



Great moments in evolution: the conquest of land by plants

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500 Ma ago the terrestrial habitat was a barren, unwelcoming place for species other than, for example, bacteria or fungi. Most probably, filamentous freshwater algae adapted to aerial conditions and eventually conquered land. Adaptation to a severely different habitat apparently included sturdy cell walls enabling an erect body plan as well as protection against abiotic stresses such as ultraviolet radiation, drought and varying temperature. To thrive on land, plants probably required more elaborate signaling pathways to react to diverse environmental conditions, and phytohormones to control developmental programs. Many such plant-typical features have been studied in flowering plants, but their evolutionary origins were long clouded. With the sequencing of a moss genome a decade ago, inference of ancestral land plant states using comparative genomics, phylogenomics and evolutionary developmental approaches began in earnest. In the past few years, the ever increasing availability of genomic and transcriptomic data of organisms representing the earliest common ancestors of the plant tree of life has much informed our understanding of the conquest of land by plants.

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Current Opinion in Plant Biology 2018, 42:49–54

This review comes from a themed issue on **Genome studies and molecular genetics**

Edited by **Yves Van de Peer** and **J Chris Pires**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 8th March 2018

<https://doi.org/10.1016/j.pbi.2018.02.006>

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Introduction

‘We can state unequivocally that without green land plants there would be no land animals, including humans.’ [1]. Hence, occupation of land by plants was a crucial evolutionary step (Figure 1), not only for humans/animals, but also for biodiversity in general. Photosynthesis by cyanobacteria since ca. 3000 Ma ago, and later (ca. 1500 Ma ago) eukaryotic algae, led to the

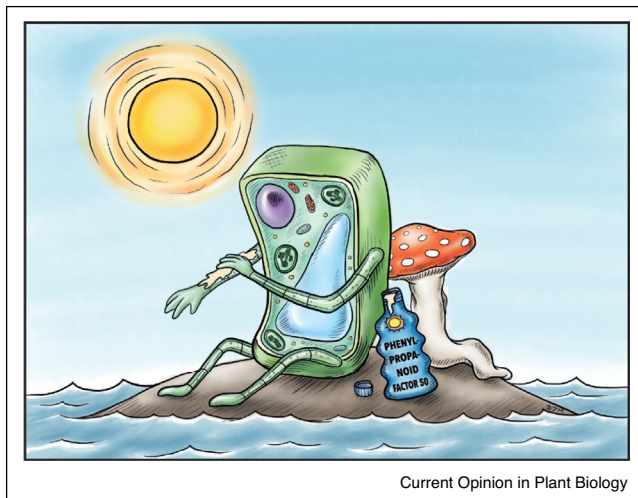
steady increase of atmospheric oxygen [2]. Although not as pronounced as today [3], the ozone layer reduced the amount of ultraviolet radiation hitting the ground, probably representing one factor that allowed organisms to emerge from the water. Early land plants then not only generated even larger amounts of oxygen, but they also significantly weathered the rock [4,5].

The likely sequence of events leading to the colonization of land by plants is that some marine green algae (Chlorophyta) first adapted to freshwater habitats, and from there some evolved into land plants [6]. It is, however, also conceivable that green algae evolved in freshwater, and subsequently made the habitat transition to seawater as well as to land [7]. In any case, it is important to note that the habitat transition that enabled plant life was from freshwater to land. Consequently, one needs to study the closest freshwater relatives of land plants in order to better understand plant terrestrialization. Since the fossil record is scarce, extant species have to be used to infer evolutionary events.

The **Streptophyta** are a **monophyletic clade** within the **Viridiplantae** (green plants or green lineage, including green algae). **Streptophyta** encompass several lineages of streptophytic (**charophytic**) algae, as well as the land plants (**Embryophyta**). The streptophytic algae are a **polyphyletic grade** and it has only recently been accepted that among them most probably the **Zygnematomyceae** are the closest relatives to land plants [8[•],9,10[•]]. Because of the high morphological complexity of the **Charophyceae**, and their land plant-like body plan, they were earlier considered to be the land plant sister group [11]. Three of the lineages of charophytes, namely **Charophyceae**, **Coleochaetophyceae** and **Zygnematomyceae**, exhibit a microtubular array that helps to establish the new cell wall after division, the **phragmoplast**. Together with the land plants, these three lineages are thus united in the monophyletic clade **Phragmoplastophyta** (or **Streptophytina**) [12].

The group of organisms that first evolved on land is probably best represented by extant **bryophytes**, comprising **mosses**, **liverworts** and **hornworts** [13[•]]. The branching order of this group has been highly debated and is as yet unresolved. Recent phylogenomics data suggest that mosses and liverworts are monophyletic, and that the hornworts might represent the sister lineage to all other land plants [8[•]]. In any case, the bryophytes are sister to the vascular plants. Within the latter, lycophytes and

Figure 1



Another great moment in evolution. Inspired by the classical 'Great moments in evolution' cartoon by Gary Larson, this figure illustrates some of the key features that probably enabled early plants to thrive on land: the rigid cell wall, several plastids per cell, phenylpropanoids enabling protection for example, to ultraviolet-B radiation, and the mutualistic interaction with fungi to gain access to inorganic nutrients; artwork by Debbie Maizels.

ferns are successively sister to the seed plants. In summary, in order to infer how land plants evolved one needs to study the extant lineages representing the closest freshwater relatives of land plants, the algae at the basis of the Phragmoplastophyta, as well as extant descendants of those non-vascular lineages that diverged early after the water-to-land-transition from their common ancestor with vascular plants, the bryophyte, and compare them with vascular plants. In this review I will focus on studies using these organisms to unravel early land plant evolution.

The move to land

The last common ancestor of the Phragmoplastophyta was hypothesized to have been filamentous and to have possessed the ability to generate side branches, that is to direct the cell division plane [10[•]]. The land plant-like cell wall, enabled among others by the phragmoplast and the rosette-like cellulose synthase complexes, was one of the key features enabling terrestrialization (Figure 1). Some extant charophytes are able to live on land, and hence it has been proposed that the adaptation to land via a rigid cell wall preceded the evolution of other important land plant features [14[•]].

As pointed out above, all Phragmoplastophyta share unique land-plant like features. However, the Zygnematomyceae, the sister group to land plants display some molecular changes that most probably evolved in the last common ancestor of Zygnematomyceae and land plants.

Among those is the transfer of some **plastid**-encoded genes to the nucleus, that has been argued to have been instrumental in establishing the 'embryoplast', a type of plastid that enabled the subsequent evolution of poly-plastidy (i.e. coordination of cell and plastid division; Figure 1), as well as the subfunctionalization into specialized plastid types as known from flowering plants (e.g. **amyloplasts** or **chromoplasts**) [15[•]]. Indeed, coordination of plastid division might have been an important feature during land plant evolution. Plastids were originally engulfed by **peptidoglycan**, and there is evidence that the genes controlling the division of this plastid wall (present in charophytes and bryophytes) were replaced together with the peptidoglycan shell during vascular plant evolution [16,17].

The alternation of generations and embryogenesis

The observation that all land plants alternate between two multicellular stages ('generations'), the **haploid gametophyte** and the **diploid sporophyte**, was made more than 150 years ago [18]. All green algae and charophytes are **haplonts**, that is, the only diploid stage is the zygote, while all land plants are **haplodiplonts**, possessing two mitotically dividing stages of different ploidy [19[•]]. Around a century ago, it was hypothesized that by establishment of mitotic division in the diploid zygote the alternation of generations evolved in the last common ancestor of land plants [20]. Land plants are Embryophyta (embryo plants), which is due to the fact that they perform embryogenesis, that is the early developmental progression from zygote to embryo, the latter possessing a three-dimensional body plan characterised by polarity and symmetry breaking [19[•]]. Recent studies primarily conducted in the model moss, *Physcomitrella patens* [21,22[•]], have revealed by comparison with vascular plants details about the evolution of the alternation of generations and embryogenesis. For example, it has been shown that **homeodomain** (HD) transcription factors (TF) of the KNOX family repress the execution of the gametophytic *bauplan* in the diploid generation [23]. Another HD TF, **BELL**, is involved both in the formation or division of the zygote, and in sporophyte development [24,25]. In the liverwort *Marchantia polymorpha*, the genome sequence of which has recently been published [26[•]], it has been shown that an RWP-RK family TF keeps egg cells quiescent in the absence of fertilization [27] and controls the formation of germ cells [28]. Comparison of such studies with data from flowering plants, in which the gametophyte is highly reduced and harder to access, allows inference of the ancestral situation. For example, gametangia development in *M. polymorpha* is controlled by MpBNB, an ortholog of the AtBNB1/2 gene pair that controls pollen generative cell formation [29]. Since MpBNB can complement AtBNB function, the involvement of these TFs in sexual reproduction has apparently been conserved since the earliest land plants. The

prevalent hypothesis currently is that genes and gene regulatory networks of the gametophyte were recruited during vascular plant evolution to serve the sporophyte [13^{••}].

Evolution of protective phenylpropanoids

The presence of absorbing pigments is related to the amount of UV-B irradiation [3], and UV-B absorbing pigments such as flavonoids and their biosynthesis genes are an ancestral molecular adaptation of land plants [30] (Figure 1). Flavonoids are phenylpropanoids, secondary metabolites that have many protective functions. For example, sporopollenin is a major protective compound of the moss spore and seed coat [3,31]. Lignin precursor metabolism evolved in early land plants and allows the formation of cuticles that protect from drought [32,33]. It has recently been hypothesized that all these biosynthetic pathways evolved by gene duplication, retention and sub-functionalization and neofunctionalization based on existing biosynthetic pathways [34^{••}]. As with other features previously thought to have evolved in land plants, the phenylpropanoid pathway evolved early in the diversification of streptophytes, before the origin of land plants [35].

Phytohormones

Probably the most ancestral phytohormones are auxin and cytokinin. For example, the charophyte alga *Klebsormidium nitens* shows auxin response [36,37] and PIN auxin transporters apparently evolved in the last common ancestor of charophytes [38]; some cytokinin-related genes can be traced back to unicellular green algae, while for example, the receptor evolved in the last common ancestor of land plants [39]. Strigolactones are present in Charophyceae and stimulate the elongation of rhizoids (rooting structures) in these organisms, as well as in mosses and liverworts [40[•],41], suggesting they evolved in the common ancestor of Phragmoplastophyta. Ethylene biosynthesis and responses have been demonstrated in Zygnematophyceae [42]. Using comparative genomics and phylogenetics, it was confirmed that cytokinin, auxin and strigolactone signaling pathways evolved in the last common ancestor of charophytes, while abscisic acid, jasmonate and salicylic acid signaling evolved in the last common ancestor of land plants [43]. Abscisic acid (ABA) signaling is controlled by orthologous genes in *P. patens* and flowering plants [44], uses similar TF binding sites [45] and is synthesized in the same way [46]. However, the regulation of desiccation tolerance in *P. patens* uses genes not found in flowering plants [47], and while ABA plays a crucial role in seed germination it affects moss spores in a non-essential way [48]. Recently, how auxin, cytokinin and strigolactone control shoot formation in *P. patens* has been analysed and contrasted with knowledge from flowering plants [49]. Notable differences include the transport of auxin, which is basipetal in flowering plants and bi-directional in *P. patens*.

The mycorrhizal landing hypothesis

It was hypothesized that the conquest of land by plants was aided by mutualistic symbiotic interactions with microorganisms, in particular with fungi (Figure 1). While Glomeromycota are the fungal group involved in development of mycorrhiza in the majority of seed plants, Mucoromycotina have recently been argued to have been interacting with the earliest land plants as well [50,51], at a time when there was more CO₂ in the atmosphere and plants did not have roots. Mycorrhizal signaling is induced by the phytohormone strigolactone, its symbiotic function probably evolved with the freshwater to land habitat transition [52]. Intriguingly, although extant mosses are not known to mutualistically interact with mycorrhizal fungi, they contain most of the conserved genetic toolkit for such interactions [52,53], even though these genes are usually lost in flowering plants that do not engage in symbiosis [54]. Synthesis of strigolactones in moss is controlled by phosphate starvation [55], a condition that — in flowering plants — can be remedied by interaction with mycorrhizal fungi.

Conserved transcriptional control and signaling

Extant bryophytes have a dominant gametophyte, the sporophyte is nutritionally dependant. Ferns possess free-living gametophytes and sporophytes, while in seed plants the sporophyte is dominant and the gametophyte heavily reduced. Most probably, these extant examples exemplify the gain of sporophytic complexity during land plant evolution [20,56,57]. Given this theory, regulatory networks controlling the ever more complex sporophyte should arise by co-option of gametophytic genes, and by gene duplication followed by sub-functionalization and neofunctionalization [58]. Indeed, there is now ample evidence that gametophytic genes were co-opted during land plant evolution [59], and that ancestral TF networks are controlling similar developmental processes, for example, in the moss gametophyte and the flowering plant sporophyte [60]. For example, bHLH TFs control the formation of rhizoids and other protrusions in bryophytes, and the formation of root hairs in flowering plants [61[•],62]. Light signaling via phytochrome interacting factors (PIF, also bHLH TFs) was present in the earliest land plants [63,64] and might have its evolutionary roots in charophytes. The UV-B receptor has been largely functionally conserved since the earliest land plants [65], as well as downstream signaling components like COP/SPA and HY5 [66,67].

Conclusions and outlook

The first genomes of flagellated plants (non-seed plants) have much informed our understanding of land plant evolution [21,26[•],68]. *Marchantia* features a very much reduced set of genes and shows no evidence of ancestral polyploidization [26[•],69[•]], but mutualistically interacts with mycorrhizal fungi [70]. *Physcomitrella* went through

two genome duplications, features gene redundancy rivaling flowering plants (but shows a different genome structure lacking evidence of large eu-chromatic and heterochromatic regions [22*]) and is thought not to associate with mycorrhizal fungi. Are these differences peculiar for certain lineages, or generalizable for liverworts and mosses? Since liverworts and mosses apparently form a monophyletic clade [8**,69*], which features had their common ancestor, and how do hornwort genomes compare to them (that might be part of a monophyletic Bryophyta clade [69*])? Recently, transcriptomic data of charophyte algae and bryophytes were used to infer further details of early evolutionary events around the water-to-land-transition. Since transcriptomic data, however, are usually incomplete we need more genome sequences representing all early branches of the Phragmoplastophyta, to answer pending questions. Such data is forthcoming and will be used to further our understanding of early land plant evolution.

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