Biology in Bloom: A Primer on the *Arabidopsis thaliana* Model System

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ABSTRACT *Arabidopsis thaliana* could have easily escaped human scrutiny. Instead, *Arabidopsis* has become the most widely studied plant in modern biology despite its absence from the dinner table. Pairing diminutive stature and genome with prodigious resources and tools, *Arabidopsis* offers a window into the molecular, cellular, and developmental mechanisms underlying life as a multicellular photoautotroph. Many basic discoveries made using this plant have spawned new research areas, even beyond the verdant fields of plant biology. With a suite of resources and tools unmatched among plants and rivaling other model systems, *Arabidopsis* research continues to offer novel insights and deepen our understanding of fundamental biological processes.

KEYWORDS model organism; reference plant

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HUMANS have experimented with plants since the dawn of agriculture. The logic of modern science, the invention of analytical technology, and the adoption of *Arabidopsis thaliana* as a model organism have created an explosion in our understanding of plant structure and function. *Arabidopsis* research has helped form the foundation of modern biology.

Historically, human interactions with plants were often focused on crop yields. Many modern crops have been subjected to millennia of artificial selection and only bear passing resemblance to their wild relatives (Doebley *et al.* 1995; Tanksley and Mccouch 1997). Selection for greater yield and seedlessness has, in many cases, involved polyploidy

(Özkan *et al.* 2002; Rapp *et al.* 2010; Perrier *et al.* 2011), which complicates genetic research. In contrast, the *Arabidopsis* varieties commonly used in laboratories are recently descended from wild plants (Mitchell-Olds 2001) and remain diploid.

Beyond their essential underpinning of human nutrition, plants offer many advantages as research organisms. Compared to most organisms, the metabolic complexity of plants is staggering, offering fertile ground for biochemical research. Plant development is plastic and modular, tolerating many experimental insults. Perhaps the most convenient trait among seed plants is dormancy—seeds can be easily stored and shared. Among plants, *Arabidopsis* is small, grows quickly, and flourishes indoors (Figure 1). A wealth of *Arabidopsis* tools, resources, and shared experiences facilitate efficient generation of data and new understanding.

Arabidopsis History

The ancestors of *A. thaliana* diverged to become a distinct *Arabidopsis* clade ~6 MYA (Hohmann *et al.* 2015). Early descriptions of the plant used aliases. The plant is native to Europe and Asia (Hoffmann 2002), and at the same time that Elizabeth I ruled England and Tycho Brahe was documenting the comet of 1577, the physician Johannes Thal was finishing a book describing the plants of the Harz Mountains in what is now Central Germany. Thal's descriptions included a plant he named *Pilosella siliquata* (Thal 1588). Linnaeus renamed the plant, placing it in the genus *Arabis* and assigning a species name in honor of Thal, hence *Arabis thaliana* (Linnaeus 1753). The plant was later called by the varied appellations *Pilosella thaliana*, *Conringia thaliana*, and *Sisymbrium thalianum* (Holl and Heynhold 1842; Rydberg 1907). When the *Arabis*-like genus *Arabidopsis* was created, the species *thaliana* was initially retained in *Arabis* (De Candolle 1824). Only later was *thaliana* migrated into the genus *Arabidopsis* (Holl and Heynhold 1842). After continuing controversy about the placement of the species into the *Arabidopsis* genus, the Berlin code cemented the name by establishing *Arabidopsis thaliana* as the type for the genus (Greuter *et al.* 1988).

Early observers did not esteem *Arabidopsis*. In *Flora Londinensis*, William Curtis remarked that "we have it frequent enough on our walls, and sometimes on dry ground, about town: and it may be found in great abundance on the south side of Greenwich Park Wall... No particular virtues or uses are ascribed to it" (Curtis 1777). To modern science, *Arabidopsis* is a most useful plant. The number of *Arabidopsis* publications over the last decade has exceeded those of model plants that double as crops like maize and rice, as well as the classic genetic model organism *Drosophila melanogaster* (Figure 2); over 50,000 *Arabidopsis* articles had been published by 2015 (Provart *et al.* 2016). Many of these are cited in articles focused on other organisms, highlighting the fundamental importance of *Arabidopsis* research to biology.

The Utility of *Arabidopsis* as a Model Organism

Arabidopsis research is fast, cheap, and convenient. *Arabidopsis* plants can develop from a seed to a plant bearing mature seeds in as few as 6 weeks, depending on growth conditions (Figure 1). They can grow indoors under feeble fluorescent lighting that is easy to achieve in the laboratory but inadequate for many plants. Seeds and seedlings are small enough to germinate by the hundreds on a single Petri dish. No coculture of any other species is required for *Arabidopsis* to flourish, allowing aseptic growth conditions and maximal control of variables.

Beyond speed and size, several additional features make *Arabidopsis* amenable to genetic research. The genome is small (~132 Mbp) for a plant, with ~38,000 loci, including >20,000 protein-coding genes dispersed among five nuclear chromosomes (Arabidopsis Genome Initiative 2000; Cheng *et al.* 2017). Unlike many genetic models (and many other plants), *Arabidopsis* can tolerate a high degree of homozygosity and is self-fertile; each individual can produce tens of thousands of offspring.

Whereas animals eat, autotrophic plants weave themselves from thin air by capturing carbon dioxide and solar energy. Animal defenses are tooth and claw, horn and hoof. Plants prefer poisons. *Arabidopsis* chemically deters herbivores in part by producing pungent glucosinolates (Hogge *et al.* 1988). Both autotrophy and chemical defenses contribute to the tremendous chemical and enzymatic diversity in *Arabidopsis* that is fertile ground for study.

Unlike most microbial autotrophs, plants are multicellular. The added dimension of differentiation offers exciting research avenues. *Arabidopsis* models most typical features and specialized cell types of seed plants, including perfect flowers ("perfect" referring to the presence of both stamens and carpel; Figure 3), stems, apical meristems, simple leaves, trichomes (defensive leaf hairs; Figure 4), epidermal pavement cells that interlock to form an outer barrier (Figure 5), stomata that open or close to regulate gas exchange between the leaf and atmosphere (Figure 5), roots, root hairs, vascular tissue, pollen (Figure 6), and female gametophytes. Furthermore, as a winter annual, *Arabidopsis* undergoes biphasic development. It first produces a compact set of rosette leaves. Then, given appropriate environmental and genetic factors, the plant develops inflorescences that bear self-fertile flowers and, later, siliques (seed pods) (Figure 1). *Arabidopsis* survival and development are influenced by many environmental signals, including temperature,

doi: https://doi.org/10.1534/genetics.118.300755
Manuscript received September 18, 2017; accepted for publication January 23, 2018.
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photoperiod, and the presence (Figure 7), wavelength, and intensity of light.

Arabidopsis research has revealed the inner workings of other plants. About three out of four gene families present in *Arabidopsis* are present in other flowering plants (Figure 8). Therefore, gene functions discovered in *Arabidopsis* are often similar in other plants (Figure 9). For example, hormones often function similarly across plant species, and the receptors and signaling pathways of almost all plant hormones have been elucidated in *Arabidopsis* (Provart *et al.* 2016).

The *Arabidopsis* Toolkit

Most tools available in nonplant model systems are available in *Arabidopsis*. Forward-genetic screens are routinely initiated by mutagenizing seeds with ethyl methanesulfonate (Koornneef and Van Der Veen 1980), irradiation (Reinholz 1947), fast-neutron bombardment (Timofeev-Resovskii *et al.* 1971), or sodium azide (Blackwell *et al.* 1988). The M_2 progeny of these self-pollinated M_1 plants are then screened for phenotypes of interest, allowing isolation of homozygous recessive mutations. Targeted mutagenesis is also possible, most recently using the CRISPR/Cas9 gene editing system (Li *et al.* 2013). *Arabidopsis* can be transformed using a facile dip of plants that have begun to flower into *Agrobacterium tumefaciens* culture (Clough and Bent 1998). The transferred DNA (T-DNA) that is inserted into the plant genome by *Agrobacterium* as part of the natural lifestyle of the microbe (Yajko and Hegeman 1971) has been modified to include genes or reporters of interest or can be exploited as an insertional mutagen (Alonso *et al.* 2003), allowing for reverse-genetics research (*e.g.*, Figure 7).

Beyond the *Arabidopsis* techniques available to individual research groups, there are useful curated community collections. Mutants can be obtained for reverse-genetics projects from the *Arabidopsis* Biological Resource Center (https://abrc.osu.edu/) or the Nottingham *Arabidopsis* Stock Centre (http://www.arabidopsis.info), which maintain sequence-indexed collections of >30,000 homozygous T-DNA insertional lines (O'Malley and Ecker 2010) from hundreds of thousands of insertion events (Alonso *et al.* 2003). Full-length complementary DNAs for most genes (Yamada *et al.* 2003) also are available from the *Arabidopsis* Biological Resource Center. Further, there are collections of *Arabidopsis* expression vectors (Curtis and Grossniklaus 2003; Earley *et al.* 2006) and yeast two-hybrid vectors (Trigg *et al.* 2017) for conducting overexpression, localization, and interaction studies.

Beyond material resources, there is a wealth of shared *Arabidopsis* data available on The *Arabidopsis* Information Resource (TAIR; www.arabidopsis.org), Araport (www.araport.org), and ePlant (Waese *et al.* 2017; https://bar.utoronto.ca/eplant/). Other shared informational resources include databases of gene expression (Schmid *et al.* 2005; Kilian *et al.* 2007; Winter *et al.* 2007) and protein–protein interactions (Trigg *et al.* 2017). In the realm of proteomics, available data include

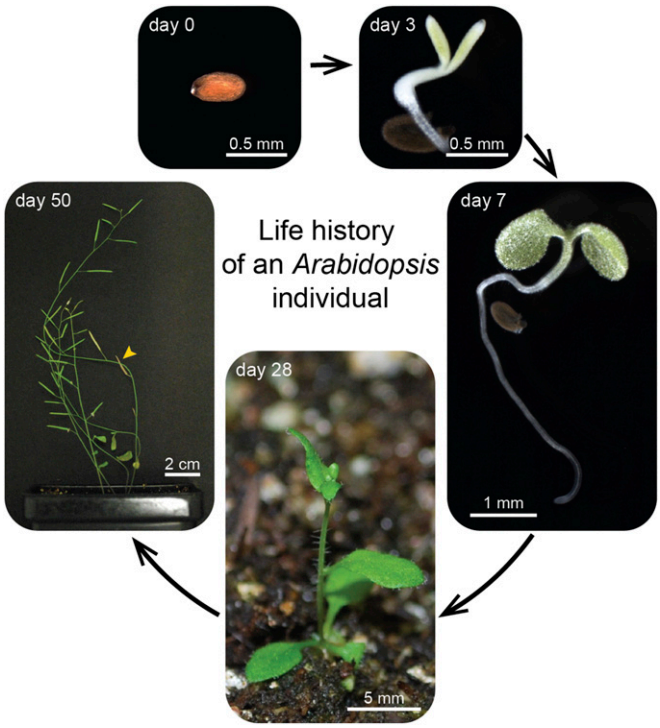

Figure 1 Life history of an *Arabidopsis* plant. The seed was photographed prior to surface sterilization and placement on plant nutrient medium (Haughn and Somerville 1986) solidified with 0.6% (w/v) agar. The plate was sealed against contaminants using surgical tape and incubated vertically at 22° under continuous light. The radicle (embryonic root) had emerged from the testa (seed coat) by 3 days. Green cotyledons (embryonic leaves), emerging true leaves, an expanded hypocotyl (embryonic stem), and an elongated root were apparent by 7 days. After 13 days, the seedling was transferred to soil and grown at room temperature under continuous fluorescent light, then photographed shortly after the transition to flowering (28 days) and after dry seed pods (siliques; arrowhead) containing mature seeds were apparent (50 days).

protein sequences (Baerenfaller *et al.* 2008), membrane protein topology (Schwacke *et al.* 2003), subcellular localization (Hooper *et al.* 2017), phosphorylation (Sugiyama *et al.* 2008), and ubiquitination (Kim *et al.* 2013).

An Educational Model

Arabidopsis is a useful model in the classroom. High school and college students have successfully employed *Arabidopsis* to explore gravitropism (Kiss *et al.* 2000), genetics (Zheng 2006), and genomics (Brooks *et al.* 2011). Experiments with an *Arabidopsis* relative, a set of *Brassica rapa* varieties known as Wisconsin fast plants, also are popular for teaching experiments that explore plant development (Williams 1997). Whereas Wisconsin fast plants have larger structures and fast life cycles (Williams 1997), the wealth of bioinformatics resources, mutants, and published studies that *Arabidopsis* brings to the classroom is unrivaled.

Arabidopsis is almost uniquely suited for undergraduate research projects. Unlike animal model organisms for which the preservation of lineages often involves uninterrupted

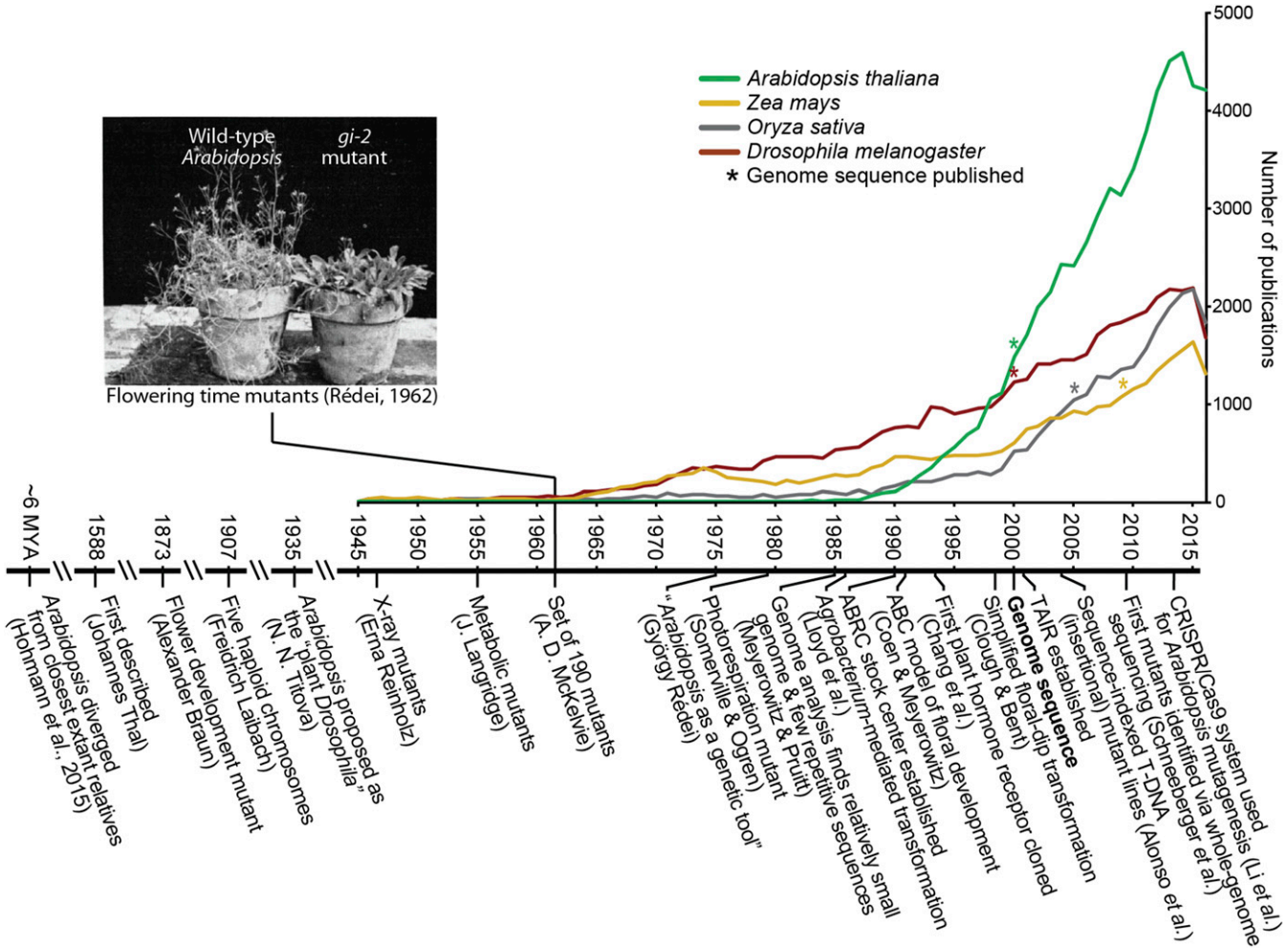

Figure 2 *Arabidopsis* publications and selected milestones. The graph plots the number of publications since 1945 featuring selected model organisms gathered from PubMed (NCBI Resource Coordinators 2017) searches using full genus and species names as search terms. Asterisks indicate the date when the genome sequence was first published for each model. The photograph of wild type and a late-flowering mutant is adapted from an early *Arabidopsis* paper in *Genetics* (Rédei 1962). The timeline highlights selected events in *Arabidopsis* history (Thal 1588; Braun 1873; Laibach 1907; Titova 1935; Reinholz 1947; Langridge 1955; McKelvie 1962; Rédei 1975; Somerville and Ogren 1979; Meyerowitz and Pruitt 1985; Lloyd *et al.* 1986; Coen and Meyerowitz 1991; Chang *et al.* 1993; Clough and Bent 1998; Alonso *et al.* 2003; Schneeberger *et al.* 2009; Li *et al.* 2013; Hohmann *et al.* 2015).

ongoing work, *Arabidopsis* seeds can survive for years without attention at room temperature and even longer with refrigeration. Likewise, there are few ethical and safety concerns with experimental design, treatment, and handling of *Arabidopsis*.

Limitations of the Model

Of course, any single plant species cannot fully embody the characteristics of all others. *Arabidopsis* allows the analysis of many features of plant development, environmental response, and biochemistry. However, not all genes used by other plants are represented in *Arabidopsis* (Figure 8). Likewise, some interesting research problems are intractable in *Arabidopsis*.

The relatively small mass of an *Arabidopsis* plant, advantageous for genetics, can impede the extraction of measurable amounts of sparse biochemicals, and some interesting metabolites are absent from *Arabidopsis* altogether. For example, *Beta vulgaris* (sugar beet) produces betalains, vivid antioxidants (Brockington *et al.* 2011), and the anticancer drug paclitaxel (Taxol) is present in yew trees (genus *Taxus*) but not in *Arabidopsis* (Besumbes *et al.* 2004). Although *Arabidopsis* does not produce wood, a related secondary growth process is present (Dolan and Roberts 1995) and can be stimulated by certain manipulations (Zhao *et al.* 2000).

Some plant cell structures, such as trichomes and chloroplasts, differ in *Arabidopsis* as well. Trichomes are single-cell extensions from the surfaces of leaves and stems (Figure 3). Although *Arabidopsis* genetics has elucidated trichome development [reviewed in Pattanaik *et al.* (2014)], *Arabidopsis* trichomes do not produce the diverse chemical secretions present in many plant species, including tomato, in which glandular trichomes can be investigated (McDowell *et al.* 2011). *Arabidopsis* chloroplasts lack the bacterium-like peptidoglycan cell wall present in many plants and algae, but *Arabidopsis* harbors genes that appear to encode some, but

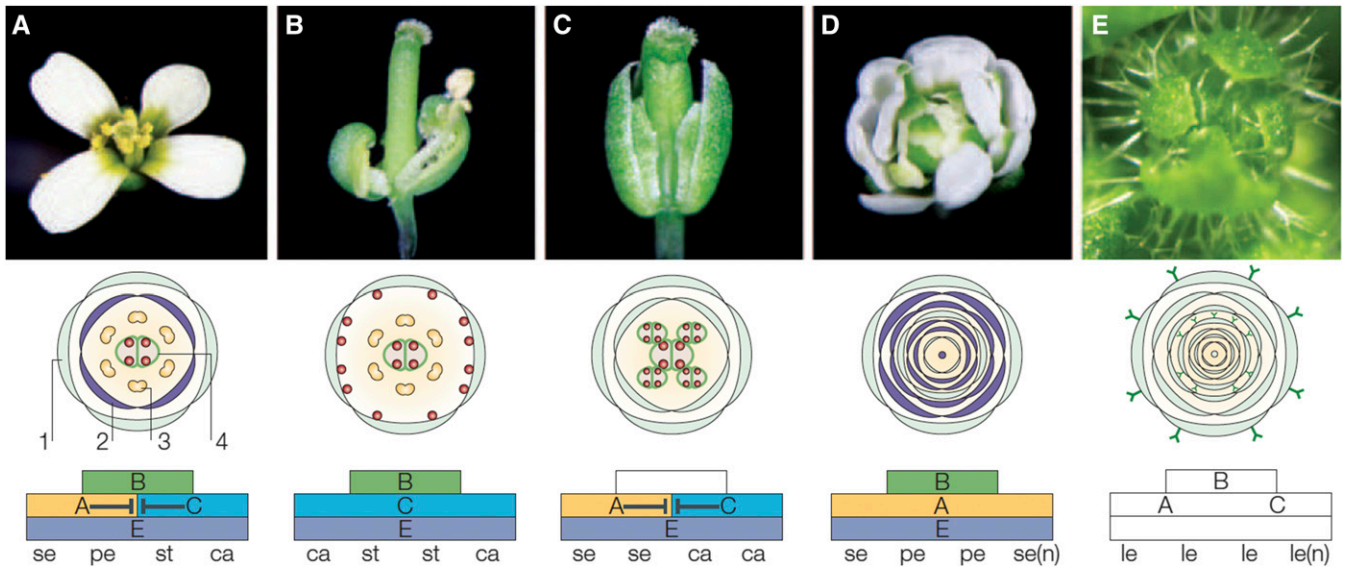

Figure 3 The ABCE model of floral development is supported by *Arabidopsis* research. Wild-type *Arabidopsis* flowers consist of four floral whorls: 1 - sepals (se), 2 - petals (pe), 3 - stamens (st), and 4 - carpels (ca), shown in panel A. Sepals result from the combined activity of A and E genes; petals from B, A, and E genes, stamens from B, C, and E genes, and carpels from C and E genes. A and C genes are mutually repressive. To the right of wild type, four cases of disrupted floral development are shown. (B) In the absence of A-gene activity, only carpels and stamens form. (C) In the absence of B-gene activity, only sepals and carpels form. (D) In the absence of C-gene activity, only numerous sepal and petal structures form. (E) In the absence of E-gene activity, no floral structures form, and the numerous whorls resemble leaves (le), including the presence of leaf hairs (trichomes) decorating the surfaces. Figure modified from Krizek and Fletcher (2005).

not all, of the enzymes for peptidoglycan production. Loss of one such *Arabidopsis* gene in the pathway does not cause any notable phenotype (Hirano *et al.* 2016), suggesting that the genes are vestiges of a lost peptidoglycan biosynthesis pathway in *Arabidopsis*.

Arbuscular mycorrhizal fungi are crucial for nutrient and water absorption and colonize 80% of land plants (Wang and Qiu 2006). *Arabidopsis* flourishes in aseptic conditions in part because it does not associate with mutualistic arbuscular mycorrhizae (Smith and Read 2008). Despite this absence, *Arabidopsis* research has revealed many aspects of the strigolactone chemical signals that promote arbuscular mycorrhizae in other plants (Kohlen *et al.* 2011). Furthermore, although *Arabidopsis* also does not associate with the endosymbiotic bacteria that fix nitrogen, *Arabidopsis* is useful for studying root colonization by the mutualistic fungus *Piriformospora indica* (Jacobs *et al.* 2011) that can facilitate *Arabidopsis* phosphate uptake (Shahollari *et al.* 2005).

Arabidopsis Genetics

Norms and nomenclature

A. thaliana is often indicated simply by the genus name *Arabidopsis*, even though other species within the genus also are subjects of investigation. Some authors consider *Arabidopsis* to be a common name, printing the nonitalicized word with or without capitalization. Other English names for the plant, including Thale cress and mouse-ear cress, are rarely used by researchers.

Arabidopsis genes newly identified through mutant analysis are named for the mutant phenotype (Meinke and Koornneef 1997), whereas those identified via reverse genetics are often named for the encoded protein. Gene names are typically abbreviated to three letters. When a gene that has already been described is rediscovered in a new experiment, the previously published name is often used to avoid creating long lists of synonymous gene names. Genes and genotypes are italicized; protein names are not. Wild-type names are written using capital letters; mutant names are lowercase. A locus number follows the letters to distinguish different genes that can mutate to a given phenotype (for genes identified by mutation) or various homologs (for genes identified by homology), and various alleles of the same gene are enumerated following a hyphen. For example, the *TRANSPORT INHIBITOR RESPONSE1* (*TIR1*) gene encodes the TIR1 protein (Ruegger *et al.* 1998). In this example, the numeral one denotes the first mutant isolated in the transport inhibitor response mutant screen. The tir1-1 protein contains a glycine-to-aspartate change caused by the *tir1-1* missense mutation in the *tir1-1* mutant, whereas the *tir1-9* mutant harbors a T-DNA insertion in the *TIR1* gene (Ruegger *et al.* 1998).

Following the completion of the *Arabidopsis* sequencing project (Arabidopsis Genome Initiative 2000), genes also have standardized names assigned by TAIR. The standard gene name includes *At* for *A. thaliana*, the nuclear chromosome number (or C for chloroplast or M for mitochondrion), and the letter *g* for gene followed by a unique, five-digit numerical identifier that reflects the chromosomal position. In this system, the *TIR1* gene is *At3g62980*, indicating that the gene is on

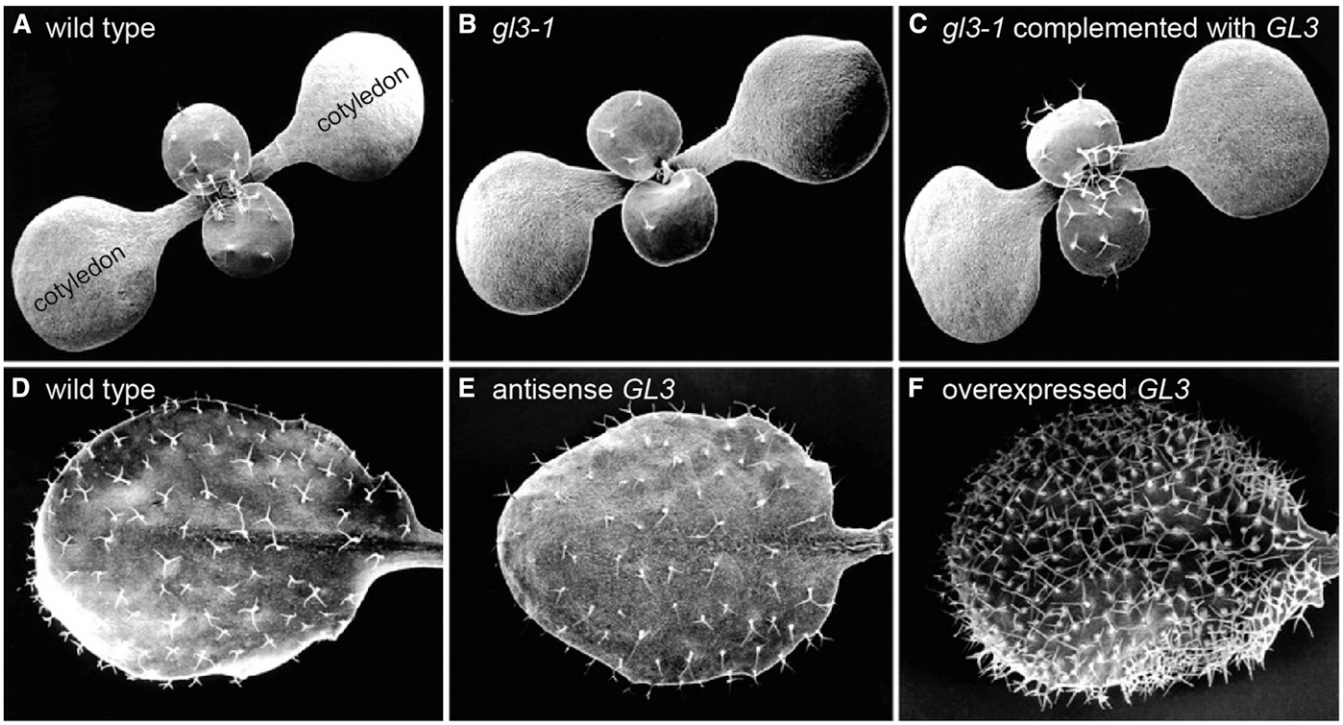

Figure 4 Leaf epidermal development: A gene regulating *Arabidopsis* trichome density. Scanning electron micrographs of (A) wild-type seedlings or (D) leaves show trichomes (leaf hairs) distributed on the top surface of true leaves (A and D) but not cotyledons (A). Reducing function of the GL3 transcription factor by (B) mutation or by (E) expressing a *GL3* antisense construct results in fewer epidermal cells entering the trichome lineage. Introducing a wild-type copy of the gene restores trichome formation on true leaves in *gl3-1* (C), and overexpressing *GL3* in wild type results in excessive trichome formation (F). Figure modified from Payne *et al.* (2000).

chromosome 3 with the large number reflecting a position near the bottom of the chromosome. The original annotators spaced the numbers 10 digits apart, leaving room for discovery of genes overlooked in the first annotation.

Independently collected *Arabidopsis* lineages are known as accessions. *Arabidopsis* "accessions" are groupings within the species analogous to "breeds" within animal species or "varieties" of crop plants. The differences between accessions range from easily distinguished ecotypes to nearly identical plants that were independently collected and named. The most commonly used wild type is Columbia-0 (Col-0); Landsberg *erecta* (L*er*) and Wassilewskija (Ws) are also commonly studied. Although a number of different accessions of Col-0 may have been used for generating the reference *Arabidopsis* genome sequence, the Col-0 accession CS70000 has been proposed by TAIR as the reference stock (Huala *et al.* 2001).

Plant care and growth conditions

Seeds can be germinated directly on the surface of moistened soil. To distribute seeds more evenly when sowing, they can be suspended in a 0.1% (w/v) agar solution and distributed volumetrically using a pipette. It is not necessary to bury the seeds. However, seeds on the soil surface are susceptible to desiccation, and plastic domes or tented plastic wrap can be used to reduce evaporation for the first week or longer. If atmospheric humidity is low, plants may be damaged by sudden removal of the cover, and partially removing the plastic dome or cutting slits in plastic wrap a few days before entirely removing the cover aids survival.

For more carefully controlled experiments, such as those using specific additives or investigating aspects of root development, seedlings can be germinated and grown on sterile media in Petri dishes. For this purpose, seeds are first surface sterilized (gently enough not to kill the embryo) using bleach and detergent (Haughn and Somerville 1986), ethanol (Nelson *et al.* 2009), or other disinfectants. Two types of media are commonly used: (MS) medium (Murashige and Skoog 1962) and plant nutrient (PN) medium (Haughn and Somerville 1986). MS offers the convenience of commercial, premeasured media packets. PN medium is less convenient, requiring preparation of several stock solutions and mixing of these stocks for each batch of medium (Haughn and Somerville 1986), but offers more user control over the composition of the growth medium. Media may be supplemented with sucrose to promote even germination and to allow the early development of certain metabolic mutants (Pinfield-Wells *et al.* 2005). Even mutants that require supplemented growth medium for germination can often survive transfer to soil once established (Zolman *et al.* 2000). Transfer to soil is generally required for a robust seed set.

It is possible to grow *Arabidopsis* in soil or aseptically on plates in ambient air under common lights, including LED, fluorescent, or incandescent bulbs. Lighted plant growth chambers allow precise control of day length and circulate air to maintain

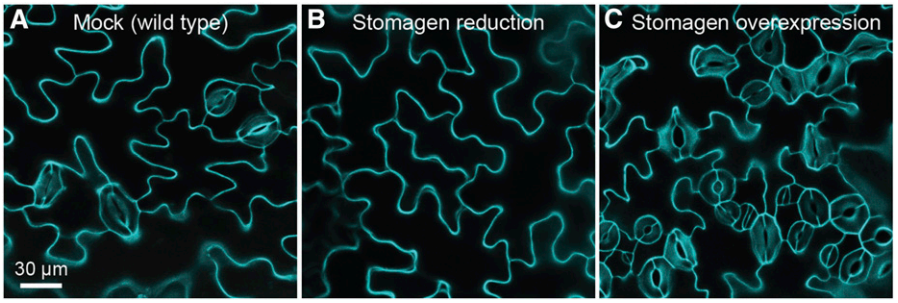

Figure 5 Tissue-level research: A secreted peptide controlling differentiation of *Arabidopsis* stomata. Confocal micrographs show the top surface of cotyledons from 10-day-old seedlings stained with propidium iodide to outline epidermal cells. (A) Stomata, the two-celled pores that regulate gas exchange, are distributed among interlocked pavement cells in wild type. Decreasing (B) or increasing (C) levels of the stomagen peptide eliminates or increases, respectively, formation of stomata (Lee *et al.* 2015). Images provided by Jin Suk Lee and Keiko Torii.

stable, user-defined temperatures while limiting condensation in closed Petri dishes. For experiments testing responses to light or to protect photosensitive chemicals, LED-equipped growth chambers offer fine control of light wavelength and intensity. Alternatively, white light can be filtered through colored plastic sheets (Stasinopoulos and Hangarter 1990), or plates can be wrapped in foil to provide darkness. To test plant responses to other environmental parameters, some incubators can regulate humidity and atmospheric gases such as carbon dioxide.

Arabidopsis plants generally self-pollinate, but the small flowers can be manually crossed with some practice. The ovules of a flower are receptive before the pollen is mature. Therefore, the sepals, petals, and anthers are removed from a recipient (female) unopened flower bud with forceps and then anthers from a mature (open) donor flower are used to dust the exposed stigmatic papillae with pollen. F_1 seeds are ready for harvest in ~2 weeks.

Breakthrough Discoveries Made using Arabidopsis

Many biological processes were first discovered in *Arabidopsis* (Provart *et al.* 2016). Other research areas that were initiated in other organisms prompted major discoveries when advanced in *Arabidopsis*. Below, we sample a few items from the smorgasbord.

Novel insights in biochemistry and plant development

In hot, dry conditions, plants sometimes capture oxygen rather than carbon dioxide during the photosynthetic Calvin–Benson cycle. This photosynthetic flaw impedes the productivity of most crops (Walker *et al.* 2016). The resulting products can be salvaged in a process called photorespiration, collaboratively achieved by chloroplasts, peroxisomes, and mitochondria (Bauwe *et al.* 2010). Much of the photorespiratory pathway was revealed using *Arabidopsis* genetics (Somerville 2001). Furthermore, introducing certain *Escherichia coli* genes into *Arabidopsis* decreases the need for photorespiration and increases the efficiency of photosynthesis (Kebeish *et al.* 2007), providing proof-of-concept work that might be applied to improve crop productivity.

Arabidopsis research was key to developing the ABCE model of floral development (Figure 3). Data from a collection of *Arabidopsis* and *Antirrhinum majus* (snapdragon) mutants converged to reveal a set of conserved MADS-box transcription factors that, combined, specify the identity of each whorl (ring) of flower organs (Coen and Meyerowitz 1991). In this model, E-class genes are needed for all floral structures. The combination of A and E activity generates sepals, the leaf-like outer whorl. A, B, and E activity yields petals. B, C, and E activity produces stamens, the pollen-bearing male structures. Finally, C and E activity produces the innermost carpel (female) reproductive structures (Krizek and Fletcher 2005). Developed using *Arabidopsis* and snapdragon data, the ABCE model of flower development explains floral structures in a variety of plants (Di Stilio 2011).

Arabidopsis offers insight into a host of other plant developmental and cellular processes. One example is the formation of elegant epidermal architecture. Leaves of most plants are decorated with trichomes, or leaf hairs. The isolation of *Arabidopsis* mutants with sparse or abundant trichomes has revealed that trichome density is regulated by bHLH, MYB, and WD40 transcription factors. The bHLH protein GLABRA3 (GL3) promotes the formation of trichomes (Payne *et al.* 2000); reduced *GL3* expression results in few trichomes, whereas overexpression increases trichome density (Figure 4). Intriguingly, many of the same transcription factors that regulate trichome formation also are used to regulate formation of root hairs (Schellmann *et al.* 2002), the protrusions from single root epidermal cells that increase root surface area.

Stomata are pores allowing gas exchange that are spaced among the beautifully jigsaw-shaped pavement cells of the leaf epidermis. In stomatal development, the stomagen signaling peptide plays a similar role to GL3 in trichome formation. Decreased stomagen decreases formation of stomata whereas stomagen overexpression increases stomatal density (Figure 5).

Advances in cell and molecular biology

Arabidopsis also offers a window into plant subcellular structures. Although most of the typical eukaryotic organelles are present, there are some special structures, and familiar organelles sometimes take on specialized functions in plant cells. Plastids, including chloroplasts and a variety of other specialized versions, are cyanobacteria-like organelles that conduct photosynthesis but also impart fruit colors, assist in gravity detection, and play key roles in plant metabolism and development. Much fundamental knowledge of plastid function emerged from *Arabidopsis* (Martin *et al.* 2002; Singh *et al.* 2015; van Wijk and Kessler 2017).

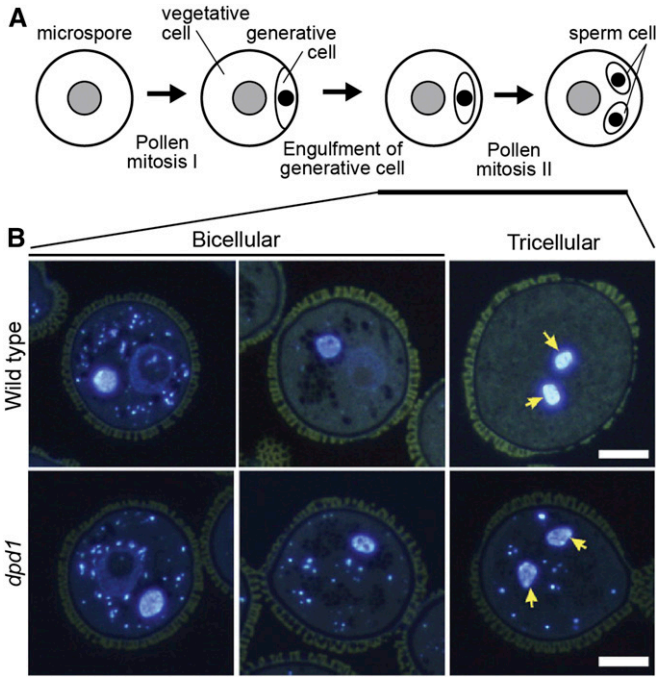

Figure 6 Subcellular research in *Arabidopsis*: Pollen organellar DNA degradation. (A) Microspore cells develop into pollen by two rounds of mitosis, producing two sperm cells within a generative cell. (B) shows microscopic sections at different developmental stages with DNA stained blue using DAPI. In wild type, organellar DNA in the vegetative cell is degraded. The *dpd1* mutant, defective in an exonuclease, has persistent organellar DNA (plastidial and mitochondrial) through the tricellular stage of development. Yellow arrows indicate nuclear DNA visible in the selected section at the tricellular stage of development. Figure modified from Matsushima *et al.* (2011) with permission from the American Society of Plant Physiologists.

Figure 7 *Arabidopsis* at the intersection of genes and environment: Sensitivity to extended darkness in autophagy mutants. Reverse-genetics mutants carrying T-DNA insertions in genes essential for autophagy (*atg* mutants) fail to recover from the return to light after extended darkness. Figure modified from Phillips *et al.* (2008).

Among other fascinating processes, the complex dance of the alternation of generations is subject to dissection in *Arabidopsis*. Morphologically, this flowering-plant lifestyle involves the formation of male and female gametophytes within the larger sporophyte plant body (Rudall and Bateman 2007). Remarkable processes occur at the cellular level, also. For example, during pollen development the formation of two sperm cells within a surrounding vegetative cell is accompanied by degeneration of the plastids and mitochondria of the vegetative cell (Figure 6). Thus male gametophyte development is reminiscent of animal spermatogenesis, wherein spermatogonia develop within Sertoli cells, and sperm mitochondria usually degenerate after fertilization (Griswold 2016). Unlike in animals, the two sperm cells are used for double fertilization to produce both embryo and endosperm tissues in angiosperm plants (Hamamura *et al.* 2011).

The first plant microRNAs (miRNAs) were discovered in *Arabidopsis* (Llave *et al.* 2002a; Park *et al.* 2002; Reinhart *et al.* 2002). ARGONAUTE, a key component of the RNA-Induced Silencing Complex (RISC) through which miRNAs act, was first discovered in *Arabidopsis* (Bohmert *et al.* 1998) thanks to the leaf deformities resulting from missing miRNA regulation in the *ago1* mutant. Likewise, phased miRNA-directed *trans*-acting small interfering RNAs were first found in *Arabidopsis* (Allen *et al.* 2005). Moreover, the high complementarity between plant miRNAs and their targets allowed systematic, high-confidence miRNA target identification (Rhoades *et al.* 2002) and validation (Llave *et al.* 2002b; Mallory *et al.* 2004) well before such predictions were feasible in metazoans.

Signaling pathway breakthroughs

The diverse discoveries from the field of light response offer a case study in *Arabidopsis* utility. Although *Arabidopsis* research has revealed novel proteins and processes, most *Arabidopsis* research grew up in the shadow of other plants. For example, Charles Darwin and his son Francis conducted pioneering experiments investigating plant phototropisms—growth toward or away from light—in oat (*Avena*), canary grass, asparagus, and beet, as well as the *Arabidopsis* cousins white mustard and *Brassica oleracea* (Darwin and Darwin 1880). It was >100 years before pea proteins were isolated that had characteristics consistent with being a phototropin receptor (Gallagher *et al.* 1988). Ultimately, the gene encoding the blue-light photoreceptor responsible for phototropism, *NPH1/PHOT1*, was identified via analysis of an *Arabidopsis* mutant that was blind to blue light (Liscum and Briggs 1995), and the photoresponsiveness of the *Arabidopsis* protein was confirmed in an insect heterologous system (Christie *et al.* 1998).

Plant hormone research is also rooted in the Darwin tropism experiments. The Darwins interpreted their data to "imply the presence of some matter in the upper part which is acted on by

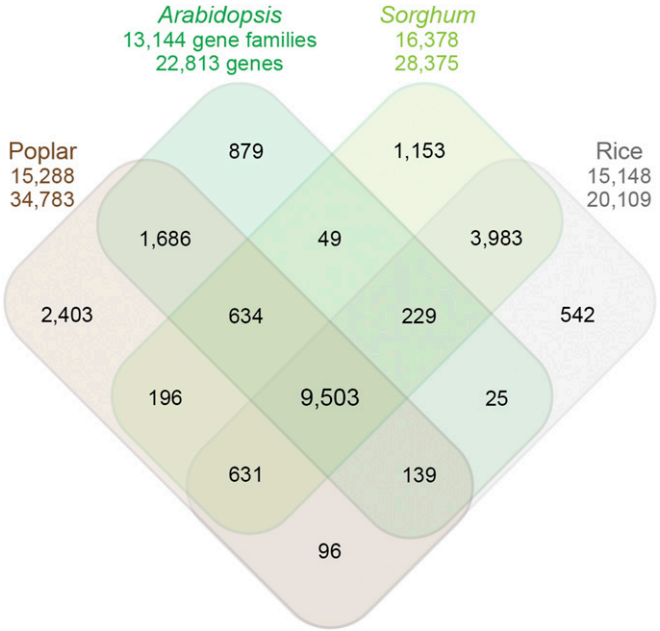

Figure 8 Comparative genomics of *Arabidopsis thaliana*, *Populus trichocarpa* (poplar) trees, and the grain crops *Sorghum bicolor* and *Oryza sativa* (rice). The number of genes and gene families for each species is shown. The Venn diagram shows the number of unique and shared gene families. *Arabidopsis* and *Populus* are dicotyledonous plants; *Sorghum* and rice are monocots. Approximately two-thirds of *Arabidopsis* gene families (9503) are shared among all of these plant species. Figure modified from Paterson *et al.* (2009) with permission from Springer Nature.

Figure 9 Translational research: *Arabidopsis* MYB12 increases tomato flavonol content. Wild-type tomatoes of the Micro-Tom variety are red (top). When an *Arabidopsis* gene that increases phenolic content is introduced into tomato, the increase in yellow flavonols in the presence of the typical red lycopene results in an orange appearance (bottom). Thus, the gene has a similar impact on this crop plant as was first demonstrated in *Arabidopsis*. Image modified from Zhang *et al.* (2015).

light, and which transmits its effects to the lower part" (Darwin and Darwin 1880). Indeed, subsequent experiments in oat revealed a diffusible chemical signal (Went 1926), later named auxin (Kögl and Haagen Smit 1931). The long-sought receptors for auxin were discovered via genetic approaches in *Arabidopsis* (Ruegger *et al.* 1998; Dharmasiri *et al.* 2005; Kepinski and Leyser 2005). Interestingly, the auxin receptors belong to a class of proteins not previously suspected to act as receptors. F-box proteins are the specificity-determining components of Skp1-Cullin-F-box (SCF) complexes that target proteins for ubiquitination and degradation (Zheng *et al.* 2002). The receptor role was first discovered for the *Arabidopsis* TRANSPORT INHIBITOR RESPONSE1 (TIR1) F-box protein that is sufficient to target AUX/IAA transcriptional repressors for degradation in heterologous systems (Dharmasiri *et al.* 2005; Kepinski and Leyser 2005). Likewise, the F-box CORONATINE-INSENSITIVE1 (COI1) protein, also discovered through *Arabidopsis* forward genetics, is a receptor for the jasmonate phytohormone (Sheard *et al.* 2010). In a fascinating parallel, auxin and jasmonate (jasmonoyl-L-isoleucine) molecules bind between the F-box protein and the targeted repressor, stabilizing the interaction to ensure target protein ubiquitination and degradation (Tan *et al.* 2007; Sheard *et al.* 2010). Both the F-box and the target protein participate in hormone binding and can therefore be considered coreceptors. Like with auxin and jasmonate, the hormones gibberellin and strigolactone also signal through F-box proteins that promote the destruction of repressors in the corresponding pathways (Morffy *et al.* 2016).

Arabidopsis mutants that fail to respond appropriately to the absence of light allowed the discovery of the COP9 signalosome, a multiprotein complex that regulates ubiquitination enzymes. The *de-etiolated* (*det*) and *constitutive photomorphogenic* (*cop*) mutants develop in darkness as if they were growing in light: In darkness, these mutants expand their cotyledons, fail to elongate their hypocotyls (embryo-derived stems), and accumulate the normally light-induced anthocyanin pigments (Chory *et al.* 1989; Deng *et al.* 1991). In fact, several of these *cop* and *det* mutants are allelic with *fusca* (*fus*) mutants that were isolated because they accumulate excess anthocyanins in seeds (Müller 1963; Castle and Meinke 1994). The genes identified in these *Arabidopsis* mutant screens encode the founding members of the COP9 protein regulatory complex (Wei and Deng 1992, 2003). Later discovered in other organisms, the COP9 signalosome is now of key interest in cancer formation and therapy (Schlierf *et al.* 2016).

Insights from Comparing Arabidopsis to Other Organisms

Arabidopsis is also an effective platform for reverse-genetic research. In one application of reverse genetics, a documented function in another organism inspires a hypothesis of similar function for the closest-related *Arabidopsis* genes (Krysan *et al.* 1996). For example, components of the autophagy pathway involved in degrading cellular aggregates and organelles were first identified in yeast (Tsukada and Ohsumi 1993). When mutants carrying T-DNA insertions in the closest *Arabidopsis* homologs of yeast autophagy genes were examined, autophagy-defective phenotypes were indeed observed (Phillips *et al.* 2008).

This work allowed the discovery of plant-specific roles for autophagy, including recovery from darkness-induced starvation (Figure 7; Phillips *et al.* 2008).

Arabidopsis data and components have been used in translational projects in crop plants. For example, the *Arabidopsis* transcription factor MYB12 stimulates the production of flavonol chemicals (Mehrtens *et al.* 2005). Flavonol intake is correlated with markers of cardiovascular health (Perez-Vizcaino and Duarte 2010), so increasing crop flavonol content is an attractive ambition. Expressing *Arabidopsis MYB12* in tomato had the hypothesized effect of increasing flavonol content, profoundly enough to change fruit color from red to orange (Figure 9; Luo *et al.* 2008).

Research using *Arabidopsis* has greatly expanded our knowledge of plants—the organisms that provide most human nutrition and atmospheric oxygen—and revealed key, common processes in diverse organisms beyond plants. With the application of inexpensive whole-genome sequencing (Ossowski *et al.* 2010; Yamamoto *et al.* 2010) and CRISPR/Cas9-based gene editing tools (Jiang *et al.* 2013; Li *et al.* 2013), many plants are now amenable to analysis that was once only feasible in *Arabidopsis*. Nonetheless, the depth of understanding and ease of manipulation in the *Arabidopsis* system is unrivaled, and *Arabidopsis* will remain the reference plant for the foreseeable future. Careful cultivation of an obscure garden weed has taught us much about both the garden and the gardener.

Acknowledgments

We thank Jin Suk Lee, Keiko Torii, and Richard Vierstra for images and Abigail Garcia, Kim Gonzalez, Kathryn Hamilton, Yun-Ting Kao, Roxanna Llinas, Michael Passalacqua, Melissa Traver, Pierce Young, Zachary Wright, and two anonymous reviewers for helpful comments on the manuscript and Dominic Palesch for assistance with translation. We apologize to the many *Arabidopsis* researchers whose work we could not highlight in this sampling because of length limitations. Our research is funded by faculty development grants from The University of Mary Hardin-Baylor Provost (to A.W.W.), the National Institutes of Health (R01GM079177 to B.B.), the National Science Foundation (MCB-1516966 to B.B.), and the Robert A. Welch Foundation (C-1309 to B.B.).

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Communicating editor: E. De Stasio