Telomeres, the essential terminal regions of linear eukaryotic chromosomes, consist of G-rich DNA repeats bound by a plethora of associated proteins. While the general pathways of telomere maintenance are evolutionarily conserved, individual telomere complex components show remarkable variation between eukaryotic lineages and even within closely related species. The recent genome sequencing of the lycophyte Selaginella moellendorfii and the availability of an ever-increasing number of flowering plant genomes provides a unique opportunity to evaluate the molecular and functional evolution of telomere components from the early evolving non-seed plants to the more developmentally advanced angiosperms. Here we analyzed telomere sequence in S. moellendorfii and found it to consist of TTAGGG repeats, typical of most plants. Telomere tracts in S. moellendorfii range from 1 to 5.5 kb, closely resembling Arabidopsis thaliana. We identified several S. moellendorfii genes encoding sequence homologs of proteins involved in telomere maintenance in other organisms, including CST complex components and the telomere-binding proteins, POT1 and the TRF1 family. Notable sequence similarities and differences were uncovered among the telomere-related genes in some of the plant lineages. Taken together, the data indicate that comparative analysis of the telomere complex in early diverging land plants such as S. moellendorfii and green algae will yield important insights into the evolution of telomeres and their protein constituents.

Keywords: telomere, Selaginella, POT1, TRF1, CST complex
in telomere biology. Our analysis indicates that S. moellendorffii harbors short telomere tracts consisting of canonical TTTAGGG repeats. Furthermore, we find a full complement of the telomere-associated genes that have previously been described in other plants. Comparative studies of S. moellendorffii with other early diverging plants may be useful for studying the evolution of telomere proteins in plants.

RESULTS AND DISCUSSION

SELAGINELLA MOELENDOFFII TELOMERES

Sequence analysis of terminal chromosomal scaffolds indicates that S. moellendorffii telomeres, like those of most other plants, are composed of tandem arrays of (TTTAGGG)ₙ repeats (Ranks et al., 2011). To gauge the size of S. moellendorffii telomere tracts, we performed terminal restriction fragment (TRF) analysis using TvuI. The blot was hybridized with probe corresponding to four repeats of TTTAGGG. As shown in Figure 1A, S. moellendorffii telomere tracts migrated as a smear ranging from 1.5 to 5.5 kb, closely resembling telomere profile in many A. thaliana accessions (Richards and Ausubel, 1988; Shakirov and Shippen, 2004).

We verified that sequences detected by TRF analysis correspond to chromosome ends using the non-specific Bal31 exonuclease. Bal31 preferentially degrades DNA ends versus more internal genomic regions. DNA was pre-incubated with Bal31 prior to digestion with TvuI, and a Southern blot was performed. After 15 min of Bal31 digestion, the hybridization products migrated faster on the gel and showed reduced intensity (Figure 1B, lane 2). With continued Bal31 incubation, the telomeric signal disappeared completely (Figure 1B, lanes 3–6). In contrast, several cross-hybridizing bands, corresponding to interstitial telomeric DNA were insensitive to Bal31 digestion for up to 90 min, supporting the conclusion that the Bal31-sensitive hybridization signal corresponds to terminal telomeric DNA. Thus, S. moellendorffii telomeres are comprised of 1.5–5.5 kb tracts of TTTAGGG repeats.

TELOMERE-RELATED GENES IN S. MOELENDOFFII POT1 proteins

Single-strand (ss) telomere-binding proteins represent a key component of the telomere cap. Such proteins control telomerase access to the telomere and ensure chromosome end protection (de Lange, 2009). Overall, ss telomere binding proteins share limited sequence similarity, but they all bear signature N-terminal oligomeric/dodecamer/oligosaccharide folds (Osemlaks). One key ss telomere binding protein is Protection of telomeres (POT1; Baumann and Cech, 2001). In the moss Physcomitrella patens, a single-copy POT1 gene encodes a typical DNA binding protein that efficiently binds ss telomeric substrates in vitro (Shakirov et al., 2010). Furthermore, similar to its mammalian and fission yeast counterparts, P. patens POT1 is involved in telomere end protection (capping). While PyPOT1-deficient moss can survive long-term in culture, the mutant strain is sterile and shows end-to-end chromosome fusions, indicating that the overall telomere protective function of POT1 is conserved between early diverging land plants and other eukaryotes (Shakirov et al., 2010).

Despite conservation of POT1 function in the earliest land plant lineages, several lines of biochemical and genetic evidence indicate that the functions of POT1 in vascular plants (starting with S. moellendorffii) may have changed substantially. First, biochemical analysis of POT1 proteins from 13 plants representing major evolutionary branches of plants has indicated that the ability to bind telomeric DNA has been lost for most plant POT1 proteins, including POT1 from S. moellendorffii (Shakirov et al., 2009a,b). In fact, besides the P. patens POT1 protein and its ortholog from the green alga Ostreococcus lucimarinus, only two other POT1 proteins (from Asparagus officinalis and Z. mays) out of a total of 16 surveyed have retained the capacity to bind telomeric DNA in vitro (Shakirov et al., 2009b). However, both A. officinalis and Z. mays are unusual plants with respect to telomere biology. A. officinalis possesses unconventional telomere repeats TTAGGG instead of the canonical TTTAGGG, while Z. mays belongs to the only plant family surveyed other than Brassicaceae that harbors duplicated POT1 genes (Shakirov et al., 2010).
Thus, the ability of POT1 proteins from A. officinalis and Z. mays to bind telomeric DNA may have been conserved due to unusual changes in organismal telomere biology (A. officinalis) or protein sub-functionalization (Z. mays). Alternatively, the ability of A. officinalis and Z. mays POT1 proteins to bind telomeric DNA may have evolved independently through parallel evolution.

The second line of evidence supporting unusually fast evolution of POT1 functions in vascular plants comes from the studies of A. thaliana. Unlike the situation in humans and most other organisms, A. thaliana and other members of the Brassicaceae family possess two full-length POT1 proteins (Shakirov et al., 2005, 2009b). Genetic and biochemical studies indicate that APOT1a is a positive regulator of telomere length working in the context of telomeres holostemymene (Sunovska et al., 2007). In contrast, POT1b is implicated in chromosome end protection (Shakirov et al., 2005). Notably, APOT1a has a high binding specificity for the RNA subunit of telomerase (Cifuentes-Rojas et al., 2011), an unexpected mode of action for an OB-fold containing protein originally evolved to bind DNA. Unlike A. thaliana, but similar to the situation in P. patens, the S. moellendorffii genome encodes only a single POT1 protein. As expected from phylogenetic positions of their corresponding species, S. moellendorffii POT1 shares more amino acid similarity with P. patens POT1 (46%), than with A. thaliana POT1 proteins (46% to APOT1a and 47% to APOT1b; Shakirov et al., 2009b). Despite the overall higher amino acid conservation between P. patens and S. moellendorffii POT1 proteins, the loss of telomeric DNA binding capacity (Shakirov et al., 2009b) clearly suggests that the functional role of POT1 in S. moellendorffii telomere biology may in fact be more analogous to the situation in A. thaliana than in P. patens. Determining whether P. patens POT1 binds telomerase RNA must await the identification of this molecule in moss.

**TRF proteins**

The second class of telomeric DNA binding proteins associates with ds telomeric DNA. This family of telomere repeat binding factors (TRF) shares a conserved Myb-related DNA binding domain in the C-terminals and a central dimerization domain (Bilaud et al., 1996). Mammals and other vertebrates encode two ds telomere binding proteins, TRF1 and TRF2, with distinct functions in telomere homeostasis. TRF1 is thought to act primarily in telomere length control, while TRF2 is required for chromosome end protection through participation in T-loop formation (Broccoli et al., 1997; Griffith et al., 1999).

Unlike vertebrates, plants possess two related families of TRF-like (TRF) proteins, class I and class II (Chen et al., 2001; Hwang et al., 2001; Karamysheva et al., 2004). In A. thaliana, there are 12 TRF proteins, 6 in class I and 6 in class II. Members of class II do not bind ds TTAGGG repeats in vitro. In contrast, all six members of class I specifically bind ds telomeric DNA (Karamysheva et al., 2004). This interaction is dependent on the presence of a unique plant-specific Myb-extension motif, located at the extreme C-terminals of the TRF1 protein (Figure 2). Overall, plants display remarkable variation in the number of class I TRF genes. In dicot species, TRF1 gene amplification appears to be a common theme, with three genes in grapes (Vitis vinifera), five genes in poplar (Populus trichocarpa), and six genes in A. thaliana (Table 1). In contrast, sequenced genomes of monocots and non-flowering plants, including S. moellendorffii, harbor 2 or 3 TRF1 genes. While the precise role of individual TRF1 proteins in plants remains unclear, amplification of TRF1 gene family may provide a route for sub- and neo-functionalization with the potential for more dynamic control of telomere length or telomerase activity.

We also examined the evolutionary relationship of the available class I full-length plant TRF1 proteins, using three A. thaliana class II proteins as the outgroup (Figure 3). As expected, class II proteins form a separate clade distinct from class I, consistent with the lack of the C-terminal Myb-extension motif. The evolutionary relationship of class I proteins correlates with the phylogenetic position of the corresponding plant species. Notably, the two TRF1 proteins from green algae form a sister clade to all TRF1 proteins from land plants, suggesting significant sequence divergence in this ancestral lineage.

**CST components**

A third group of evolutionarily conserved plant telomere proteins is a trimeric complex composed of CTC1, STN1, and TEN1, termed CST (Price et al., 2010). In the budding yeast Saccharomyces cerevisiae, a similar complex, composed of Cdc13, Stn1, and Ten1 proteins, was described over 20 years ago, but only recently has this complex come to light in multicellular eukaryotes (Wellinger, 2009). Individual CST components are highly divergent, with only 10–20% amino acid sequence identity between corresponding proteins from different eukaryotic lineages (Price et al., 2010). A. thaliana mutants deficient in STN1 and CTC1 are characterized by severe defects in telomere maintenance, massive end-to-end chromosome fusions, and elevated rates of telomere recombinant DNA replication (Song et al., 2008; Sunovska et al., 2009). As in vertebrates (Casted et al., 2009), the A. thaliana CTC1 subunit of CST physically interacts with the catalytic subunit of DNA polymerase α (Price et al., 2010), thus linking the CST complex to the telomere replication pathway.

To gain a better understanding of the evolution of CST complex in plants, we looked for the presence of genes encoding CST complex subunits in selected plant species with completely sequenced genomes. Single-copy STN1 and TEN1 genes were found in all organisms surveyed (Table 2). In addition, with the exception of the green alga O. lucimarinus, a single copy of CTC1 gene was also identified in all plant species analyzed, including S. moellendorffii (Table 2). The apparent absence of a clear CTC1 homolog in O. lucimarinus is intriguing. Strikingly, none of the CTC1 orthologs can be readily identified in several species of genera Chlamydomonas, Micromonas, and Chlorella, which belong to evolutionarily distinct lineages of green algae. These data indicate that either CTC1 sequence has diverged beyond recognition or that in green algae this protein has been functionally replaced by an unrelated polypeptide. This observation is in line with the observed sequence divergence of green algae TRF1 proteins and suggests that many components of the telomere complex in green algae diverged substantially from their counterparts in land plants.
**Figure 2**: Multiple alignment of C-terminal regions of plant group I TRFL proteins. Position of conserved plant-specific MYB-extension motif is indicated. Abbreviations: At, *Arabidopsis thaliana*; Cp, *Carica papaya*; Pt, *Populus trichocarpa*; Vv, *Vitis vinifera*; Oy, *Oryza sativa*; Sb, *Sorghum bicolor*; Bd, *Brachypodium distachyon*; Pp, *Physcomitrella patens*; Sm, *Selaginella moellendorffii*; Ol, *Ostreococcus lucimarinus*.

Accession IDs: AtTBP1, NP_196886; AtTRP1, NP_200751; AtTRFL1, NP_190243; AtTRFL2, NP_172234; AtTRFL4, NP_190947; AtTRFL9, NP_187862; CpTRFL1, EU909205; CpTRFL2, EU909206; PtTRFL1, XM_002316243; PtTRFL2, XM_002311138; PpTRFL1, XP_001771004; PpTRFL2, XP_001767955; SmTRFL2, XP_002979224.1; SmTRFL3, EF J24726; SmTRFL1, XP_002984862.1; OlTRFL1, XP_001421395.1; OlTRFL2, XP_001416857.1. Protein alignment was generated using MEGA5 software (Tamura et al., 2011) and visualized in the BOXSHADE format.

**Table 1**: Putative TRFL genes in selected plants with sequenced genomes.

| Species               | Plant lineage | Number of TRFL genes | Sequence IDs                                                                 | References                                |
|-----------------------|---------------|-----------------------|------------------------------------------------------------------------------|-------------------------------------------|
| *Vitis vinifera*      | Dicot         | 3                     | CBI30542, CBI16113, CB31661                                                  |                                            |
| *Populus trichocarpa* | Dicot         | 5                     | XM_002316243, XM_002311138, XP_002313432, XM_002316852, XM_002306128         | Hwang et al. (2001), Chen et al. (2001)    |
| *Carica papaya*       | Dicot         | 2                     | EU909205, EU909206                                                          | Shakirov et al. (2008)                    |
| *Arabidopsis thaliana*| Dicot         | 6                     | NP_196886, NP_200751, NP_190243, NP_172234, NP_190947, NP_187862             | Hwang et al. (2001), Chen et al. (2001)    |
| *Oryza sativa*        | Monocot       | 2                     | AF242398.1, ABF95241                                                         | Yu et al. (2003)                          |
| *Brachypodium distachyon* | Monocot     | 3                     | XP_003565159, XP_00356519, XP_003558236                                     |                                            |
| *Sorghum bicolor*     | Monocot       | 2                     | XP_00246687.1, XP_002468104                                                  |                                            |
| *Selaginella moellendorffii* | Monocot | 3                     | XP_002979234, XP_002984862                                                  |                                            |
| *Physcomitrella patens* | Bryophyte   | 2                     | Bp0173004.1, BP0173004.1                                                    |                                            |
| *Ostreococcus lucimarinus* | Green alga  | 2                     | XP_001421395.1, XP_001416857                                                 |                                            |
Interestingly, it has been argued that the budding yeast *S. cerevisiae* replaced CTC1 with Cdc13 (Mitton-Fry et al., 2002). The two proteins share little sequence similarity, but possess structurally similar OB-fold DNA binding domains and interact with well-conserved protein binding partners (STN1 and TEN1). Our genome analysis indicates that single-copy genes encoding CST complex subunits are present in all land plants analyzed, from the earlier evolved non-seed plant lineages, represented by *P. patens* and *S. moellendorffii*, to the more developmentally advanced flowering plants. Thus, the important functions of CST complex in chromosome end protection and/or telomere replication are likely to be conserved throughout evolution of land plants.

### CONCLUSION AND OUTLOOK

Lycophytes occupy a unique phylogenetic position in the evolution of land plants, as they are ancient representatives of vascular plants and sister to Euphyllophytes (which include flowering plants). Since most components of the telomere maintenance machinery have previously been analyzed only in Angiosperms, we examined the telomere repeat array and sequence homologs of telomere-related factors in *S. moellendorffii*. As in *A. thaliana* and *P. patens*, telomere tracts are short and consist of the canonical TTAGGG repeat. Furthermore, similar to the situation in Angiosperms and other land plants, the *S. moellendorffii* genome harbors homologs of POT1, TRF1, STN1, CTCL, and TEN1 genes. Finally, our study revealed marked sequence divergence in telomere components of green algae relative to *S. moellendorffii*, arguing that future comparative studies among these organisms may provide important insight into the evolution of the telomere complex in plants.

### MATERIALS AND METHODS

#### TELOMERE LENGTH ANALYSIS AND Bal31 DIGESTION

*Selaginella moellendorffii* DNA was extracted as described by Cocciolone and Cone (1993). To detect telomeric DNA repeats, genomic DNA was digested with *Tsp*11 (Fermentas; recognition sequence TTAA) and subjected to Southern blotting with 32P-labeled (TTTAGGG)4 as a probe (Fitzgerald et al., 1999). Radioactive signals were scanned by a STORM PhosphorImager (Molecular Dynamics), and the data were analyzed by IMAGEQUANT software (Molecular Dynamics). For the Bal31 exonuclease assay, 100 μg of *S. moellendorffii* genomic DNA was incubated with 50 units of Bal31 (New England Biolabs) or with H2O (0 min time point) in 1 × Bal31 reaction buffer at 30°C. Equal amounts of sample were removed at 15 or 30 min intervals for 90 min. Reactions were stopped by the addition of 20 mM EDTA and heating to 65°C for 15 min. DNA in each sample was precipitated with isopropanol and ammonium acetate, followed by *Tsp*11 digestion. Digested DNA was separated on 0.8% agarose, blotted onto a nitrocellulose membrane and subjected to hybridization as described above.

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**Table 2 | Putative CST complex proteins from selected plants with sequenced genomes.**

| Species          | STN1  | TEN1  | CTCL  |
|------------------|-------|-------|-------|
| Vitis vinifera   | XP_003623221 | CB_03529 | CAN_0783971 |
| Papuus trichocarpa | EEE94597     | EEF08821  | XM_002302411 |
| Carex papaya     | JX198668    | JX198687  | JX19865   |
| Arabidopsis      | NP_0637581.1| NP_170222.2| NP_00118660.1 |
| Selaginella      | EEE9510     | EAZ28641  | EEE96801.1 |
| Physcomitrella   | XP_00357913 | JX198668  | XP_003576480.1 |
| Oryza sativa     | ERI0221.1   | ERE95890.1| XP_002462303.1 |
| Arabidopsis      | PS012678    | PS02686   | PS029653031.1 |
| Physcomitrella   | EDQ7436     | XP_001782219.1| EDGA49634 |
| Oryza sativa     | EEE5910     | EER95890.1| XP_002462303.1 |
| Arabidopsis      | EFJ12878    | EFJ2686   | EFJ26866 |
| Brachypodium     | XP_00357913 | JX198668  | XP_003576480.1 |
| Oryza sativa     | EEF08821    | XP_002302411 |         |
| Physcomitrella   | EEE9510     | EAZ28641  | EEE96801.1 |
| Oryza sativa     | EEF08821    | XP_002302411 |         |

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ADDENDUM

The occurrence of Arabidopsis-type telomeres was previously shown by FISH in Selaginella martensii [J. Fuchs and I. Schubert “Arabidopsis-type telomere sequences on chromosome termini of Selaginella martensii (Pteridophyta)” Biol. Zent. Bl. 115, 260–265, 1996].