Physcomitrella patens: mosses enter the genomic age
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The sequenced genome of the moss Physcomitrella patens provides a powerful tool for comparative analyses of land plant genomes. In parallel, several tools for studying gene function have been developed in P. patens, including RNA interference, inducible promoters and gene targeting, a unique attribute of this plant system. The results of these initiatives are now being realized. For example, transcriptomic analyses illustrate commonalities among plant lineages in gene content, structure, and regulation. Transgenic studies show that the regulatory factors ABSCISIC ACID INSENSITIVE3 (ABI3) and LEAFY (LFY) have molecular functions that are conserved between moss and angiosperms, in spite of the fact that they function in non-homologous tissues. Future work in P. patens will contribute to our understanding of the molecular basis of plant development and evolution.

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Introduction
Recent reviews have highlighted the use of the moss Physcomitrella patens [1–4] as an experimental system and we will not duplicate the topics covered in these reviews. In this review, we focus on recent work on the genomics and molecular biology of P. patens, and on new tools and resources available for experimental analysis of gene function. We discuss specific examples of their use in addressing important questions in plant biology.

Tools for gene discovery and functional analysis
An assembled P. patens genome (circa 487 Mbp), representing 8X coverage, has been released by the Joint Genome Institute, USA (http://shake.jgi-psf.org/Phyapa1/Phyapa1.home.html). In parallel, full-length cDNAs, additional expressed sequence tags (ESTs), and bacterial artificial chromosome (BAC)-end sequences are being developed, and updates can be accessed through the Physcomitrella Genome Consortium website (http://www.mossgenome.org). Various libraries and vectors are available (http://biology4.wustl.edu/moss/links.html), as is the Agilent microarray (MOgene, St. Louis, USA; http://www.mogene.com), which contains approximately 20,000 features that are based on 80,000 ESTs of Physcomitrella, Japan (http://moss.nibb.ac.jp). Additionally, efforts to identify polymorphisms among isolates of P. patens are proceeding and will enable both map-based cloning of ethane methyl sulfonate (EMS)-generated mutants and quantitative trait locus mapping of natural variants ([5]; Plant Biology, University of Freiburg, Germany: http://cosmoss.org/cont).

Several tools for the functional analysis of genes in P. patens are now available. The dexamethasone (M Chakhparonian, PhD thesis, Université de Lausanne, 2001), heat shock [6] and homoserine lactone [7] inducible promoter systems have all been shown to function successfully. Forward genetics can be employed to dissect gene function using a shuttle-mutagenesis library [8,9]. Alternatively, a targeted deletion library has been created using ESTs [10], and has been used for functional analysis [11]. Somatic hybridization has also been used to analyze mutants genetically [12]. Reverse genetics using gene targeting is a tool of choice for manipulating single genes in P. patens, but RNA interference (RNAi) allows the downregulation of gene families. An RNAi system has been developed in P. patens [13] that silences a nuclear-localized green fluorescent protein::β-glucuronidase (GFP::GUS) fusion protein at the same time as it silences the gene(s) of interest (see Figure 1a–d). This system was used to analyze the role of ARPC1, a member of the Arp2/3 complex, in tip growth [14].

Gene targeting
Unlike angiosperms, P. patens shows high levels of gene targeting, comparable with those shown by Saccharomyces cerevisiae [15]. Transformation constructs containing genomic sequence are targeted at high frequency to the cognate genomic locus, allowing genes to be inactivated by targeted gene replacement (TGR). Understanding the mechanism of gene targeting should allow its use to be extended to other species.

TGR involves the insertion of a selection cassette into a cloned gene, preferably replacing the coding sequence. Transformation is carried out using linear DNA, comprising the selection cassette flanked by two stretches of
Haploid tissues (filaments and gametophores) for developmental studies. (a–d) Protonemal filaments from P. patens plants expressing the nuclear localization signal (NLS)–GFP–GUS construct [13]. Wildtype filaments are shown (a) under white light and (b) viewed for GFP. GFP is localized to the nucleus whereas numerous chloroplasts (red auto-fluorescence) are visible in each cell. When (c) wildtype filaments are (d) transformed with a RNAi construct containing both the sense and antisense sequences of the GFP and the P. patens FtsZ gene (PpFtsZ) [13], GFP expression is silenced and chloroplast division is inhibited. This results in the formation of one large chloroplast. The same phenotype was reported for TGR of PpFtsZ [55].

The deletion of the single copy actin-related protein complex 4 subunit gene (arp4) resulted in the severe restriction of tip extension growth [18]. Replacement of the deleted gene with the wildtype gene fused with two copies of YFP complemented the deletion phenotype and revealed the specific cellular localization of this protein at the tip of the apical cell. In vivo localization of ARPC4 is consistent with its role in the extension of the apical cell. Scale bar represents 50 μm.

Scale bar in (a) represents 1 mm. (e,f) P. patens filaments expressing GFP in response to ABA. P. patens protoplasts were stably transformed with the wheat Em promoter linked to the GFP reporter gene (Em–GFP). When (e) seven-day old cultures were (f) treated with 1 μM ABA for six hours, GFP was observed in every cell of the developing plant. The response can be observed as early as 15 minutes after application of ABA to the medium. This response was shown to use the same ABA response elements in the Em promoter as in seed plants. Furthermore, the protein complex from the protonemal filaments displays the same DNAase footprint on the Em promoter, as does the protein complex from seed plants [42]. Scale bar in (e) represents 1 mm. (g) Tip localization of YFP–ARPC4-expressing caulonema cells of P. patens. The deletion of the single copy actin-related protein complex 4 subunit gene (arp4) resulted in the severe restriction of tip extension growth [18]. Replacement of the deleted gene with the wildtype gene fused with two copies of YFP complemented the deletion phenotype and revealed the specific cellular localization of this protein at the tip of the apical cell. This in vivo localization of ARPC4 is consistent with its role in the extension of the apical cell. Scale bar represents 50 μm.

(h) Expression of the GUS–LFY fusion protein in a gametophore of P. patens. Expression is localized to terminal and lateral apices of the gametophore. Although the site of activity is similar between P. patens and Arabidopsis (apical cells and meristems, respectively), the timing of activity and DNA-binding specificity have diverged between angiosperm and moss (from [45]). Scale bar represents 1 mm.

Targeted gene insertion (TGI) involves the insertion of the transforming construct into the corresponding sequence in the genome without removing genomic sequence [19*,20**]. The relative frequency of replacement and insertion is dependent on the lengths of genomic sequence in the construct and their symmetry. In all cases of TGI investigated, both ends of the targeting construct could be detected, consistent with non-homologous end joining (NHEJ) occurring before integration. NHEJ could occur either between the two ends of a single construct, forming a circle, or between the ends of different copies of the construct, generating a concatemer (Figure 2). The latter model is favored because all cases of TGI involve the insertion of a concatemer and because transformation with circular constructs results in low levels of integration [20**]. Gene targeting occurs in another moss, Ceratodon purpureus, where TGR has been used to substitute a functional allele for a mutant allele [21]. As in P. patens, about half of the targeted C. purpureus transgenics contained more than one copy of the targeting construct.

The only candidate genes implicated in TGR that have been investigated are homologs of rad51. P. patens has two
such genes. Inactivation of either of these genes by TGR reduces TGR: double knockouts no longer show TGR. In addition, spore formation is dramatically reduced in these double knockouts (U Markmann-Mulisch et al., pers. comm.). Inactivation of the single copy P. patens msh2 gene, the product of which plays a central role in the repair of mismatched DNA, results in a highly mutable phenotype and hyper-sensitivity to UV irradiation, and also affects TGR [22]. The frequency of TGR in the mutant lines was slightly reduced when targeting constructs having exact homology to the corresponding genomic sequence were used. In wildtype strains, targeting constructs that have mismatches show a reduced frequency of TGR, with 3% mismatch leading to about a 20-fold reduction in targeting. The msh2 knockout lines were tolerant of mismatches, showing no reduction in targeting with constructs containing 5% mismatches [22]. This evidence suggests that MSH2 must play a role in sequence recognition during double-strand break repair.

Comparative genomics

The development of P. patens as a model system has enabled comparative genomics across land plants. Recent publications have examined gene family evolution in P. patens and seed plants (Tables 1 and 2). Analysis of 71 cytochrome P450 (CYP) genes from P. patens reveals that all major angiosperm CYP clans were present in moss but not in algae (e.g. Chlamydomonas), indicating an expansion of the family coincident with the origins of land plants or shortly thereafter [23]. Further analysis of specific CYPs in P. patens indicates that only the first part of certain biosynthetic pathways (e.g. biosynthesis of lignin and gibberellic acid) are present, reflecting the lack of these end products in P. patens [24].

Two large-scale transcriptome analyses [25,26] of about 100,000 ESTs have revealed a high degree of sequence similarity (circa 65%) between P. patens and angiosperms [25]. Additionally, splice sites and codon usage are conserved among similar genes of P. patens and Arabidopsis thaliana [26]. A characteristic of the P. patens transcriptome is that it is enriched in metabolism-related genes [27]. Using transcript levels, enzymatic activity and thiol peptide profile, Cd²⁺ has been shown to induce activation of both the assimilatory sulfate reduction pathway and glutathione biosynthesis in P. patens [28]. Investigation of the protein phosphorylation state of the proteome upon cytokinin treatment has identified several new proteins never previously associated with the cytokinin signaling pathway [29].

No close homolog of 8% of the P. patens annotated genes are present in angiosperms, but are found in bacteria, fungi or animals [26]. For example, angiosperms have four classes of major intrinsic proteins that evolved from a bacterial type I glycerol transporter [30]. P. patens has an additional fifth class, GlpF-like intrinsic protein (GIP;1), whose sequence alignment is more closely related to that of bacterial type II glycerol transporters. This gene was also identified as being of bacterial origin by others [25]. Genes in P. patens that are not conserved in angiosperms appear to be enriched for certain functional classes, including DNA repair, which might account for the high frequency of gene targeting in P. patens [25,26].

Small RNA molecules (microRNAs [miRNAs] and short interfering RNAs [siRNAs]) form an abundant class of non-coding RNAs that are important regulatory factors common to a variety of organisms, including seed plants [31]. Recently, 561,102 small RNAs were identified in P. patens, representing 214,996 unique sequences, of which 127,135 had at least one perfect match in the P. patens genome [32]. Slightly less than half of the unique sequences could be classified as miRNA, whereas almost 60% did not appear to arise from loci with characteristics of known miRNAs, including four loci that give

Table 1

<table>
<thead>
<tr>
<th>Characteristics of the P. patens genome compared to those of a dicot (Arabidopsis) and a monocot (rice).</th>
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<tr>
<td>Genome size</td>
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<td>No. of chromosomes</td>
</tr>
<tr>
<td>Average intron length</td>
</tr>
<tr>
<td>Average intron number</td>
</tr>
<tr>
<td>Intron G/C</td>
</tr>
<tr>
<td>Exon G/C</td>
</tr>
</tbody>
</table>

* Data from The Institute of Genomic Research, USA website: http://www.tigr.org/tdb/e2k1/osa1/riceInfo/info.shtml#Genes.

(Figure 2 Legend) Models for targeted gene insertion in P. patens. (a) Target gene. a1, a2, b and c are regions of the gene labeled to clarify the mechanism of targeting. (b) Cloned targeting construct. The selection cassette (sel) has replaced segment b of the genomic sequence. The black and gray ends represent short distinct, non-homologous sequences (e.g. Gateway® sequences). (c) Model for targeted insertion of a circularized construct. (i) The construct is circularized by non-homologous end joining (NHEJ). The grey arrow indicates that further copies of the construct can be included if concatemer formation by NHEJ precedeses circularization. (ii) A double-strand break is induced in the circle as the precursor to integration. (iii) The 5' strand of the break is digested. (iv) The 3' strand seeks the homologous genomic sequence. The resulting single-stranded sequences are nicked (grey arrows). (v) Repair can result in homologous recombination. (d) Model for targeted insertion of a concatemer. (i) Concatemers are formed by NHEJ. A dimer is shown but further copies could be included at the site indicated by the grey arrow. (ii,iii) One end of the concatemer initiated double-strand-break repair using the homologous genomic sequence, as in (c)(iv). If the other end of the concatemer is now repaired using the genomic c sequence, replacement of the genomic sequence by the concatemer will result. (iv) Alternatively, the double-strand break in the genome, generated by the initial repair process, can be repaired by using a sequence in the concatemer. (v) Repair results in the insertion of one or more copies of the construct adjacent to the targeting sequence. (e) Both models lead to the same outcome, but model D requires that only concatemers are inserted.
rise to siRNA of the trans-acting class. This work with *P. patens* and *Arabidopsis* led to the model of a two-hit trigger for siRNA formation in plants [32]. Five angiosperm miRNA homologs were found in *P. patens*, as were six additional miRNAs that were regulated in gametophores by auxin [33]. Similarly, the target sequence of two other miRNAs, which are known to regulate genes in the class III homeodomain-leucine zipper (HD–Zip) gene family of *Arabidopsis*, is conserved in homologous sequences of *P. patens* and other non-seed plants [34]. All of these emerging results on small RNAs from *P. patens* suggest that, like *Arabidopsis*, *P. patens* expresses many endogenous siRNAs and miRNAs. These molecules will lead to a better understanding of both the controls that operate in *P. patens* development and the evolution of this process in land plants.

**Evolution of gene regulation across land plants**

The molecular genetic and genomic tools now available in *P. patens* allow an insight into the evolution of specific gene regulatory networks across the land plants. In *Arabidopsis*, an increasingly detailed picture is now emerging of the means by which environmental or developmental signals control plant morphogenesis [35,36]. It is clear, however, that homologs of many genes that are involved in the regulation of angiosperm-specific traits are found in distantly related lineages that lack such traits [37,38]. A current challenge is to understand how the evolution of these gene regulatory networks relates to physiological or morphological diversification. Here, we highlight recent work on the networks governed by regulatory factors such as the seed maturation gene *ABSCISIC ACID INSENSITIVE3 (ABI3)*, which is largely conserved between angiosperms and *P. patens*, and the floral homeotic gene *LEAFY (LFY)*, which has diverged between angiosperms and non-vascular plants.

The ability to withstand desiccation is a crucial component in the normal development of seeds and bryophyte vegetative tissues. In angiosperm seeds, the hormone abscisic acid (ABA) and the transcriptional factor ABI3 together control a set of genes that are required for seeds to survive desiccation [36]. The enzymes for ABA synthesis and degradation are present in *P. patens* [25,39]. ABA elicits both physiological [40,41] and molecular responses [42]; for example, *P. patens* responds to ABA by activating gene expression from the ABA-responsive wheat Em promoter linked to a reporter gene (Figure 1e,f; [42]). The same Em promoter was used to determine if ABI3-like regulators are present and whether they play a similar role in the response pathway [43**]. Three copies of an ABI3-like gene in *P. patens* (PpABI3) have been characterized, one of which can activate Em–GUS expression in the absence of exogenous ABA, and can strongly enhance Em–GUS expression in tissues treated with ABA. Furthermore, PpABI3A was also able to enhance Em–GUS expression in barley aleurone in the absence of ABA. Elements of the ABA-response pathway were, therefore, present in the common ancestor of angiosperms and mosses, and were conserved at least in these two lineages.

Furthermore, it was demonstrated that PpABI3A driven by the *Arabidopsis* ABI3 promoter (P*AtABI3–PpABI3A*) partially complemented the phenotypes of the *Arabidopsis* *abi3-6* mutant [43**]. The seed color and size phenotype of the *abi3-6* was fully complemented, but the ability to become desiccation tolerant was not complemented. In the P*AtABI3–PpABI3A*/*abi3-6* complementation lines, the expression levels of several ABI3-regulated genes were similar to wildtype (Table 3). The partial molecular complementation of *abi3-6* might be due in part to a failure of PpABI3A to interact with the bZIP transcription factor ABI5, which is required for proper expression of the remaining ABI3-regulated genes in *Arabidopsis* [43**]. Nevertheless, a major portion of the ABI3 signaling pathway was used for both angiosperm seed development and bryophyte function, possibly for desiccation tolerance.

The general role of the *LFY* gene in apical cell fate appears to be conserved in mosses and angiosperms. Deletion analyses of *LFY* in *Arabidopsis* (At*LFY*) indicate

### Table 2

**Comparison of gene families between *P. patens* and *Arabidopsis***

<table>
<thead>
<tr>
<th>Gene family</th>
<th><em>P. patens</em></th>
<th><em>Arabidopsis</em></th>
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<tr>
<td></td>
<td>No. of families</td>
<td>No. of genes</td>
</tr>
<tr>
<td>P450</td>
<td>29a</td>
<td>71</td>
</tr>
<tr>
<td>Chalcone synthase</td>
<td>NA</td>
<td>19</td>
</tr>
<tr>
<td>Cellulose synthase</td>
<td>4</td>
<td>30</td>
</tr>
<tr>
<td>Monosaccharide transporter</td>
<td>7</td>
<td>20</td>
</tr>
<tr>
<td>Peptidoglycan biosynthesis</td>
<td>NA</td>
<td>5</td>
</tr>
<tr>
<td>GLYCOCEN SYNTHASE KINASE 3</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>CONSTANS-like</td>
<td>NA</td>
<td>17</td>
</tr>
<tr>
<td>Germin-like</td>
<td>7</td>
<td>10</td>
</tr>
</tbody>
</table>

*a* 13 of which are shared with Arabidopsis.

*b* 59 families for angiosperms.
that the amino-terminal conserved region binds to the enhancers of several floral homeotic genes, while the carboxy-terminal (C-terminal) conserved region modulates the activity of the DNA-binding region [44**]. Arabidopsis mutants that were deficient in LFY activity failed to initiate proper flowering but exhibited no other mutant phenotypes. In P. patens, LFY (PpLFY) is expressed in gametophytic tissues (Figure 1h), although gametophyte development appeared normal in the deletion lines. *MFLY* expression is necessary only for the late stages of sporophyte development but the initiation of proper sporophyte development was impaired in *PpLFY* disruptants [45]. When the *PpLFY* disruptant lines were selfed, the first mitotic cell division was arrested in the developing diploid embryo, although these lines were capable of producing sporophytes when crossed to a *LFY* wildtype individual.

To determine whether the *LFY* regulatory network was conserved, but expressed in different tissues in *Arabidopsis* and *Physcomitrella*, *LFY* homologs from representatives of several land plant lineages were expressed in an *Arabidopsis* *lfy* mutant background [44**]. None of the 16 LFY targets in *Arabidopsis* were induced by heterologous expression of *PpLFY* (Table 3). In yeast two-hybrid screens, *PpLFY* failed to bind to the angiosperm-specific LFY targets APETALa1 and AGAMOUS, indicating that the changes in LFY activity result in part from changes in DNA binding rather than transcriptional activity. Replacing a single amino acid in the C-terminal conserved binding region of *PpLFY* partially complemented the *Arabidopsis* *lfy* mutant. The evolution of gene regulation by changes in DNA binding sites in LFY represents a departure from the changes in repression or activation more commonly seen in metazoans [46].

These studies illustrate that the regulatory activity of some transcription factors (e.g. LFY) has continued to evolve after the divergence of angiosperms and mosses, whereas others, such as ABI3 and GOLDEN2-LIKE (GLK2), show little or no change in activity (Table 3; [47**]). The evolution of regulatory networks, by adding or removing components or by altering the interactions among existing components, probably occurred along both the bryophyte and angiosperm lineages over the 450 million years since they shared a common ancestor. A complete understanding of regulatory evolution in the ABI3 and LFY networks, therefore, requires additional knowledge of the regulation of gene expression in *P. patens*. For example, does *PpLFY* control transcripts endogenously that it fails to properly regulate in *Arabidopsis*? The heterologous expression of genes from other land plant lineages in *Physcomitrella* using TGR will provide a powerful complement to such studies in *Arabidopsis*.

### Conclusions

The initial assembly and sequencing of the *Physcomitrella* genome is the first step for the international consortium ([www.mossgenome.org](http://www.mossgenome.org)), whose main goal is to generate integrated physical and genetic maps of the genome in the next few years. These resources, coupled with the experimental tools (e.g., efficient transformation and gene targeting, constitutive and inducible promoters, forward and reverse genetics, multiple selection markers, RNAi and so on) that have already been applied to further our understanding of gene function and regulatory networks, will make *Physcomitrella* the model system of choice for many fundamental biological questions. Although some angiosperm-specific processes (e.g., development of vascular tissue and flowers) cannot be studied directly in moss, cellular processes and signaling pathways, (e.g., responses to hormone and light) can be dissected in this experimentally tractable system. The ability to exchange genes between *P. patens* and angiosperms will allow us to explore the evolution of plant regulatory proteins, such as LFY and ABI3, whose function(s) as regulators has been conserved over 400 million years. Understanding how the functions of such regulatory factors have changed at the molecular level in diverse lineages of plants will provide key insights into the evolution of land plants, and has the potential to provide exciting new findings in angiosperm physiology and developmental biology.

### Acknowledgements

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### Table 3

<table>
<thead>
<tr>
<th>Regulatory gene</th>
<th>Arabidopsis loci regulated by Arabidopsis gene</th>
<th>Arabidopsis loci regulated by Physcomitrella trans gene</th>
<th>Percent properly regulated</th>
<th>Reference</th>
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<tr>
<td>GLK2</td>
<td>LHCb1, LHCb6, HEMA1, CAO</td>
<td>LHCb1, LHCb6, HEMA1, CAO</td>
<td>100%</td>
<td>[47**]</td>
</tr>
<tr>
<td>ABI3</td>
<td>Em1, Em6, CruciferinC, Napin, Oleosin2, Rab18</td>
<td>CruciferinC, Napin, Oleosin2, Rab18</td>
<td>67%</td>
<td>[43**]</td>
</tr>
<tr>
<td>LFY</td>
<td>AP1, AP3, AG, PI, SEP1, SEP2, SEP3</td>
<td>None</td>
<td>0%</td>
<td>[44**]</td>
</tr>
</tbody>
</table>
References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


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39. aborted flower growth leaves the moss, Physcomitrella patens, with an ancestral floral regulatory network in several land plant lineages.

Diverse lineages of eukaryotes are built from a common genetic toolkit. In some groups, changes in cis-regulation of gene expression are a key factor in generating phenotypic variation. The authors of this paper use a variety of transgenic assays to demonstrate that DNA binding of a trans-acting factor is responsible for the evolution of the LFY regulatory network in several land plant lineages.


43. The Golden2-like (GLK2) transcription factor that regulates chloroplast development was targeted to determine whether chloroplast biogenesis is conserved between P. patens and angiosperms. Both P. patens and angiosperms have two genes that encode GLK2, which have overlapping function in Arabidopsis and P. patens but not in maize. Disruption of a single gene in P. patens has no effect, whereas a double disruptant is pale green and has fewer thylakoid stacks. In Arabidopsis, reduced chlorophyll levels were correlated with reduced expression of light-harvesting chlorophyll a/b binding protein (LHCB), glutamyl tRNA reduc-tase (AtHema1) and chlorophyll a oxygenase (AtCAO). Expression of the corresponding genes is reduced by at least 60% in P. patens double disruptants. Overexpression of PpGLK2 is able to rescue partially the defect in Arabidopsis glk1 glk2 double mutants. The expression patterns of AtLHCB, AtHema1 and AtCAO in complemented lines correlates with the phenotype.


53. This paper identifies a limited set of genes that are regulated correctly in seeds when the transcription factor AB13 homolog from P. patens (PpAb13) is expressed in transgenic abi3-6 mutant Arabidopsis. Not all genes or seed traits are complemented, however. For example, although transgenic seeds containing PpAb13 are formed, they are not desiccation-tolerant. This would indicate that those Arabidopsis genes that are not properly regulated by PpAb13 could account for the lack of complementation of this phenotype. This reference serves as an example of how comparative functional genomics can lead to enhanced understanding of gene function and the role of specific genes in complex traits.
