments. Seed and DNA stocks can be obtained from NASC or the Arabidopsis Biological Resource Center.

APPLICATIONS OF *ARABIDOPSIS THALIANA* IN BIOINFORMATICS

1. FLOWER DEVELOPMENT

Arabidopsis has been extensively studied as a model for flower development. The developing flower has four basic organs: sepals, petals, stamens, and carpels (which go on to form pistils). These organs are arranged in a series of whorls: four sepals on the outer whorl, followed by six petals inside this, six stamens, and a central carpel region. Homeotic mutations in Arabidopsis result in the change of one organ to another — in the case of the *Agamous* mutation, for example, stamens become petals and carpels are replaced with a new flower, resulting in a recursively repeated sepal-petal-petal pattern.

The ABC model summarizes how the presence or absence of different classes of transcription factors in the different parts of the flower regulates the development of floral organs. Two key observations have led to the ABC model. First, the discovery of homeotic mutations in which one organ develops in a location normally occupied by a different organ. Wild roses, for example, have only five petals but many stamens. Garden roses have a homeotic gene that causes some of the potential stamens to develop into petals instead. Second, each of the genes that affect the identity of organs in flowers has an effect on two groups of flower organs, affecting petals and sepals or affecting petals and stamens.

Floral organ identity genes are therefore divided into three classes, depending on which organs they affect. Mutations in class A genes affect sepals and petals. Mutations in class B genes affect petals and stamens, while those in class C affect stamens and

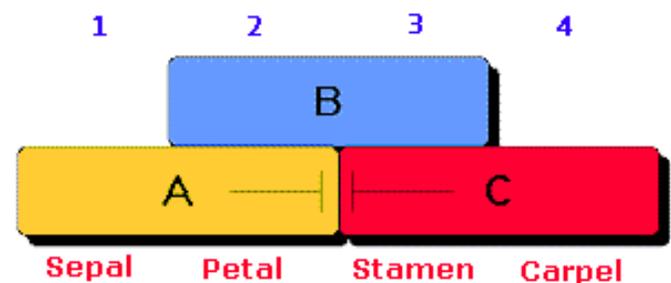
carpels. All three classes of genes are homeotic genes, which are translated into proteins.

Observations of homeotic mutations led to the formulation of the ABC model of flower development by E. Coen and E. Meyerowitz^[16]. According to this model, floral organ identity genes are divided into three classes: class A genes (which affect sepals and petals), class B genes (which affect petals and stamens), and class C genes (which affect stamens and carpels). These genes code for transcription factors that combine to cause tissue specification in their respective regions during development. Although developed through study of Arabidopsis flowers, this model is generally applicable to other flowering plants.

ABC model overview

- Simple rule that underlie the whorl specifications using floral homeotic mutants
- Class A mutants have carpels in the first whorl instead of sepals, and stamens in the second whorl in place of petals
- Class B mutants have sepals rather than petals in the second whorl and carpels in the rather than stamens in the third whorl
- Class C mutants have petals instead of stamens in the third whorl and sepals instead of carpels in the fourth

Figure 2: ABC Model



2. LIGHT SENSING

The photoreceptors phytochrome A, B, C, D and E mediate red light-based phototropic response. Understanding the function of these receptors has helped plant biologists understand the signalling

cascades that regulate photoperiodism, germination, de-etiolation and shade avoidance in plants.

Arabidopsis was used extensively in the study of the genetic basis of phototropism, chloroplast alignment, and stomatal aperture and other blue light-influenced processes^[17]. These traits respond to blue light, which is perceived by the phototropin light receptors. *Arabidopsis* has also been important in understanding the functions of another blue light receptor, cryptochrome, which is especially important for light entrainment to control the plants circadian rhythms^[18].

Light response was even found in roots, which were thought not to be particularly sensitive to light. While gravitropic response of *Arabidopsis* root organs is their predominant tropic response, specimens treated with mutagens and selected for the absence of gravitropic action showed negative phototropic response to blue or white light and positive response to red light, indicating the roots also show positive phototropism^[19].

3. NON-MENDELIAN INHERITANCE

In 2005, scientists at Purdue University proposed that *Arabidopsis* possessed an alternative to previously known mechanisms of DNA repair, which one scientist called a "parallel path of inheritance". It was observed in mutations of the *HOTHEAD* gene. Plants mutant in this gene exhibit organ fusion and pollen can germinate on all plant surfaces, not just the stigma. After spending over a year eliminating simpler explanations, it was indicated that the plants "cached" versions of their ancestors' genes going back at least four generations, and used these records as templates to correct the *HOTHEAD* mutation and other single nucleotide polymorphisms. The initial hypothesis proposed the record may be RNA-based^[20]. Since then, alternative models have been proposed which would explain the phenotype without requiring a new model of inheritance^{[21] [22]}. More recently, the whole phenomenon is being challenged as a being a simple artifact of pollen

contamination^[23]. "When Jacobsen took great pains to isolate the plants, he couldn't reproduce the [reversion] phenomenon", notes Steven Henikoff^[24]. In response to the new finding, Lolle and Pruitt agree that Peng *et al.* did observe cross-pollination, but note that some of their own data, such as double reversions of both mutant genes to the regular form, cannot be explained by cross-pollination^[25].

4. COMPARISON OF THE TRANSPORTER COMPLEMENT OF ARABIDOPSIS, C. ELEGANS AND S. CEREVISIAE IN TERMS OF ENERGY COUPLING MECHANISMS

S. cerevisiae, *C. elegans* and *A.thaliana* led to the identification of over 100 distinct families of membrane transporters^{[26] [27]}. Plant secondary transporters are typically coupled to protons rather than to sodium^{[28] [29]}. Compared with *C. elegans*, *Arabidopsis* has a surprisingly high percentage of primary ATP-dependent transporters (12% and 21% of transporters, respectively), reflecting increased numbers of P-type ATPases involved in metal ion transport and ABC ATPases proposed to be involved in sequestering unusual metabolites and drugs in the vacuole or in other intracellular compartments. These processes may be necessary for pathogen defence and nutrient storage.

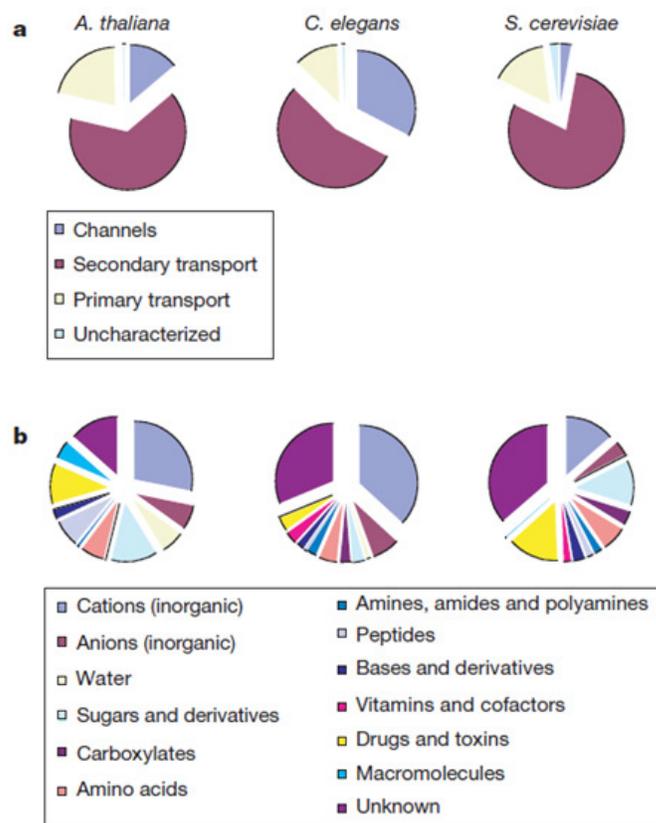
About 15% of the transporters in *Arabidopsis* are channel proteins, five times more than in any single-celled organism but half the number in *C. elegans* (Fig. 3b). Almost half of the *Arabidopsis* channel proteins are aquaporins, and *Arabidopsis* has 10-fold more Mfamily major intrinsic protein (MIP) family water channels than any other sequenced organism. This abundance emphasizes the importance of hydraulics in a wide range of plant processes, including sugar and nutrient transport into and out of the vasculature, opening of stomatal apertures, cell elongation and epinastic movements of leaves and stems. Although *Arabidopsis* has a diverse range of metal cation

transporters, *C. elegans* has more, many of which function in cell-cell signalling and nerve signal transduction.

Arabidopsis also possesses transporters for inorganic anions such as phosphate, sulphate, nitrate and chloride, as well as for metal cation channels that serve in signal transduction or cell homeostasis. Compared with other sequenced organisms, *Arabidopsis* has 10- fold more predicted peptide transporters, primarily of the proton dependent oligopeptide transport (POT) family, emphasizing the importance of peptide transport or indicating that there is broader substrate specificity than previously realized. There are nearly 1,000 *Arabidopsis* genes encoding Ser/Thr protein kinases, suggesting that peptides may have an important role in plant signalling^[30].

Virtually no transporters for carboxylates, such as lactate and pyruvate, were identified in the *Arabidopsis* genome. About 12% of the transporters were predicted to be sugar transporters, mostly consisting of paralogues of the MFS family of hexose transporters. Notably, *S. cerevisiae*, *C. elegans* and most prokaryotes use APC family transporters as their principle means of amino-acid transport, but *Arabidopsis* appears to rely primarily on the AAP family of amino-acid and auxin transporters. More than 10% of the transporters in *Arabidopsis* are homologous to drug efflux pumps; these probably represent transporters involved in the sequestration into vacuoles of xenobiotics, secondary metabolites, and breakdown of chlorophyll^[31].

Figure 3: Comparison of the transport capabilities of *Arabidopsis*, *C.elegans* and *S.cerevisiae*. Pie charts show the percentage of transporters in each organism according to bioenergetics (a) and substrate specificity (b).



5. MAGNUS NORDBORG AND JOY BERGELSON STUDIED THE EFFECT OF SEED AND ROSETTE COLD TREATMENT ON GERMINATION AND FLOWERING TIME IN SOME *ARABIDOPSIS THALIANA* (BRASSICACEAE) ECOTYPES.

The germination and flowering responses to cold treatment were investigated in 32 ecotypes of *Arabidopsis thaliana*. A month-long cold treatment at the seed stage decreased the time until flowering in all but one strain, whereas a 3-d cold treatment had little, or the opposing effect. A month-long cold treatment at the rosette stage also decreased the time until flowering, but was less effective than seed cold treatment. Seed and rosette cold treatments did not have an additive effect on time until flowering. Cold treatment usually increased the speed of germination however no clear response patterns for the probability of germination were detected. These findings are discussed in relation to the life cycle of the plant^[32].

Figure 4: The mean number of days from germination to bolting as a function of the level of seed cold treatment. Only ecotypes that germinated under all treatments are shown.

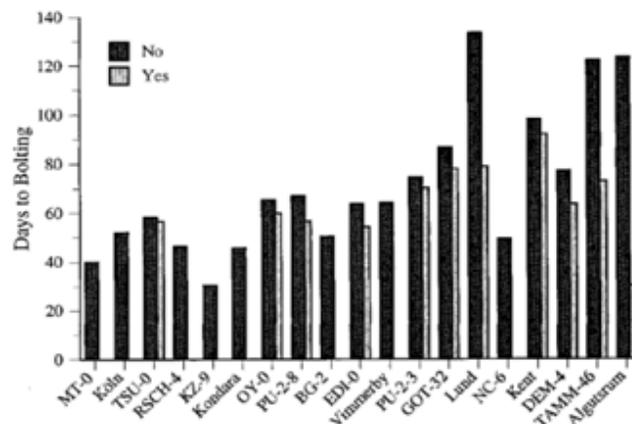
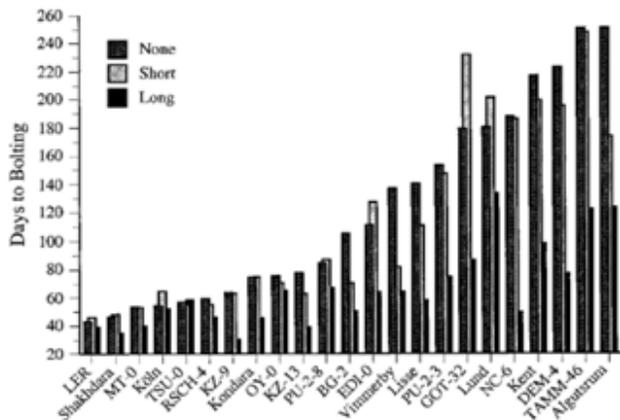
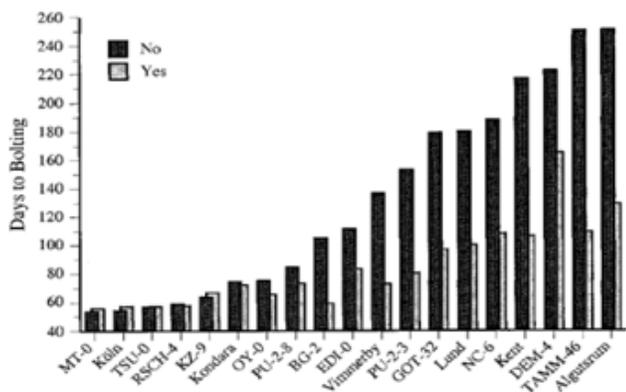


Figure 5: The mean number of days from germination to bolting as a function of whether the plants received rosette cold treatment or not. The upper chart shows the results for plants that were not treated at the seed stage, the lower shows the same for plants that received “long” seed cold treatment. Missing values in the latter indicate that the ecotype bolted too rapidly to be subjected to rosette cold treatment. Ecotypes that failed to germinate under either seed treatment are not shown, nor are those that bolted too rapidly even without seed cold treatment.



Ecotypes whose probability of germination was very strongly promoted (at least doubling the germination percentage) by the long seed cold treatment were KZ-9, KZ- 13, OY-0, Lisse, DEM-2, and MS-0 [33] [34]. The four Swedish ecotypes all responded negatively (basically eliminating germination for Vimmerby and Va”stervik) to long seed cold treatment.

The effect of cold treatment on the speed of germination, measured as the number days until 95% of the seeds that were eventually to germinate had germinated, was much simpler. In all except one case, germination was faster with long cold treatment than with short or no cold treatment, and in these cases germination was usually also faster with short than with no cold treatment. One ecotype, OY-0, showed precisely the opposite response. The long seed cold treatment decreased bolting time compared to no and/or short cold treatment in all but one ecotype, TSU-0 [35].

In contrast, short seed cold treatment had a less consistent and usually minor effect; bolting time was increased for seven ecotypes (significantly so for GOT-32 and Ko”ln) and decreased for 15 (significantly so for Vimmerby and Algenrum). Second, significant rosette cold treatment effects always entailed a decrease in bolting time, however there was often no significant effect. For many ecotypes, a combination of rosette and long seed cold treatment did not decrease bolting time relative to long seed cold treatment alone [36]. It is notable that our short seed cold treatment (3 d)

was evidently not sufficient to significantly accelerate bolting^[32].

CONCLUSION

During the last 8 to 10 years, *Arabidopsis thaliana* has become universally recognised as a model plant for study. The systematic studies of *Arabidopsis* will offer important advantages for basic research in genetics and molecular biology and will illuminate numerous features of plant biology, including those of significant value to agriculture, energy, environment, and human health.

The function of all genes within their cellular, organismal and evolutionary context of *Arabidopsis thaliana* has to be predicted. That will be the first time it is feasible for plant biologists to envision a whole system approach to study of plant form and function. This whole system approach needs a lot of additional information that comes from micro array experiments, knockout experiments, pathway databases, etc. The more information about *Arabidopsis* is generated, the more it can be used for commercial plants. This means that the use of the information generated with *Arabidopsis* will then be used to improve plants for commercial goals.

REFERENCES

1. Germplasm Resources Information Network (GRIN): *Arabidopsis thaliana*
2. Greilhuber J., Borsch T., Müller K., Worberg A., Porembski S., and Barthlott W., "Smallest angiosperm genomes found in Lentibulariaceae, with chromosomes of bacterial size", *Plant Biology*, 2006; Vol. 8: 770-777.
3. Wu Zheng-yi & P. H. Raven et al., eds. 1994-. *Flora of China* (English edition). (F ChinaEng)
4. Blamey M. & Grey-Wilson C., *Flora of Britain and Northern Europe*, 1989; ISBN 0-340-40170-2.
5. López-Bucio J, Campos-Cuevas JC, Hernández-Calderón E, et al, "Bacillus megaterium rhizobacteria promote growth and alter root-system architecture through an auxin- and ethylene-independent signaling mechanism in *Arabidopsis thaliana*", *Mol. Plant Microbe Interact*, 2007; Vol. 20 (2): 207–17.
6. Meinke D.W., Cherry J.M., Dean C., Rounsley S.D., Koornneef M., "Arabidopsis thaliana: A Model Plant for Genome Analysis", *Science*, 1998; 282 (5389): 662–682.
7. Rensink W.A., Buell C.R., "Arabidopsis to Rice. Applying Knowledge from a Weed to Enhance Our Understanding of a Crop Species", *Plant Physiol*, 2004; Vol. 135 (2): 622–9.
8. Coelho S.M., Peters A.F., Charrier B., et al, "Complex life cycles of multicellular eukaryotes: new approaches based on the use of model organisms", *Gene*, 2007; 406 (1–2): 152–70.
9. Platt A., Horton M., Huang Y.S., Li Y., Anastasio A.E., et al, "The Scale of Population Structure in *Arabidopsis thaliana*", *PLoS Gen.*, 2010; Vol. 6 (2).
10. Bennett M. D., Leitch I. J., Price H. J. & Johnston J. S., "Comparisons with *Caenorhabditis* (100 Mb) and *Drosophila* (175 Mb) Using Flow Cytometry Show Genome Size in *Arabidopsis* to be 157 Mb and thus 25% larger than the *Arabidopsis* Genome Initiative Estimate of 125 Mb", *Annals of Botany*, 2003; Vol. 91 (5): 547–557.
11. The *Arabidopsis* Genome Initiative (2000). "Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*", *Nature* 408 (6814): 796–815.
12. Clough S.J., Bent A.F., "Floral dip: a simplified method for *Agrobacterium*-mediated transformation of *Arabidopsis thaliana*", *Plant J*, 1998; Vol. 16 (6): 735–743.
13. Zhang X., Henriques R., Lin S.S., Niu Q.W. & Chua N.H., "Agrobacterium-mediated transformation of *Arabidopsis thaliana* using the floral dip method", *Nat Protoc*, 2006; Vol. 1 (2): 641–6.
14. Moreno N., Bougourd S., Haseloff J. and Fiejo J.A., Chapter 44: Imaging Plant Cells. In: Pawley JB (Editor). *Handbook of Biological Confocal Microscopy - 3rd edition*. SpringerScience+Business Media, New York. 2006: 769-787
15. Shaw S., "Imaging the live plant cell", *The Plant Journal*, 2006; 45 (4): 573–598.
16. Coen E., Henrico S., Meyerowitz E.M., "The war of the whorls: Genetic interactions controlling

flower development", *Nature* 1991; 353 (6339): 31–37.

17. Sullivan J.A., Deng X.W., "From seed to seed: the role of photoreceptors in Arabidopsis development", *Dev. Biol.*, 2003; 260 (2): 289–97.

18. Más P., "Circadian clock signaling in Arabidopsis thaliana: from gene expression to physiology and development", *Int. J. Dev. Biol.*, 2005; 49 (5–6): 491–500.

19. Ruppel N.J., Hangarter R.P., Kiss J.Z., "Red-light-induced positive phototropism in Arabidopsis roots", *Planta*, 2001; 212 (3): 424–30.

20. Lolle S.J., Victor J.L., Young J.M., Pruitt R.E., "Genome-wide non-mendelian inheritance of extra-genomic information in Arabidopsis", *Nature*, 2005; 434 (7032): 505–9.

21. Chaudhury A., "Hothead healer and extragenomic information", *Nature*, 2005; 437(7055): E1–E2.

22. Comai L., Cartwright R.A., (2005). "A Toxic Mutator and Selection Alternative to the Non-Mendelian RNA Cache Hypothesis for hothead Reversion", *Plant Cell* 2005; 17 (11): 2856–8.

23. Peng P., et al., "Plant genetics: Increased outcrossing in hothead mutants", *Nature*, 2006; 443 (7110): E8–E9.

24. Pennisi E., "Genetics: Pollen contamination may explain controversial inheritance", *Science*, 2006; 313 (5795): 1864.

25. Lolle S. J., et al., "Increased outcrossing in hothead mutants (Reply)". *Nature* 2006; 443(7110): E8–E9.

26. Paulsen I. T., Nguyen L., Sliwinski M. K., Rabus R. & Saier M. H. Jr, "Microbial genome analyses: comparative transport capabilities in eighteen prokaryotes", *J. Mol. Biol.* 301, 2000; 75-101.

27. Paulsen I. T., Sliwinski M. K., Nelissen B., Goffeau A. & Saier M. H., "United inventory of established and putative transporters encoded

within the complete genome of *Saccharomyces cerevisiae*", *FEBS Lett.* 430, 1998; 116-125.

28. Hirsch R. E., Lewis B.D, Spalding E. P. & Sussman M. R. "A role for the AKT1 potassium channel in plant nutrition", *Science* 280, 1998; 918-921.

29. Slayman C. L. & Slayman C. W. "Depolarization of the plasma membrane of *Neurospora* during active transport of glucose: evidence for a proton-dependent cotransport system", *Proc. Natl Acad. Sci. USA* 71, 1974; 1035-1939.

30. Ryan C. A. & Pearce G. "Systemin: a polypeptide signal for plant defensive genes", *Annu. Rev. Cell. Dev. Biol.* 14, 1998; 1-14.

31. Kaul Samir et al., "Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*", *Nature*, 2000, Vol. 408.

32. Nordborg Magnus and Bergelson Joy, "The effect of seed and rosette cold treatment on germination and flowering time in some *Arabidopsis thaliana* (brassicaceae) ecotypes", *American Journal of Botany*, 1999; 86(4): 470–475.

33. Baskin J. M., and Baskin C. C., "Ecological life cycle and physiological ecology of seed germination of *Arabidopsis thaliana*." *Canadian Journal of Botany*, 1972; 50: 353–360.

34. Baskin J. M., and Baskin C. C., "Seasonal changes in the germination responses of buried seeds of *Arabidopsis thaliana* and ecological interpretation." *Botanical Gazette*, 1983; 144: 540–543.

35. Koorneef M., and Karssen C. M., "Seed dormancy and germination", In C. R. Somerville and E. M. Meyerowitz [eds.], *Arabidopsis*, 1994; 313–334.

36. Martínez-Zapater J. M., Coupland G., Dean C., and Koorneef M., "The transition to flowering in *Arabidopsis*", In C. R. Somerville and E. M. Meyerowitz [eds.], *Arabidopsis*, 1994; 403–434.
