

Field Guide to Plant Model Systems

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For the past several decades, advances in plant development, physiology, cell biology, and genetics have relied heavily on the model (or reference) plant *Arabidopsis thaliana*. *Arabidopsis* resembles other plants, including crop plants, in many but by no means all respects. Study of *Arabidopsis* alone provides little information on the evolutionary history of plants, evolutionary differences between species, plants that survive in different environments, or plants that access nutrients and photosynthesize differently. Empowered by the availability of large-scale sequencing and new technologies for investigating gene function, many new plant models are being proposed and studied.

Introduction

Arabidopsis thaliana has been the major plant model system in the past three decades, allowing for tremendous advances in our understanding of plant development, signaling, hormone biology, pathogen defense, disease resistance, and abiotic stress response, to name a few (Provart et al., 2016). Discoveries in *Arabidopsis* (a eudicot) have been applicable to many other plant species (Piquerez et al., 2014; Provart et al., 2016) and have also impacted our understanding of human biology (Jones et al., 2008). One indication of the concentration upon, and utility of, this reference plant is that there are more papers published on *Arabidopsis* every year than there are on each of *Saccharomyces*, *Caenorhabditis*, Zebrafish, Chicken, or *Drosophila*, the predominant non-mammalian fungal and animal models (Dietrich et al., 2014). *Arabidopsis* is only one species, however, growing in a limited set of environments. *Arabidopsis*, like other members of the Brassicaceae family, has limited symbiotic relations with soil microorganisms, an annual lifestyle, C3 photosynthesis (one of several photosynthetic options), and the typical dicotyledonous ways of development. Most of our crop plants are grasses (monocots) with their own specialized physiology, while many others are legumes that fix nitrogen from the air, something *Arabidopsis* does not do. Furthermore, monocots and eudicots, such as *Arabidopsis*, are both angiosperms (flowering plants) and encompass only a small fraction of the evolutionary breadth of plants. The world of plants encompasses more than 400,000 species of angiosperms, gymnosperms, ferns, lycophytes, hornworts, mosses, liverworts, and green algae (Figure 1) representing immense biodiversity in terms of their ecosystems, architecture, biochemistry, reproductive systems, and much more. To understand the specifics of the growth of crop plants on the one hand and the diversity and evolutionary history of land plants on the other, requires study of additional species.

The properties that make a model system are of three types. The initial choice typically involves practical reasons such as economic value, or intrinsic properties that suit the species chosen

for laboratory use such as small size, ease of culture, fecundity, short generation time, amenability to genetic manipulations such as crossing and mutagenesis, small genome size, and the potential to manipulate gene function. As adoption proceeds, two other types of properties are added—initially they are what might be called derived properties, such as standardized and simple procedures for DNA and RNA isolation, transformation, protein extraction, and other laboratory methods. Then, as a community of users develops, the third set of reasons to use the model are developed—community properties, such as availability of genetic strains, reporter constructs, thoroughly annotated genomes, and repositories, databases, and stock centers. Proposals to use *Arabidopsis thaliana* due to intrinsic properties date as far back as the 1940s (Laibach, 1943), and there was a seed stock center by the 1960s (Röbbelen 1965; Kranz and Kirchheim 1987). Widespread adoption of *Arabidopsis* began in the 1980s (Koornneef and Meinke, 2010; Meyerowitz and Pruitt, 1985; Somerville and Koornneef, 2002), and new seed and DNA stock centers were founded in the 1990s. The fully annotated genome (135 Mb) with 27,416 annotated genes (http://plants.ensembl.org/Arabidopsis_thaliana/Info/Annotation/#assembly) was complete in 2000, and by now, this species of flowering plant is central to much of the research in plant biology (Provart et al., 2016). While past model systems were chosen for practical reasons (e.g. crop plants) and/or intrinsic ones (e.g., *Arabidopsis*), the ease of genome sequencing and improved reverse genetic tools, such as TILLING (Targeting Induced Local Lesions IN Genomes), RNAi, and CRISPR/Cas9 now allow for an expansion of models that can be based on other types of considerations, such as phylogenetic relationships. Table 1 lists some of the existing and emerging plant models and reflects the current extent of sampling of taxonomic diversity among plant species.

Algal Relatives of Land Plants

Green algae were the photosynthetic predecessors of land plants prior to the evolutionary transition to the terrestrial

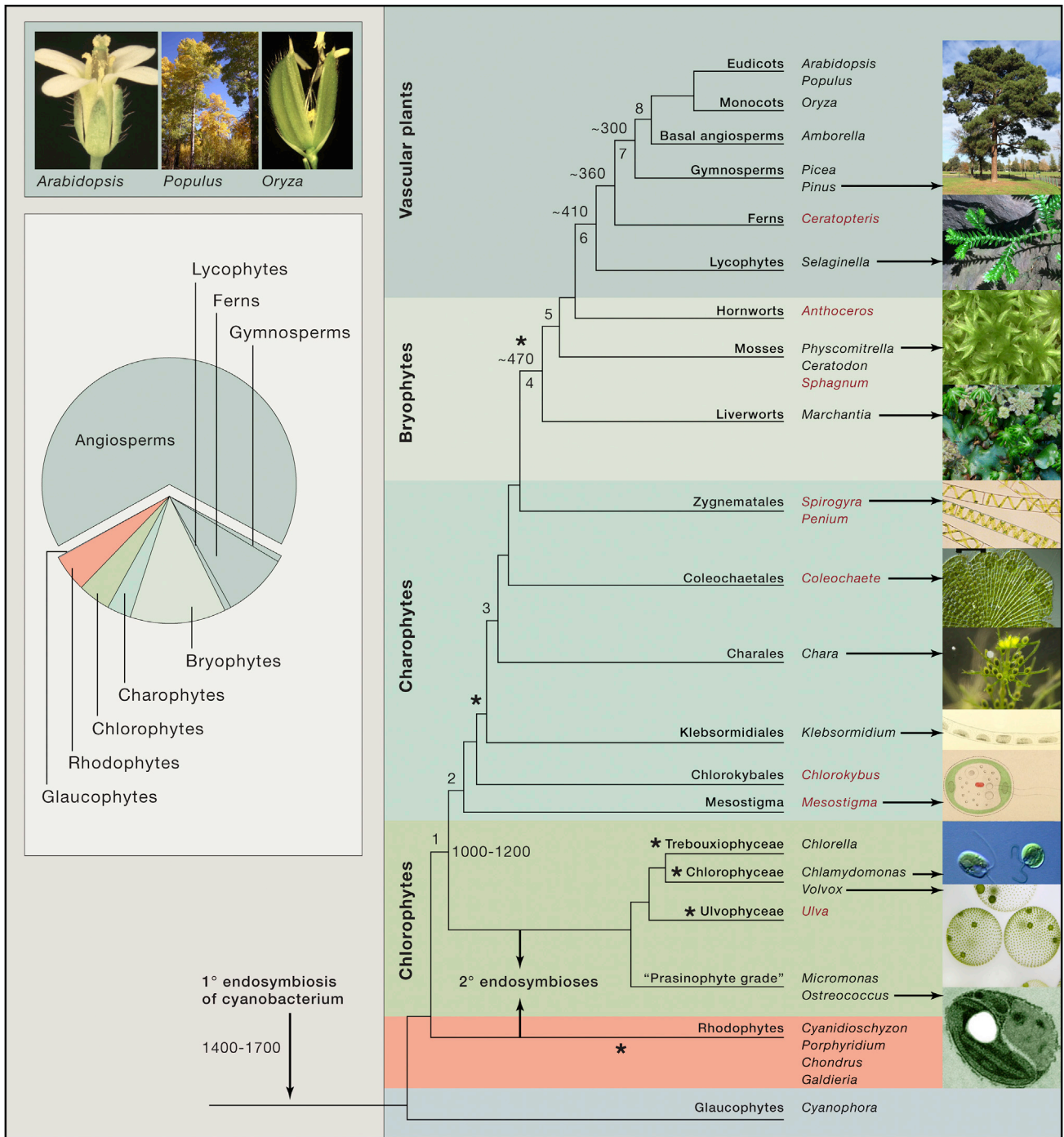


Figure 1. Plant Diversity

Depicted are relationships among the major lineages of plants: glaucophytes (freshwater algae), rhodophytes (red algae), and the Viridiplantae (chlorophytes, charophytes, and land plants [vascular plants and bryophytes]). Estimated dates for some nodes are listed in millions of years before present. The primary endosymbiotic event is estimated to have occurred at least 1.6 billion years ago. A deep split occurred within the green lineage creating the chlorophytes and the charophytes plus land plants. Note that both the charophytes and the bryophytes are grades and are not monophyletic. Key evolutionary innovations are indicated at some nodes: (1) chlorophyll a and b, highly developed chloroplast grana; (2) lateral flagella; (3) phragmoplast, plasmodesmata, apical cell growth; (4) alternation of generations (embryo), sporopollenin, three-dimensional organization, archegonia and antheridia; (5) stomata; (6) vasculature (xylem and phloem), sporophyte dominant; (7) seeds, loss of archegonia and antheridia, pollen; and (8) flowers, carpels, outer integument. Evolution of simple multicellularity (differentiation largely limited to soma and gametes) and complex multicellularity (3-dimensional tissue differentiation) are indicated by *. Taxa in red represent those whose genome sequencing are either in progress or proposed or reside at critical evolutionary positions (*Mesostigma*, *Coleochaete*). Secondary endosymbiotic events have occurred from both the red and green algal lineages. The relative species richness of the major clades is depicted in the pie chart. The

(legend continued on next page)

environment. There are two major divisions of green algae, the monophyletic chlorophytes and the paraphyletic charophytes (Figure 1), which diverged from each other well over a billion years ago (Yoon et al., 2004). Both divisions contain chlorophyll a and b, photosynthetic plastids, and cellulosic cell walls. Chlorophytes include *Chlamydomonas reinhardtii*, which is the classical model system for unicellular algae, with a long history of genetic and genomic approaches based on its intrinsic and derived properties (Harris, 2001; Merchant et al., 2007). *Chlamydomonas* can grow either photosynthetically or on acetate as a carbon source, so it is amenable to the mutational study of photosynthesis. *Chlamydomonas* bears two flagella (flagella were lost in the course of seed plant evolution (Renzaglia and Garbary, 2001; Hodges et al., 2012), and therefore, *Chlamydomonas* has also been used extensively and productively in the study of flagellar and basal body growth and function.

Close relatives of the single-celled *Chlamydomonas* include multicellular species, an example being *Volvox carteri* (131.2 Mb; 14,247 protein-coding loci) whose bodies consist of about 2,000 somatic cells and 16 germ cells (Prochnik et al., 2010). Other members of the Volvocales, to which both *Chlamydomonas* and *Volvox* belong, exhibit intermediate levels of complexity. Comparative genomic studies within this group may provide insights into the evolution of multicellularity and organismal complexity.

With its unique features, another chlorophyte, the unicellular marine alga *Ostreococcus tauri*, has attracted interest as a “minimalist” model cell. *Ostreococcus* is the smallest known free-living eukaryotic organism and is commonly found in phytoplankton. Just 0.8 μm in diameter (Courties et al., 1994), the cell has a single nucleus, a single mitochondrion, a single Golgi body with typically 5 (up to 7) cisternae, and a single chloroplast. The ultrastructure of the cell has been determined at high resolution throughout its life cycle by cryoelectron tomography, which has revealed the cell to have just one microtubule (or two in pre-divisional cells), despite having 20 chromosomes (haploid number) to segregate in mitosis (Henderson et al., 2007). This tiny cell has only about 1,250 ribosomes (compared to 200,000 in a *Saccharomyces cerevisiae* cell) (Henderson et al., 2007). The sequenced genome is small (12.56 Mb) but has a very high gene density, with 8,166 annotated genes and intergenic regions averaging <200 bp (Derelle et al., 2006). *Ostreococcus* is easy to culture and grows rapidly. Gene analysis indicates the possibility that *Ostreococcus* has C4 photosynthesis (Derelle et al., 2006), and genome-wide metabolic network analysis has allowed a complete metabolic map (with some hypothetical reactions added) showing many additional features (Krumholz et al., 2012).

Chlorophyte algae, such as *Chlamydomonas* and *Ostreococcus*, are quite distantly related to land plants. The closest

living relatives of land plants reside among the other division of green algae known as charophytes (Figure 1). Charophytes are a relatively small group of morphologically diverse freshwater and terrestrial green algae that encompass unicellular and filamentous forms, as well as structurally complex multicellular forms (Delwiche and Cooper, 2015). Land plants arose as a monophyletic group from charophyte green algae ~450 million years ago in the Ordovician Period (Delwiche and Cooper, 2015). As the closest living relatives of land plants, extant charophytes could provide insights into the origins of adaptations that allowed for the evolutionary transition to terrestrial life (Hartmann et al., 2016; Delwiche and Cooper, 2015).

Despite their phylogenetic importance, charophytes have been relatively understudied and thus lack many derived and community model system properties, including axenic cultures and methods for manipulating the complete life cycle. Recent efforts, however, suggest that charophytes may be poised to become model systems, thereby filling a large phylogenetic gap between chlorophyte algae and land plants. The first charophyte draft genome sequence (104 Mb) was recently published for *Klebsormidium flaccidum* (Hori et al., 2014), a filamentous alga in one of the basal charophyte lineages. Also available are de novo transcriptome assemblies for representative species within each of the five major charophyte lineages (Ju et al., 2015), including a desiccation response transcriptome of *Klebsormidium* (Holzinger et al., 2014). Efforts are currently underway to sequence the genomes of additional species across all the charophyte lineages. Recent studies have indicated conservation of certain plant systems in charophyte algae, including plant hormones (Holzinger and Becker, 2015; Ju et al., 2015; Viaene et al., 2013; Delaux et al., 2012), cell wall biochemistry (Domozych, 2014), and stress responses (Holzinger et al., 2014). Ethylene hormone signaling homologs in the filamentous charophyte *Spirogyra pratensis* show remarkable functional conservation with the *Arabidopsis* ethylene signaling pathway, suggesting that this hormone pathway was present in the aquatic common ancestor prior to the colonization of land (Ju et al., 2015). *Spirogyra* is within the Zygnematophyceae, a species-rich charophyte lineage that is likely to be the closest sister taxon to land plants (Delwiche and Cooper, 2015). Stable transformation has been reported for two other Zygnematophyceae species (Sorensen et al., 2014; Abe et al., 2011), including the unicellular *Penium margaritaceum*. *P. margaritaceum* is being used to study the evolution of the plant cell wall, an essential adaptation for both structural support and biotic defense for life on land (Domozych, 2014).

Land Plant Evolution

Land plants are distinguished from their algal relatives by life cycle and by morphological and physiological characteristics

vast majority of species within the Plantae are angiosperms (350,000 species), with other groups having substantially fewer described species (numbers approximated): glaucophytes, 21; rhodophytes, 7095; chlorophytes, 6263; charophytes, 4644; bryophytes, 18,200 (liverworts, 7,270; mosses, 11,000; hornworts, 215); lycophytes, 1225; ferns, 12,000; and gymnosperms, 1000.

Photos from top: *Pinus radiata*, *Selaginella kraussiana*, *Physcomitrella patens*, *Marchantia berteroana*, *Spirogyra* sp., *Coleochaete orbicularis*, *Chara* sp., *Klebsormidium flaccidum*, *Mesostigma viride*, *Chlamydomonas reinhardtii*, *Volvox* sp., and *Ostreococcus tauri*. Thanks to individuals who generously provided photos of poplar (Gayle Dupper, Institute of Forest Genetics, Placerville), *Physcomitrella* (Keiko Sakakibara), *Spirogyra* (Bram Van de Poel, University of Maryland), *Coleochaete*, *Chara* (Charles Delwiche, University of Maryland), *Chlamydomonas* (James Umen, Salk Institute), *Volvox* (Frank Fox, www.mikro-foto.de), and *Ostreococcus* (Hervé Moreau, Université Pierre et Marie Curie-Paris). Other photos by J. L. B. *Mesostigma* image from (Lauterborn, 1898) and *Klebsormidium* image from (Klebs, 1896). Figure adapted from Bowman et al. (2007).

Table 1. Some Existing and Emerging Plant Models

Classification	Family	Species Name	Genome Size (Mb) ¹	Genome Sequence Status	Properties	References
Angiosperm eudicot	Brassicaceae	<i>Arabidopsis thaliana</i> (mouse-ear cress)	135	complete	predominant plant model system	Provart et al., 2016
		<i>Arabidopsis halleri</i>	145.5	nearly complete	heavy metal tolerance/accumulation	Kubota et al., 2015 ; Kosugi et al., 2015
		<i>Arabidopsis lyrata</i> (lyrate rock cress)	207	nearly complete	self-incompatible <i>A. thaliana</i> relative	Hu et al., 2011 ; Joschinski et al., 2015 ; Wos and Willi, 2015
		<i>Eutrema salsugineum</i> formerly known as <i>Thellungiella halophila</i> (saltwater cress)	238.5	nearly complete	salt-tolerant <i>A. thaliana</i> relative	Inan et al., 2004 ; Yang et al., 2013
		<i>Cardamine hirsute</i> (bitter cress)	549 ²	in progress	compound leaves	Hay et al., 2014 ; Bar and Ori, 2015
	Fabaceae	<i>Lotus japonicas</i> (birdsfoot trefoil)	472 ³	in progress	nitrogen fixation	Sato and Tabata 2006 ; Sato et al., 2008
		<i>Medicago truncatula</i> (barrel medic)	~454–526 ⁴	nearly complete	nitrogen fixation	Young et al., 2011 ; Tang et al., 2014
	Myrtaceae	<i>Eucalyptus globulus</i> (blue gum)	530 ⁵	nearly complete	wood, lignification, biofuel	Araújo et al., 2014 ; Myburg et al., 2014
		<i>Eucalyptus grandis</i> (rose gum)	640 ⁵	nearly complete	wood, biofuel	Myburg et al., 2014
	Orchidaceae	<i>Phalaenopsis</i> spp. (moth orchid)	~1160 ⁶	nearly complete	complex flower development, commercial flower crop	Hsu et al., 2011 ; Pan et al., 2014 ; Cai et al., 2015
	Phrymaceae	<i>Mimulus guttatus</i> (seep monkeyflower)	322	nearly complete	ecological studies, flower evolution	Wu et al., 2008
	Ranunculaceae	<i>Aquilegia caerulea</i> (Colorado blue columbine)	306	nearly complete	flower evolution and ecology	Kramer and Hodges, 2010
	Rosaceae	<i>Fragaria vesca</i> (wild strawberry)	240	complete	fruit development	Shulaev et al., 2011
		<i>Prunus persica</i> (peach)	225	nearly complete	fruit tree development	International Peach Genome Initiative et al., 2013
	Salicaceae	<i>Populus trichocarpa</i> (black cottonwood)	~422.9	complete	wood	Tuskan et al., 2006 ; Wulschleger et al., 2013
	Solanaceae	<i>Solanum lycopersicum</i> (tomato)	~900	complete	fruit ripening	Tomato Genome Consortium, 2012
		<i>Petunia x hybrid</i> (petunia)	~1,300	in progress	flower development, evolution	Vandenbussche et al., 2016
	Vitaceae	<i>Vitis vinifera</i> (grape)	487	complete	wine	Jaillon et al., 2007 ; Pulvirenti et al., 2015

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Table 1. Continued

Classification	Family	Species Name	Genome Size (Mb) ¹	Genome Sequence Status	Properties	References
Angiosperm monocot	Araceae	<i>Lemna minor</i> (common duckweed)	472 ⁷	nearly complete	aquatic plant for phytoremediation and biofuel	Cantó-Pastor et al., 2015
		<i>Spirodela polyrhiza</i> (greater duckweed)	158 ⁸	in progress	aquatic plant for phytoremediation and biofuel	Wang et al., 2014
	Poaceae	<i>Brachypodium distachyon</i> (purple false brome)	~272	nearly complete	non-crop grass model	Brkljacic et al., 2011
		<i>Miscanthus sinensis</i> (Chinese silver grass)	5,500 ⁹	in progress	bioenergy plant	Ma et al., 2012; Swaminathan et al., 2012
		<i>Oropetium thomaeum</i>	245 ¹⁰	nearly complete	drought model	VanBuren et al., 2015
		<i>Oryza sativa</i> (rice)	372	complete	major crop, grass model	International Rice Genome Sequencing Project 2005
		<i>Panicum virgatum</i> (switchgrass)	~1,500 ¹¹	nearly complete	bioenergy crop	Sharma et al., 2012
		<i>Setaria viridis</i> (green foxtail)	~395	nearly complete	non-crop grass	Bennetzen et al., 2012
		<i>Sorghum bicolor</i> (sorghum)	~732	complete	potential bioenergy crop	Paterson et al., 2009
<i>Zea mays</i> (maize)	2,300 ¹²	nearly complete	genetics and development, major crop	Strable and Scanlon 2009; Schnable et al., 2009		
Basal angiosperm	Amborellaceae	<i>Amborella trichopoda</i>	748	nearly complete	flowering plant evolution	Amborella Genome Project (2013)
Gymnosperm	Pinaceae	<i>Picea abies/ Picea glauca</i> (spruce)	~20,000 ¹³	in progress	wood	Nystedt et al., 2013; Biol et al., 2013
		<i>Pinus taeda</i> (loblolly pine)	~22,000 ¹⁴	nearly complete	wood	Zimin et al., 2014
Pteridophyta	Pteridaceae	<i>Ceratopteris richardii</i> (triangle waterfern)	11,260 ¹⁵	in progress	model fern	Strain et al., 2001; Atallah and Banks, 2015
	Azollaceae	<i>Azolla filiculoides</i> (water fern)	740 ¹⁶	nearly complete	model fern, nitrogen fixation	Qiu and Yu, 2003; Sessa et al., 2014
Lycopodiophyta	Selaginellaceae	<i>Selaginella moellendorffii</i> (spikemoss)	~106 ¹⁷	complete	clubmoss evolution	Banks et al., 2011
Anthocerotophyta	Anthocerotaceae	<i>Antheroceros agresis</i> (field hornwort)	83 ¹⁸	in progress	hornwort evolution	Szövényi et al., 2015a
Bryophyta	Ditrichaceae	<i>Ceratodon purpureus</i> (fire moss)	340 ¹⁹	in progress	photosynthesis, heavy metal tolerance	Thornton et al., 2005
	Funariaceae	<i>Physcomitrella patens</i>	473	complete	moss evolution, moss development	Knight et al., 2009
Marchantiophyta	Marchantiaceae	<i>Marchantia polymorpha</i>	226	in progress	liverwort evolution	Ishizaki et al., 2016
Charophyta	Klebsormidiaceae	<i>Klebsormidium flaccidum</i>	~104 ²⁰	nearly complete	filamentous freshwater alga	Hori et al., 2014

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Table 1. Continued

Classification	Family	Species Name	Genome Size (Mb) ¹	Genome Sequence Status	Properties	References
Chlorophyta	Chlamydomonadaceae	<i>Chlamydomonas reinhardtii</i>	~120 ²¹	complete	motile unicellular freshwater alga	Harris, 2001; Merchant et al., 2007
	Mamiellaceae	<i>Ostreococcus tauri</i>	12.56 ²²	complete	miniscule unicellular marine alga	Courties et al., 1994; Derelle et al., 2006
	Volvocaceae	<i>Volvox carteri</i>	131.2	nearly complete	multicellular freshwater alga	Prochnik et al., 2010

¹<https://phytozome.jgi.doe.gov/pz/portal.html> unless otherwise noted.

²http://www.brassica.info/resource/sequencing/bmap/CSP2012Proposal_Version11_Final.pdf.

³Sato et al., 2008.

⁴Young et al., 2011.

⁵Myburg et al., 2014.

⁶Cai et al., 2015.

⁷Van Hoeck et al., 2015.

⁸Wang et al., 2014.

⁹Rayburn et al., 2009; Cichorz et al., 2015.

¹⁰VanBuren et al., 2015.

¹¹Sharma et al., 2012.

¹²Schnable et al., 2009.

¹³Nystedt et al., 2013; Birol et al., 2013.

¹⁴Zimin et al., 2014.

¹⁵Sessa et al., 2014.

¹⁶<http://www.azollagenome.net/>.

¹⁷Banks et al., 2011.

¹⁸Szövényi et al., 2015a.

¹⁹Thornton et al., 2005.

²⁰Hori et al., 2014.

²¹Merchant et al., 2007.

²²Derelle et al., 2006.

related to their life on land. Land plants exhibit an alternation of generations (Hofmeister, 1862), with complex multicellular bodies developing in both the haploid and diploid stages of their life cycle and, hence, are also known as embryophytes. Of the seven major extant lineages of land plants (Figure 1), three comprise the paraphyletic bryophytes (liverworts, mosses, hornworts), in which the haploid phase of the life cycle is dominant, with the diploid phase being nutritionally dependent upon the haploid. In contrast, the other four lineages (lycophytes, ferns, gymnosperms, angiosperms) comprise the monophyletic vascular plants, characterized by internal conducting vasculature and a life cycle in which the diploid phase is dominant, with the haploid phase being reduced and, in seed plants (gymnosperms and angiosperms), nutritionally dependent upon the diploid. In all land plants, except the seed plants, dispersal occurs via single-celled haploid spores and the haploid generation of the life cycle is free-living and produces gametes, motile sperm and eggs within specialized protective structures termed archegonia. Land plants are also distinguished from algae by exhibiting three-dimensional growth (as opposed to two-dimensional) and a host of biochemical adaptations, such as a waxy cuticle, associated with tolerating desiccation in a terrestrial environment.

Bryophytes—Non-vascular Land Plants

The bryophytes (non-vascular land plants) arose at least as early as at the end of the Ordovician Period. The phylogenetic relationships both among bryophytes and with respect to vascular plants are still being debated, with almost every possible permutation having been proposed at some time. While early phylogenies built on morphology, molecules and the fossil record suggested that liverworts were the basal land plant lineage (Kenrick and Crane, 1997; Mishler and Churchill, 1984; Qiu et al., 2006). The most recent phylogeny based on molecular data places hornworts sister to all other land plants and mosses plus liverworts as a clade sister to vascular plants (Wickett et al., 2014). However, this topology is difficult to reconcile with the fossil record, in which the earliest land plant spores (Ordovician cryptospores) more closely resemble those of extant liverworts (Wellman et al., 2003; Wellman, 2010). Likewise, the earliest Devonian bryophyte macrofossils have been classified as related to liverworts, considerably predating those thought to represent mosses and hornworts (Oostendorp, 1987; Guo et al., 2012; Edwards et al., 1995). Thus, extant liverworts appear to retain more ancestral characters of early bryophytic land plants. It is generally accepted that the three lineages of bryophytes branched from one another and from vascular plants early in the evolution of land plants, and this rapid diversification may be obscuring any remaining phylogenetic signal. Thus, to untangle early events in the origin of a land flora, models (preferably multiple) for each of the bryophyte lineages will be required.

The first bryophyte model established was the monoecious moss *Physcomitrella patens*, for which a diverse suite of techniques and resources has been developed (Knight et al., 2009). Of particular importance was the development of homologous recombination-based gene replacement, facilitating characterization of gene function (Schaefer and Zrýd, 1997). The sequence of the *Physcomitrella* genome (473 Mb; 32,926 protein-coding loci) provided an initial baseline for the identification of “land

plant” genes and revealed evidence of polyploidy, a characteristic typical of many derived mosses (Rensing et al., 2008). Experiments with *Physcomitrella* have been instrumental in elucidating the molecular basis for the alternation of generations—polycomb-repressive-complex-2-mediated gene repression is required to keep the diploid gene expression program repressed during the haploid generation (Okano et al., 2009; Mosquna et al., 2009), and conversely, TALE-homeodomain genes are required to activate or maintain the diploid gene expression following gamete fusion (Sakakibara et al., 2013; Horst et al., 2016). These studies have begun to unify the molecular genetic regulation of life cycles in land plants with those in *Chlamydomonas* (Lee et al., 2008) and more distantly related eukaryotes, such as fungi (Herskowitz, 1989). While *Physcomitrella* genomics has contributed to our understanding of land plants, it is a derived moss, and to fully appreciate moss diversity, development of other model mosses (Szövényi et al., 2015b), such as *Ceratodon purpureus* (a dioecious and heavy metal-tolerant derived moss) and a *Sphagnum* species representing a basal lineage of mosses (Shaw et al., 2016), will be informative.

The dioecious liverwort *Marchantia polymorpha* has been a model for investigating a broad range of biological phenomena for almost two centuries (Bowman, 2016) and has recently entered the molecular genetic and genomic era, with all the modern tools now available (Ishizaki et al., 2016). Critically, both homologous recombination-mediated gene replacement and CRISPR/Cas9 technologies have been shown to work efficiently in *Marchantia*. Furthermore, protocols for efficient *Agrobacterium*-mediated transformation of spores have been pioneered (Ishizaki et al., 2008), and these may be able to be adapted, with modifications to suit differences in life cycle, to other spore-producing land plants. Studies on the auxin transcriptional response machinery in *M. polymorpha* have suggested that auxin response modulates, but does not determine cell fates and, furthermore, that it is critical for the transition from 2-dimensional growth to 3-dimensional growth in the haploid generation (Kato et al., 2015; Flores-Sandoval et al., 2015). Gene knockout technologies also enabled the discovery that the molecular mechanism by which plants measure photoperiod and control the transition between vegetative growth and reproductive growth is broadly conserved across land plants (Kubota et al., 2014). These studies also hint at a lack of redundancy within the *M. polymorpha* genome (226 Mb; 19,287 protein-coding loci), a feature that would be consistent with the lack of ancient whole-genome duplications within liverworts (Berrie, 1960).

The power of comparative genomics combined with the ability to manipulate gene function is highlighted by investigations into epidermal growth that have revealed commonalities in the development of single-celled *M. polymorpha* rhizoids, multicellular *Physcomitrella patens* rhizoids, and *Arabidopsis* root hairs. The rhizoids in the two bryophyte species develop in the haploid body while the root hairs of *Arabidopsis* are part of the other generation, the diploid. Despite these differences, orthologous basic-helix-loop-helix (bHLH) transcription factors control their development, suggesting a common ancient mechanism for epidermal outgrowths to facilitate anchorage to substrates and uptake of nutrients (Menand et al., 2007; Tam et al., 2015; Proust

et al., 2016). That the *Marchantia* bHLH ortholog is also required for gemma development, also via an epidermal outgrowth, suggests that the formation of structures derived from epidermal outgrowths may have a common underlying genetic mechanism (Proust et al., 2016). As both antheridia, in which sperm will develop, and archegonia, in which egg cells are formed, are formed via epidermal outgrowths, it is possible that the formation of sex organs in most land plants will rely on a similar fundamental genetic mechanism.

Lagging behind the other bryophyte lineages in their development of models are hornworts. *Anthoceros agrestis* (83 Mb) has been proposed as a model hornwort system—culture conditions and preliminary genome sequences have been produced (Szövényi et al., 2015a). As with the other bryophyte systems, the establishment of a transformation system perhaps based on that of *M. polymorpha* would facilitate functional genetic studies. The sequencing of a hornwort genome should help to resolve the phylogenetic relationships of the three bryophytes and vascular plants by comparative genomic studies.

One caveat is that often only a single taxon in each major land plant lineage has been sequenced, as seen in Table 1. Since each of the lineages has been following their own independent evolutionary trajectory for millions of years, each species is likely to possess its own peculiarities and may not be representative of the entire lineages that they have been purported to reflect. It will be important to develop additional models within each of the lineages to conclusively address questions in evolutionary genomics.

Basal Vascular Land Plants

Vascular plants appeared in the Silurian Period (around 423 million years ago; Kenrick and Crane, 1997). The basal lineage of vascular plants is the Lycophyta (clubmosses and relatives; Figure 1). The genome sequence of the lycophyte *Selaginella moellendorffii* (~106 Mb; 22,273 protein-coding loci) has provided some insight into the evolution of vascular plants (Banks et al., 2011); however, the development of genetic tools such as transformation methods for *Selaginella* is in the future.

The sister group to seed plants is the ferns (Figure 1), a diverse clade of plants that are often the first vascular plants to colonize disturbed sites. As with lycophytes, both haploid and diploid generations of ferns may be free-living. Ferns may be either homosporous or heterosporous and comparisons may provide insight into the evolution of sexual systems. Ferns evolved leaves independently of seed plants, and whether the molecular mechanisms are similar is actively being investigated (Plackett et al., 2015). Ferns are often polyploids with large genomes, and while no draft fern genome sequences are currently available (Wolf et al., 2015), transcriptome assemblies of *Azolla filiculoides* (an aquatic fern; genome of 740 Mb) and *Equisetum giganteum* (horsetail) have provided some insight into gene content (Vanneste et al., 2015; Brouwer et al., 2014). A derived fern, *Ceratopteris richardii* (11.26 Gb) has been developed to some extent as a model system with genetic approaches; e.g., investigations of sex determination mechanisms (Strain et al., 2001; Atallah and Banks, 2015) and transformation protocols have been established (Muthukumar et al., 2013; Plackett et al., 2014).

Diversification in Eudicots Arabidopsis Satellite Systems

While there is a clear rationale for developing plant models that are distantly related to flowering plants, there is also justification for developing models as close as possible to the dominant flowering plant model *Arabidopsis thaliana*. These new plant models form what might be termed *Arabidopsis* satellite systems—plants that are phylogenetically as close to *Arabidopsis* as possible and therefore amenable to laboratory use and to the methods developed for *Arabidopsis* but with special features not found in *A. thaliana*. *Arabidopsis lyrata* is an example of such a satellite system. *A. lyrata* is generally self-incompatible in comparison to the generally self-crossing *A. thaliana*, so it can provide a view of genome evolution in an outcrossing species. As there are also self-fertilizing populations, the evolution of mating system differences can be studied (Joschinski et al., 2015). This species is also being used to address the evolution of genome size and chromosome number. This is an important question in plant evolution, as flowering plant genomes range in size from 82 Mb (*Utricularia gibba*; Ibarra-Laclette et al., 2013) to an estimated 17 Gb for wheat (Brenchley et al., 2012) and up to 148 Gb for the monocot *Paris japonica* (Pellicer et al., 2010). Genome sequencing of *A. lyrata* (Hu et al., 2011) shows a genome of 207 Mb, different from *A. thaliana* by thousands of small insertions/deletions, despite an overall 80% sequence similarity in comparable regions. The chromosomes show two reciprocal translocations and three chromosome fusions that led from the presumed ancestral eight chromosomes of *A. lyrata* to the five of *A. thaliana*. Half of the genome differences between the two species are transposable elements. Recent work examines gene expression after hybridization between different populations (Videvall et al., 2016). Future studies will likely include attempts to understand the basis of ecological differences between the two species, since *A. thaliana* is widely distributed in temperate climates, whereas *A. lyrata* is circum-polar and tolerant of cold (Wos and Willi, 2015).

Arabidopsis arenosa is another such satellite, which has both diploid and naturally formed autotetraploid populations, which has enabled the study of the evolutionary differences that accumulate after autopolyploidy (Hollister et al., 2012), as well as differences between natural and artificially formed autotetraploid lines (Yant et al., 2013).

Another example of what could be considered an *Arabidopsis* satellite is a salt-tolerant mustard, *Thelungiella halophila* (also published under a newer designation, *Eutrema salsugineum*) (Inan et al., 2004; Yang et al., 2013). Comparative studies of osmolytes, ion channels, and responses to additional stresses are leading to an understanding of responses to abiotic stress that could be of considerable importance to agriculture in dry or drought-prone areas.

Additional *Arabidopsis* satellites are under development and are already revealing physiological and developmental processes distinct from those in *A. thaliana*. These satellites include *Cardamine hirsuta* for compound leaf development (Hay et al., 2014; Bar and Ori, 2015), *Arabidopsis halleri*, a cadmium and zinc hyperaccumulating plant (Kubota et al., 2015; Kosugi et al., 2015), *Boechera* species that exhibit apomixis (asexual reproduction) (Rushworth et al., 2011), and *Arabis alpina*, a

model for the ecology of alpine and arctic environments that has a perennial rather than annual life cycle (Wang et al., 2009). Some *A. alpina* populations are self-fertilizing, while others appear to manifest sporophytic self-incompatibility (Tedder et al., 2011).

Additional Eudicot Models

Prior to the development of *Arabidopsis* as a model system, a number of other plant models had been established, primarily among the angiosperms. Angiosperms have been a major focus of model studies as they form the largest and most diverse group of plants (Figure 1), consisting of several hundred thousand species of herbaceous plants, shrubs, grasses, and most species of trees. A variety of established and emerging models are discussed below and in subsequent sections of this article. This section focuses on plants within the asterid clade, which diverged from the rosid clade (in which *Arabidopsis* resides) early in angiosperm evolution, ~120 million years ago.

Antirrhinum majus (snapdragon) has numerous intrinsic qualities and derived properties, as well as an extensive history in plant research spanning the past 100 years (Schwarz-Sommer et al., 2003). The elucidation of the molecular basis of floral organ identity came from studies in *A. majus* in conjunction with studies in *Arabidopsis* (Coen and Meyerowitz, 1991). This member of the Plantaginaceae family has been also used to study the basis of floral scent, flower pigmentation, floral asymmetry, leaf development, and population genetics (Schwarz-Sommer et al., 2003). In the Solanaceae family, petunia has a similarly extensive history in plant genetics and has been recently proposed to serve as a representative model for the asterid clade (Vandenbussche et al., 2016). *Mimulus* in the Phrymaceae family of asterids is a proposed model for plant adaptation and speciation, based on the broad ecological and genomic diversity of this genus (Wu et al., 2008).

The Asteraceae or Compositae (commonly known as the daisy family) is thought to be the largest and perhaps most diverse family in the asterid clade. The most developed model within this family is lettuce (*Lactuca sativa* L.), which has a life cycle of 3–5 months, routine transformation methods, and a genome size of ~2.7 Gb (http://compgenomics.ucdavis.edu/compositae_data.php?name=Lactuca+sativa). Another economically valuable member of the Asteraceae is sunflower (*Helianthus annuus*), an oilseed crop that may be useful not only for oil and seed production, but also for studying plant genome evolution. The sunflower genome is quite large (~3.5 Gb) (Kane et al., 2011) mainly due to transposable elements that comprise 81% of the genome (Staton et al., 2012).

Nitrogen Fixation

Nitrogen fixation is a physiological and developmental process that is not only fascinating, but also agriculturally of great importance. Many legumes have a symbiotic association with nitrogen fixing bacteria, whereby the plants create nitrogen-fixing nodules in their roots that provide an anaerobic environment where the bacteria can convert atmospheric nitrogen to nitrate, which can be used as a nitrogen source by the plants. Two plants used for study of nitrogen fixation are *Medicago truncatula*, an alfalfa relative with a small and sequenced genome (~454–526 Mb) (Young et al., 2011), small size, large seed production, and good transformation protocols (Barker et al., 1990; Crane et al., 2006), and *Lotus japonicus*, also with a manageable

genome size (472 Mb), short life cycle, and a different (determinate versus indeterminate) type of nitrogen fixing nodule (Sato and Tabata 2006; Sato et al., 2008).

Fruit Development

Arabidopsis has a dry fruit known as a silique, which is typical of the mustard family to which it belongs. *Solanum lycopersicum* (tomato) is another well-established reference plant for the study not only of fruit ripening, but also plant growth, compound leaf development, and disease resistance. There are many cultivars of tomato, and one in particular has been proposed for its *Arabidopsis*-like properties, cultivar Micro-Tom, a dwarf and determinate growth variety originally produced as an ornamental (Emmanuel and Levy, 2002; Martí et al., 2006). Its rapid life cycle (2–3 months), small size (10–20 cm), and ability to grow when planted at high density (>1,000 plants per m²) and in glasshouses suit it well for mutant screens. Insertional mutagenesis protocols allow for isolation and molecular cloning of genes that give novel mutant phenotypes, and chemical mutagenesis is also highly effective. The published genome sequences of tomato are from another, closely related cultivar and show a genome of ~900 Mb (Tomato Genome Consortium, 2012). As for *Arabidopsis*, tomatoes can be considered to have satellite systems. One of particular note is potato, a member of the same family, which serves as a model not only for tuber development (Navarro et al., 2011), but also for agriculturally relevant disease resistance.

To study the development of different types of edible fruits at a genetic and genomic level requires different models. Many fruits are non-climacteric (ripen without a burst of respiration), in contrast to tomato fruit, which is climacteric. Cultivated strawberry is non-climacteric and has a complex octaploid genome that is thought to derive from four different diploid ancestors. *Fragaria vesca*, a wild strawberry species, is diploid and has a small sequenced genome of 240 Mb (Shulaev et al., 2011). *F. vesca*, with its simpler genome, in vitro regeneration, short generation time, small size, and available transformation methods, has been proposed as a reference system for the Rosaceae family, which includes peach. *Prunus persica* (peach) also has been proposed as a model due to considerable genetic resources, and especially because of its small genome, which at 225 Mb is less than twice that of *Arabidopsis* (International Peach Genome Initiative et al., 2013). It too is diploid, unlike sour cherries and plums, its close polyploid relatives. It cannot be said that peach is rapid-growing, however, as the time from germination to fruiting, while much shorter than in related trees, is 2 or 3 years, and its size precludes simple indoor growth.

Monocot Models

Grasses

Grasses constitute the most important plants for human use: the three major crops in the world are maize, rice, and wheat. Long before *Arabidopsis* came to prominence as a model, researchers studied the genetics and development of maize (*Zea mays*), as well as the genetic basis of its domestication from the wild grass teosinte, and particularly, the genetic contributions to yield and agronomic properties of this major crop (Strable and Scanlon 2009). One of the initial reasons for the use of *Arabidopsis* was the difficulty in dealing with the enormous genome of maize,

which at ~2.3 Gb is similar in size to that of humans (Schnable et al., 2009). Maize is also a large and slow growing plant, with one or two generations a year, requiring considerable field space or highly illuminated growth room areas. To avoid these difficulties, and still study the growth and physiology of grasses, grass satellite systems are also intensively studied.

Rice (*Oryza sativa*) is the predominantly studied non-maize model genomic system for grasses, not only because it is a major crop itself, but also because it has a manageable genome and is a smaller plant, more easily suited to laboratory growth. The haploid genome of 389 Mb has been sequenced and annotated (International Rice Genome Sequencing Project 2005), and there are efficient transformation methods (Hiei et al., 1997). The generation time is ~4 months, depending on strain (compared to ~2 months for *Arabidopsis thaliana*).

While a great advantage of maize and rice is that anything learned is directly relevant to agriculture, there are two non-crop grasses that have been proposed as even more convenient laboratory model systems, *Brachypodium distachyon* and *Setaria viridis*. *Brachypodium* has a genome of only 272 Mb, about twice that of *Arabidopsis* and an eighth that of maize, with a small content (~20%) of repetitive elements, making cloning by chromosome walking feasible. The plant grows to 15–20 cm, similar to *Arabidopsis*, and has an 8–12 week generation time. It is transformable with high efficiency using *Agrobacterium* and tissue culture methods (Brkljacic et al., 2011). Thus, the intrinsic properties are not too different from those of *Arabidopsis*, and the derived and community aspects are under rapid development. *Brachypodium*, like rice, wheat, and *Arabidopsis*, has C3 photosynthesis, in which carbon dioxide from the air is directly combined with ribulose biphosphate to make 3-phosphoglycerate, starting the Calvin-Benson cycle. *Setaria viridis* (green foxtail) like maize uses C4 photosynthesis, in which CO₂ is incorporated into malate and then from malate reacts with ribulose biphosphate, allowing carbon dioxide uptake at night when humidity is high, and its use during the day without the water loss consequent on stomatal opening. *Setaria* thus can serve as a model for the specializations (anatomical and biochemical) that allow this type of light utilization, which is particularly efficient in hot and dry conditions (Doust et al., 2009; Brutnell et al., 2010). The genome is ~395 Mbp (Bennetzen et al., 2012). An additional grass, *Oropetium thomaeum*, with the smallest known grass genome (245 Mbp), is a drought-tolerant monocot (VanBuren et al., 2015) in much the same way that *Eutrema* is a salt-tolerant satellite of *Arabidopsis*. Additional grasses are proposed and used as models for bioenergy production, discussed below.

Monocot “Trees”

Palms (oil, date, coconut), bananas, and pineapples have great economic importance in arid, tropical, and/or subtropical regions. These monocotyledonous flowering plants are sometimes referred to as “trees,” although they are distinct from woody plants that have secondary xylem growth. Comparison of the genome sequences of diploid African oil palm (*Elaeis guineensis*; 1.8 Gb) and diploid South American oil palm (*E. olifera*) revealed that their common ancestor was tetraploid (Singh et al., 2013). Genome sequencing is underway or nearly complete for date palm (*Phoenix dactylifera*; 658 Mb) (Al-Dous et al., 2011), banana

(*Musa acuminata*; 523 Mb) (D’Hont et al., 2012), and pineapple (*Ananas comosus*; 526 Mb) (Ming et al., 2015).

Bioenergy Crops

An additional important use for plants beyond their use for food is their use for energy, either by burning, the traditional route, or for conversion to high-energy transportation fuels (bioethanol and biodiesel). *Sorghum bicolor* is one model energy crop, with low input, high drought tolerance, and accumulation of large amounts of sugars in stems, which grow to high biomass (Carpita and McCann 2008; Calviño and Messing 2012). It is also a potential model for study of C4 photosynthesis (Mullet et al., 2014). The ~732 Mb genome is partly sequenced (Paterson et al., 2009). Genomic analysis by high-resolution genetic mapping and sequencing of the sugarcane relative *Miscanthus sinensis* (a parental species of the hybrid energy crop *Miscanthus x giganteus*) has also been started (Ma et al., 2012; Swaminathan et al., 2012) as has sequencing of *Miscanthus x giganteus* (Swaminathan et al., 2010). Another high-yielding energy crop is switchgrass, *Panicum virgatum*, which is also the subject of genome analysis projects that show a close relationship to sorghum (Sharma et al., 2012). The duckweeds are highly reduced aquatic monocots. A truly tiny (2 cm) member, the fast-growing *Lemna minor*, has additionally been proposed as a model for aquatic plants, as a biofuel source, and because of its sensitivity to environmental toxins, for ecophysiological studies (Van Hoeck et al., 2015). The diploid genome is 472 Mb (Van Hoeck et al., 2015), and efficient genetic transformation and gene silencing via artificial microRNAs have been established (Cantó-Pastor et al., 2015). The smallest known monocot genome (158 Mb) belongs to another duckweed, *Spirodela polyrhiza*, whose genome sequence suggests that reductions in several biochemical pathways accompany its aquatic lifestyle and that its neotenus life cycle is reflected in changes in paralog numbers of promoters and repressors of the juvenile-to-adult transition (Wang et al., 2014).

Medicinal Plants

There are hundreds of medicinal plants, and many of our drugs are either derived from plants or based on compounds originally identified in plants, e.g., aspirin from *Salix* species, morphine from *Papaver somniferum*, digitalin from *Digitalis purpurea*, quinine from *Cinchona* species, vincristine from *Catharanthus roseus*, and taxol from *Taxus* species. However, the compounds often exist in minute quantities, in sometimes rare plants, making the identification of the genetic basis for biochemical pathways and their transfer to more tractable systems of both economic and environmental interest. Targeted genomic or transcriptomic sequencing of medicinal plant species (Hao et al., 2012; Sharma and Shrivastava, 2016) could lead to synthetic biology approaches to produce specific bioactive compounds in yeast or *E. coli*, as has been done with *Artemisia annua*, the source of artemisinin, a potent anti-malarial drug (Ro et al., 2006; Westfall et al., 2012), and the opium poppy *Papaver somniferum*, the source of medical opiates (Thodey et al., 2014).

Trees

Trees (both eudicot hardwoods and gymnosperm softwoods) exhibit dormancy and secondary wood formation, and have

economic, environmental, and ecological importance, due to their use for wood-based products (timber, pulp, and paper), carbon mitigation, and watershed protection. The reference tree *Populus trichocarpa* (black cottonwood or California poplar) was the first tree (and the third angiosperm, after *Arabidopsis* and then rice) to have its genome (~422.9 Mb) sequenced (Tuskan et al., 2006) and is readily transformable (Song et al., 2006). The genus *Populus* includes poplars, cottonwoods, and aspens. Poplar is a valuable source of timber because of its rapid growth, maturing in ~5 years. Genome information from poplar has been used to study wood formation, salt stress, and other relevant characteristics (Dharmawardhana et al., 2010; Wulschleger et al., 2013; Zang et al., 2015). The genome sequences of the fast-growing hardwood trees, *Eucalyptus grandis* (640 Mb) and *E. globulus* (530 Mb), offer the opportunity for comparative angiosperm tree genomics as well as investigation of specialized metabolites, such as terpenes and oils (Myburg et al., 2014). While not a model for trees per se, transcriptome sequencing of *Ulmus minor* (elm) genotypes has shed insight on the impact that Dutch elm disease has had on *Ulmus* species and may illuminate possible avenues for conservation of *Ulmus* species (Perdoguero et al., 2015).

Gymnosperms, the sister group of angiosperms, are the oldest lineage of the seed plants (Figure 1). Gymnosperms are mostly long-lived species with relatively large genomes, so there is a dearth of model gymnosperms at even the first level, despite genome sequences being available for a few northern hemisphere conifers: the Norway spruce (20 Gb genome) (*Picea abies*; Nystedt et al., 2013), white spruce (20 Gb) (*Picea glauca*; Birol et al., 2013), and the loblolly pine (22 Gb) (*Pinus taeda*; Zimin et al., 2014). However, due to their value as timber, genome-wide association mapping approaches have been applied in conifer species, identifying allelic variation influencing wood properties and environmental responses (González-Martínez et al., 2007; Dillon et al., 2010; Eckert et al., 2010).

Conclusion

In summary, both the list of what are considered model systems for plants and the definition of model systems, are undergoing rapid change. Few of the plants listed have the full set of intrinsic, derived, and community properties that characterize the established models *Arabidopsis*, tomato, maize, rice, and *Chlamydomonas*. What they do have is a group of laboratories that have particular reasons, based on unique physiology, development, phylogenetic position, or societal value to warrant deeper study, and a genome sequence (or a plan to obtain one) that can give the list of parts—important prerequisites for a generally accepted model status. Many also have demonstrated transformation protocols, amenable genetic systems, and ease of laboratory culture. Classical genetic manipulation, which was a critical feature of *Arabidopsis*, may no longer be essential, given the availability of rapid whole-genome sequencing and targeted gene editing by CRISPR/Cas9. Whether the future holds continued concentration on the current set of models, a more diverse approach in which the overall effort of the plant research community is spread among many systems—a “return” to the situation prior to the advent of *Arabidopsis* as a model, a greater concentration on crop plants, or some mix of the above, is yet to

be seen. One thing that is clear is that the choice of possibilities for plant researchers is large and open—and that any information obtained about any plant model will be applicable to studies of other plants, improving our understanding of the evolution, diversification, and fundamental properties of plants. The expansion of knowledge will enhance our ability to modify plants and make use of plant biodiversity. Like the original discoveries in plants of cells, the nucleus, genetic principles, genes, viruses, transposons, the cytoskeleton, microRNAs, DNA methylation, and much else, the information may also be relevant to those who study animals.

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