Evo-physio: on stress responses and the earliest land plants

Janine M.R. Fürst-Jansen, Sophie de Vries, and Jan de Vries

Abstract

Embryophytes (land plants) can be found in almost any habitat on the Earth’s surface. All of this ecologically diverse embryophytic flora arose from algae through a singular evolutionary event. Traits that were, by their nature, indispensable for the singular conquest of land by plants were those that are key for overcoming terrestrial stressors. Not surprisingly, the biology of land plant cells is shaped by a core signaling network that connects environmental cues, such as stressors, to the appropriate responses—which, thus, modulate growth and physiology. When did this network emerge? Was it already present when plant terrestrialization was in its infancy? A comparative approach between land plants and their algal relatives, the streptophyte algae, allows us to tackle such questions and resolve parts of the biology of the earliest land plants. Exploring the biology of the earliest land plants might shed light on exactly how they overcame the challenges of terrestrialization. Here, we outline the approaches and rationale underlying comparative analyses towards inferring the genetic toolkit for the stress response that aided the earliest land plants in their conquest of land.

Keywords: Charophytes, earliest land plants, exaptations, plant evolution, plant terrestrialization, streptophyte algae, stress physiology, terrestrial algae.

Introduction

Green evolution: from the origin of photosynthetic eukaryotes to the earliest land plants

Photosynthetic eukaryotes probably first emerged >1.5 billion years ago (Butterfield, 2000; Eme et al., 2014; Bengtson et al., 2017). Underlying the origin of photosynthetic eukaryotes was the endosymbiotic uptake of a free-living cyanobacterium by a heterotrophic protist—an event that gave rise to the Archaeplastida (reviewed by Archibald, 2015; Martin et al., 2015; de Vries and Gould, 2018). There are three types of Archaeplastida: the red algae (rhodophytes), the glaucophytes, and the green lineage (Keeling, 2013; Archibald, 2015; Jackson et al., 2015). The green organisms make up the Chloroplastida (Fig. 1)—a name that should be given preference over the previous label for that clade, Viridiplantae (Adl et al., 2005, 2019). Within the Chloroplastida, we find both green algae and the land plants (reviewed by Leliaert et al., 2012; de Vries et al., 2016).

The green lineage separated roughly a billion years ago into the chlorophytes and the streptophytes (Zimmer et al., 2007; Parfrey et al., 2011; Morris et al., 2018). While the chlorophytes are generally perceived as the clade comprising famous
green algae (such as Volvox, Ulva, and Chlamydomonas), the streptophytes are best known as the clade containing the land plants. However, there is more to the lineage of streptophytes. In the phylogeny of streptophytes sits—next to the land plants—the paraphylum of streptophyte algae (Fig. 1). It is this grade that one must turn to in order to understand the origin of land plants.

All land plants evolved from a single streptophyte algal progenitor (reviewed in de Vries and Archibald, 2018). The streptophyte algae are a group of mainly freshwater and terrestrial algae—with a few representatives living in brackish environments (Lewis and McCourt, 2004; Becker and Marin, 2009; Fig. 1). That the streptophyte algal ancestors of land plants lived in freshwater—as opposed to marine—environments is considered a major factor leading to terrestrialization: starting from a freshwater environment such as a pond, there was smooth passage along the hydrological gradient towards land (see discussions in Becker and Marin, 2009; Delwiche and Cooper, 2015; de Vries and Archibald, 2018). It is this stepwise conquest of land along the hydrological gradient where the earliest land plants—or the first common ancestors of land plants—are evolutionarily and ecologically situated (Figs 1, 2). This ecological setting, however, does not constitute a reason for the singular global conquest of land by streptophytes. Indeed, photosynthetic eukaryotes might have had a freshwater origin (Delwiche and Cooper, 2015; de Vries and Archibald, 2017; Lewis, 2017; Ponce-Toledo et al., 2017; Sánchez-Baracaldo et al., 2017). Streptophytes are also not the only photosynthetic eukaryotes that dwell in freshwater environments and on land. Various other algae, including chlorophytes (for an overview, see Holzinger and Karsten, 2013), diatoms (for an overview, see Souffreau et al., 2013), red algae (e.g. Porphyridium, see John,

Fig. 1. Terrestrial organisms are found across the green lineage. A cladogram shows the deep split of the green lineage into the clades Chlorophyta and Streptophyta. The Streptophyta are composed of the paraphylum streptophyte algae and the monophyletic Embryophyta (land plants). Streptophyte algae can be broken up into the paraphyla KCM (for Klebsormidiophyceae, Chlorokybophyceae, and Mesostigmatophyceae) and ZCC (for Zygnematophyceae, Coleochaetophyceae, and Charophyceae; de Vries et al., 2016). ZCC streptophyte algae and land plants form the monophyletic clade Phragmoplastophyta. Taken in their entirety, Chlorophyta occur in habitats ranging from marine saltwater, to freshwater, to terrestrial (row of dots). Streptophyte algae mainly occur in freshwater and terrestrial environments; some Charophyceae live in a brackish habitat. While the Embryophyta are mainly terrestrial, some have secondarily moved back to a freshwater habitat; some have even conquered a new habitat: saltwater (e.g. sea grasses). Inset: the Zygnematophyceae are the closest algal relatives of land plants and they hence share with the clade of Embryophyta the last common ancestor of land plants and algae (yellow dot); along the trajectory from that last common ancestor of land plants and algae (yellow dot) to the last common ancestor of land plants (red dot) are the earliest land plants to be found (orange dot). Inferring the biology of the earliest land plants requires a subtraction of the traits (“adaptations”) that were gained on land, that is en route to the last common ancestor of land plants (from the orange to the red dot; see also Fig. 2).
1942), and many more, are terrestrial, too (Hoffmann, 1989). Hence, the question is not only what allowed for the origin of land plants but also what allowed for their unique success—a success that resulted in the global conquest of land. In this review, we will explore the complexities underlying these questions and make a case for dissecting one—which is by far not the only—key aspect of the biology of the earliest land plants: adequately responding to terrestrial stressors.

**Synapomorphies and the global success of land plants**

Embryophytes (land plants) are defined by a series of traits. For example, land plants undergo a cycle where they alternate between a diploid sporophyte and a haploid gametophyte. An alternation of generations that involve two multicellular generations of different ploidy is one of the features of land plants that sets them apart from their algal ancestors (for more on this topic, see Bowman et al., 2016; Horst et al., 2016; Rensing, 2018). Among such embryophytic traits, we also might find those features that allowed for the success of the monophylum of land plants.

As the name implies, having embryos and embryogenesis is a signature feature of embryophytes. Broadly speaking, the embryo is a parentally supported complex structure with different tissue types. The exact organization and structure of embryos varies across the diversity of land plants concomitant with the dominance of sporophyte and gametophyte (for an overview of the underlying process, see Rensing, 2016). Support both through the parent organism and the structural framework that the embryo defines is thought to have been adaptive for living on land: the pre-defined structure of the embryo leads to an upright body plan with specialized tissues, both of which can foster nutrient uptake and nuanced responses to environmental cues via specialized cells (Rensing, 2016). When pondering the evolution of plant embryos, the seed of spermatophytes comes...
to mind. The seed is a structure that is highly resistant to terrestrial stressors (principally desiccation—see stimulating discussions in Oliver et al., 2000). Seeds obtain their stress resistance through molecular mechanisms such as the accumulation of LATE EMBRYOGENESIS ABUNDANT (LEA; e.g. Dure et al., 1981; Xu et al., 1996) proteins and seed dormancy regulation via abscisic acid (ABA; reviewed in Holdsworth et al., 2008); more on this below. While the seed clearly is a derived structure of spermatophytes, the molecular framework that underpins their stress resilience is probably conserved across the breadth of land plant diversity (Cuming et al., 2007; Eklund et al., 2018). This framework was hence likely to have been present in the last common ancestor of land plants—and potentially even before.

Land plants have evolved a number of complex structures that are adaptive in a terrestrial habitat (Harrison, 2017). Among these structures are stomata. There is much debate about the exact trajectory of stomata evolution; for an overview, see Chater et al. (2017). Yet, it is considered probable that some sort of stomata were a feature of the last common ancestor of land plants (e.g. Duckett and Pressel, 2018). The ancestral function of stomata is, however, ambiguous and much debated (see, for example, Duckett and Pressel, 2018; Pressel et al., 2018). A similar case applies to water-conducting tissues. Land plants need to allocate water from their substrate, which is facilitated by rooting structures that range from rhizoids in non-vascular plants to the ‘true roots’ of vascular plants (reviewed by Jones and Dolan, 2012; Kenrick and Strullu-Derrien, 2014; Hetherington and Dolan, 2017). Root-mediated water conduction from the substrate through the entire plant is a textbook process of vascular plants that is clearly adaptive in aeroterrrestrial environments. Some mosses and liverworts have water-conducting tissues such as hydroids—yet these probably evolved multiple times independently (Ligro et al., 2000) and most do not have water-conducting tissues. Surprisingly, Xu et al. (2014) highlighted that the same group of transcription factors (TFs), the NACs, that regulate xylem differentiation in the vascular plant Arabidopsis thaliana also regulate hydroid differentiation in the moss Physcomitrella patens. This has potential implications for vascular or non-vascular water-conducting cells in the last common ancestor of land plants (see Fig. 2). The findings of Xu et al. (2014) thus underscore the genetic capacity for the earliest land plants to have gained a complex system for water conduction.

This list could be continued but there is a stumbling block to most of the above-named traits: they define land plants as we know them today. These traits were likely to have been present in the last common ancestor of all land plants. Yet, it is difficult to put the gain of these traits into the right order that might enable us to reconstruct a scenario for the origin of land plants. Here the closest streptophyte algal relatives of land plants can help. Among streptophyte algae, we find (i) traits that were once classified as land plant specific and (ii) genes that are required for realizing such traits—even if they are not fully realized in the algae or used in an entirely different manner as in land plants.

**Inferring trait evolution towards understanding the singularity of plant terrestrialization**

The last common ancestor of land plants was an embryophyte. As elaborated in the previous paragraph, this common ancestor must have had an array of the synapomorphic traits that define embryophytes. These traits give a post-hoc perspective on the singularity of the origin of the embryophytic clade: The last common ancestor was probably already established on land. However, when did the decisive traits evolve if we consider the earliest land plants and, thus, the organisms that conquered land (see Fig. 2)? To pinpoint those features that might have allowed for the conquest of land, we have to look at what happened before the last common ancestor of land plants lived—we have to resolve features of the biology of the earliest land plants (Figs 1, 2). To do so, we need to add an informative set of streptophyte algae to the picture.

In the past few years, garnering phylogenetic (e.g. Wickett et al., 2014; Puttick et al., 2018; Leebens-Mack et al., 2019) and sequence data (e.g. Hori et al., 2014; Delaux et al., 2015; Ju et al., 2015; de Vries et al., 2018a; Nishiyama et al., 2018) for streptophytes has gained momentum, resulting in a changing picture of early land plant evolution. In light of these new data, the notion that the embryophyte lineage might be split into two monophyletic groups (Puttick et al., 2018) raises the question of what the properties of the common ancestor of embryophytes might be; its repertoire of traits could have entailed features of both bryophytes (mosses, liverworts, and hornworts) and tracheophytes (vascular plants). Here, a streptophyte algal perspective will help, too. Disentangling the transition from the earliest common ancestor to the last common ancestor of land plants (see also Fig. 2) will not only illuminate the properties present and relevant during the earliest steps of plants on land, but also those at the base of the land plants.

In the previous section, we have listed a number of adaptations of embryophytes to living on land. If we projected their origin onto the trajectory from streptophyte algal ancestor to extant embryophytes, we would find that the streptophyte algal progenitor probably possessed a few of these key traits—at least in a rudimentary fashion. Palpably, these include rhizoids and multicellular growth.

Rhizoids or similar structures can be found in all phragmoplastophytic streptophyte algae. The most obvious cases of these are the multicellular rhizoids of Charophyceae, whose stololiths are even involved in the modulation of gravitropism (e.g. Leitz et al., 1995). The Coleochaetophyceae do not form rhizoids, but have special hairs that rest in a sheath, whose possible homology with rhizoids was discussed by Graham et al. (2012). Among the Zygnematophyceae, which are phylogenetically most closely related to land plants, rhizoid formation for providing anchorage to a substrate has been meticulously described in Spirogyra (Yoshida et al., 2003; Ikegaya et al., 2008; Yoshida and Shimmen, 2009). Rhizoid formation is, hence, a probable feature of the earliest land plants (Fig. 2).

Multicellularity in phragmoplastophytic streptophyte algae can be supported by a simplex meristem/apical cell structure.
Charophyceae have an apical cell at the tip of the shoot-like structure that confers its erect growth (Pickett-Heaps, 1967). In Coleochoae, varying growth morphologies occur that range from branched filaments to discoidal parenchymatous growth (for an overview, see Delwiche and Cooper, 2015). The body plan of the latter is underpinned by meristems (Dupuy et al., 2010). During the course of evolution, the zygnematophycean body plan probably experienced some reduction—as, for example, seen in the desmids that reverted to unicellularity. However, as already indicated previously, some filamentous Zygmatophyceae have a few morphological surprises up their sleeves, including the formation of rhizoidal holdfasts (e.g., Ikegaya et al., 2008) and branching (e.g., Stancheva et al., 2014). Altogether, this suggests that the earliest land plants probably had a body plan that entailed at least branching filaments—if not parenchymatous growth—likely to resemble to some degree the body plans found among the diversity of the genus Coleochoae (Fig. 2; Delwiche and Cooper, 2015). A multicellular body plan facilitates the differentiation of cells that can specialize in the responses to environmental stressors, for example, the uppermost layer of a hypothetical body plan being particularly rich in compounds that act as sunscreens. Thus, multicellularity might have provided selective advantages for the earliest land plants when facing stress on terra firma.

Genetic potential and the evolution of decisive traits

The embryophytic transcriptionally active protein (TAP) repertoire has often been proposed to explain the complex developmental phenotypes and high plasticity in environmental responses of land plants (Lang et al., 2010; Mähönen et al., 2014; Harrison, 2017; Scheres and van der Putten, 2017; Wilhelmsson et al., 2017). Recent studies (Catarino et al., 2016; Wilhelmsson et al., 2017), however, showed that >80% of the TAP family repertoire of land plants is present in streptophyte algal genomes and transcriptomes. It may therefore be assumed that an interconnected network of TAPs and their downstream targets already fine-tuned the biology of the earliest land plants. Importantly, the TAP repertoire does more than the actual function—targets already fine-tuned the biology of the earliest land plants. It may therefore be assumed that an interconnected network of TAPs and their downstream targets already fine-tuned the biology of the earliest land plants.

During the course of evolution, the zygnematophycean body plan probably experienced some reduction—as, for example, seen in the desmids that reverted to unicellularity. However, as already indicated previously, some filamentous Zygmatophyceae have a few morphological surprises up their sleeves, including the formation of rhizoidal holdfasts (e.g., Ikegaya et al., 2008) and branching (e.g., Stancheva et al., 2014).

Altogther, this suggests that the earliest land plants probably had a body plan that entailed at least branching filaments—if not parenchymatous growth—likely to resemble to some degree the body plans found among the diversity of the genus Coleochoae (Fig. 2; Delwiche and Cooper, 2015). A multicellular body plan facilitates the differentiation of cells that can specialize in the responses to environmental stressors, for example, the uppermost layer of a hypothetical body plan being particularly rich in compounds that act as sunscreens. Thus, multicellularity might have provided selective advantages for the earliest land plants when facing stress on terra firma.

GRAS TFs. GRAS TFs regulate both development and stress response of land plants (Hirsch and Oldroyd, 2009; B. Zhang et al., 2018). In the recently reported genome sequence of the two Zygmatophyceae Spirogrca muscicola and Mesotaenium endlicherianum (Cheng et al., 2019), the authors found that already the ancestor of Zygmatophyceae and land plants shared an expanded repertoire of genes coding for GRAS TFs. Some of these GRAS TFs are thus strong candidates for regulating conserved stress responses. Altogether, TAPs offer a plausible explanation for the rapid diversification in form and function (including stress-related) that we see across the diversity of land plants; the potential for this TAP-based radiation of form and function was already present in the algal relatives of land plants.

A tangible example of the fertile ground that the genetic material of streptophyte algae offers is the genetic toolkit to establish an interaction with symbiotic fungi (Delaux et al., 2015). Most (>70%) of the extent diversity of embryophytes engage in symbiosis with arbuscular mycorrhiza that aid in obtaining nutrients from the substrate (Delaux et al., 2014; Field and Pressel, 2018). Land plants use a core signaling toolkit to establish such symbioses (Parniske, 2008). Symbioses with beneficial substrate microbiota are thought to have aided the earliest land plants in gaining a foothold in the terrestrial habitat (Delaux et al., 2013; Field et al., 2015), and orthologous genes that are involved in upstream signaling processes required for the establishment of arbuscular mycorrhizal symbiosis in land plants are present in streptophyte algae (Delaux et al., 2015). Indeed, zygnematophycean orthologs of calcium- and calmodulin-dependent protein kinase (CaCaMK; a key component of the symbiosis toolkit) rescued Medicago mutants defective in this gene and hence mycorrhization (Delaux et al., 2015). Yet, the genetic framework for the downstream signaling has only emerged after diversification of the respective gene families in the ancestor of land plants (Delaux et al., 2015). Thus, building on a conserved chain of upstream signaling, elaborate developmental processes could emerge.

Symbionts are recognized by plants through receptor-like kinases (RLKs), a major family among which are the LysMs (reviewed by Oldroyd, 2013). Pivotal to the establishment of symbioses is the recognition of lipochitoooligosaccharides secreted by arbuscular mycorrhizae via specific LysMs (Oldroyd, 2013; Sun et al., 2015). However, LysMs and other RLKs do not only play a role in formation of arbuscular mycorrhizae but are general players during symbiotic and pathogenic interactions. Fabaceae LysM receptors are involved in the recognition of lipochitoooligosaccharides of rhizobia to establish colonization and nodulation of their hosts’ roots (Limpens et al., 2003; Madsen et al., 2003; Radutoiu et al., 2003; Arrighi et al., 2006; Smit et al., 2007). In addition to their role in symbiotic interactions, different RLKs, including LysMs, are also the gatekeepers of pathogen responses in angiosperms, recognizing conserved molecular patterns of microbes, such as flagellin or chitin (Gómez-Gómez and Boller, 2000; Kaku et al., 2006; Miya et al., 2007). While we have little insight into RLK function in pathogen recognition outside of angiosperms, important insights have come from the moss Physcomitrella patens. Physcomitrella patens is able to sense and respond to chitin and encodes at least one functional chitin sensing CERK1 homolog (Bressendorff et al., 2016). CERK1 is thus one of the few LysM-RLKs that was probably involved in plant immune
signaling (upon being challenged by fungi) in the last common ancestor of all land plants.

The genome of *Chara braunii* provided some insight into the evolutionary history of LysM receptors (*Nishiyama et al.*, 2018). It appears that the common ancestor of *C. braunii* and land plants may have had a single LysM member and that each lineage has undergone their specific family expansions. Without functional studies, it is thus equally plausible that LysMs of streptophyte algae function in response to pathogens or symbionts—or both; hence, the same ambiguity currently applies to inferences of LysM function in the earliest land plants. What we know, however, is that streptophyte algae have the genetic toolkit to sense microbial associates, mutualistic or pathogenic microorganisms. Streptophyte algae associate with an entire microbiome of fungi and bacteria (*Knack et al.*, 2015) and we can predict, based on the presence of LysMs, that they are able to recognize and respond to these microbes in some manner. A similar prediction may be made for the earliest land plants.

It was argued that fungi evolved the ability to degrade plant material before land plants came to be (*Berbee et al.*, 2017). This suggests, as one would expect, that not all of the earliest land plants’ microbiome was friendly; they might have been assaulted by foes that their ancestor already faced in freshwater habitats. Another type of pathogen receptor is shared by streptophyte algae and land plants: the intracellular resistance (*R*) genes that encode proteins with nucleotide-binding domain and leucine-rich-repeat (NBS-LRR) domains (*Gao et al.*, 2018; *Han*, 2019). Yet, again, streptophyte algae seem to have evolved different domain associations from land plants and only a few land plant-like proteins of the toll interleukin 1 receptor (TIR)-NBS-LRR class are present in some streptophyte algae (*Gao et al.*, 2018; *Han*, 2019).

Only through detailed studies of the interactions between streptophyte algae and their microbiome (see *Delaux et al.*, 2015; *Knack et al.*, 2015; *Gao et al.*, 2018; reviewed in *de Vries et al.*, 2018; *Han*, 2019) will we be able to infer the plant–microbe interaction toolkit of the earliest land plants. Yet as to the exact components that the earliest land plants used, the power of inference based on extant systems might be limited: receptor families have undergone many lineage-specific expansions and reductions, and are co-opted for their specific environment, of which further hinges on the duration of a stress (*Kranmer et al.*, 2010). The connection between stress input and adjustment is mediated by the plant perceptor. The plant perceptor is a layered network of input signals converging in signal transduction pathways that target regulators of plant growth and physiology (*Scheres and van der Putten*, 2017). This response system can be considered as an additional defining trait of embryophytes. It is conceivable that the roots of this trait run deeper—already the earliest land plants had to successfully overcome the challenges that the terrestrial stressors posed in order to first colonize land and then radiate on it.

Streptophyte algae are now known to have genes for stress response that were previously thought to be characteristic for land plants. While the functions of many of these genes have not yet been tested, their mere presence warrants attention. These genes represent the ancestral gene pool from which the embryophytic genes with functions in stress response have evolved. When exactly the embryophytic function (if there is a unique function among all embryophytes) evolved can only be identified by a combination of comparative functional and bioinformatic approaches across and outside the monophyletic land plants. Independent of the function they hold nowadays in streptophyte algae, it is these genes that are prime candidates for being part of the ‘terrestrialization toolkit’. The idea is that this toolkit entitled adaptive and exaptive genes that provided a selective advantage during plant terrestrialization (see also *de Vries and Archibald*, 2018). Standing out among these candidates is the notion that streptophyte algae have the genetic capacity to utilize phytohormone-based signaling pathways (*Delaux et al.*, 2012; *Hori et al.*, 2014; *Ju et al.*, 2015; *Van de Poel et al.*, 2016; *Ohtaka et al.*, 2017; *de Vries et al.*, 2018a; *Mutte et al.*, 2018; *Nishiyama et al.*, 2018). In land plants, phytohormones interact in converging networks of regulatory circuits (*Kohli et al.*, 2013) many of which are part of the plant perceptor that is put to use when dealing with environmental cues (*Scheres and van der Putten*, 2017).

Auxin is arguably the most famous phytohormone. Polar transport of auxin is a cornerstone in the development of land plants (e.g. *Friml et al.*, 2003) and it orchestrates developmental processes throughout the plant body (*Weijers and Wagner*, 2016). In recent years, auxin has further been recognized to be a major player in the adjustment of the cell biology of plants to stress cues (*Naser and Shani*, 2016; *Blakeslee et al.*, 2019). Auxin has been detected in streptophyte algae and its polar transport has been described in Klebsormidiophyceae and Charophyceae—suggesting that polar auxin transport was an early invention (*Cooke et al.*, 2002; *Boot et al.*, 2012; *Hori et al.*, 2014; *Ohtaka et al.*, 2017). It appears however, that polar auxin transport is not present in all streptophyte algal lineages. Indeed, the KtPIN homolog of *Klebsormidium flaccidum* is an

---

**Streptophytic stress signaling: the evolution of an essential prerequisite for the conquest of land**

Dwelling on *terra firma* comes with various challenges. Foremost among these are various abiotic stressors, including drought and desiccation, UV irradiation, and rapid changes in temperature—but also changes in substrate quality such as pH, salinity, and nutrient variation. Land plants have evolved an elaborate stress response framework. This framework includes the perception of stressors, signal transduction involving ubiquitous molecules such as reactive oxygen species (ROS) and specific phytohormones such as ABA, and finally the appropriate adjustment of the physiology of the plant cell—all of which further hinges on the duration of a stress (*Kranmer et al.*, 2010). The connection between stress input and adjustment is mediated by the plant perceptor. The plant perceptor is a layered network of input signals converging in signal transduction pathways that target regulators of plant growth and physiology (*Scheres and van der Putten*, 2017). This response system can be considered as an additional defining trait of embryophytes. It is conceivable that the roots of this trait run deeper—already the earliest land plants had to successfully overcome the challenges that the terrestrial stressors posed in order to first colonize land and then radiate on it.

Streptophyte algae are now known to have genes for stress response that were previously thought to be characteristic for land plants. While the functions of many of these genes have not yet been tested, their mere presence warrants attention. These genes represent the ancestral gene pool from which the embryophytic genes with functions in stress response have evolved. When exactly the embryophytic function (if there is a unique function among all embryophytes) evolved can only be identified by a combination of comparative functional and bioinformatic approaches across and outside the monophyletic land plants. Independent of the function they hold nowadays in streptophyte algae, it is these genes that are prime candidates for being part of the ‘terrestrialization toolkit’. The idea is that this toolkit entitled adaptive and exaptive genes that provided a selective advantage during plant terrestrialization (see also *de Vries and Archibald*, 2018). Standing out among these candidates is the notion that streptophyte algae have the genetic capacity to utilize phytohormone-based signaling pathways (*Delaux et al.*, 2012; *Hori et al.*, 2014; *Ju et al.*, 2015; *Van de Poel et al.*, 2016; *Ohtaka et al.*, 2017; *de Vries et al.*, 2018a; *Mutte et al.*, 2018; *Nishiyama et al.*, 2018). In land plants, phytohormones interact in converging networks of regulatory circuits (*Kohli et al.*, 2013) many of which are part of the plant perceptor that is put to use when dealing with environmental cues (*Scheres and van der Putten*, 2017).

Auxin is arguably the most famous phytohormone. Polar transport of auxin is a cornerstone in the development of land plants (e.g. *Friml et al.*, 2003) and it orchestrates developmental processes throughout the plant body (*Weijers and Wagner*, 2016). In recent years, auxin has further been recognized to be a major player in the adjustment of the cell biology of plants to stress cues (*Naser and Shani*, 2016; *Blakeslee et al.*, 2019). Auxin has been detected in streptophyte algae and its polar transport has been described in Klebsormidiophyceae and Charophyceae—suggesting that polar auxin transport was an early invention (*Cooke et al.*, 2002; *Boot et al.*, 2012; *Hori et al.*, 2014; *Ohtaka et al.*, 2017). It appears however, that polar auxin transport is not present in all streptophyte algal lineages. Indeed, the KtPIN homolog of *Klebsormidium flaccidum* is an
auxin-specific transporter, which in heterologous experiments localizes in a non-polar manner in the plasma membrane; in *K. flacidum*, *KfPIN* is localized at the peripheral plasma membrane rather than at positions of cell–cell contact (Skokan et al., 2019). In contrast, in *Chara vulgaris*, auxin transporters appear to be localized in a polar manner (Zabka et al., 2016), which Skokan et al. (2019) hypothesized to have evolved convergently in the algae and embryophytes. Further, the canonical auxin perception and transduction pathway probably first emerged in land plants, as inferred from transcriptional responses and the presence of the required signaling components (Mutte et al., 2018).

Streptophyte algae are predicted to have pathways for utilizing phytohormones that are predominantly known as relevant for the response to environmental cues. Foremost among those is the homologous genetic framework for the signaling cascade that all land plants use in ABA-mediated responses (Umezawa et al., 2010; Eklund et al., 2018). ABA is known as a major stress phytohormone; the signaling ABA triggers is involved in responses to abiotic cues such as salt, drought, and temperature (reviewed by Ingram and Bartels, 1996; Shinozaki et al., 2003; Yoshida et al., 2014; Fahad et al., 2015). This ABA signaling cascade consists of a three-component core signaling module (see Cutler et al., 2010) that is a chain of negative regulation: when ABA is present, it binds to a receptor of the PYRA/ACTIN RESISTANCE1/PYR1-LIKE/REGULATORY COMPONENTS OF ABA RECEPTOR (PYR/PYL/R/CAR) family that inhibits the PROTEIN PHOSPHATASE 2C (PP2C) proteins that usually would prevent activity of the SUCROSE NONFERMENTING 1-RELATED PROTEIN KINASEs (SnRKs). The SnRKs are the components that activate the downstream targets, such as ion channels or TFs (Furihata et al., 2006; Geiger et al., 2009). The presence and functional conservation of the interaction of PP2Cs, SnRKs, and downstream targets such as ion channels have been investigated through experimental work for proteins of the streptophyte alga *Klebsormidium* (Holzinger and Becker, 2015; Lind et al., 2015; Shinozawa et al., 2019).

Recently, a transcript probably coding for an orthologous protein of the land plant *PYL* was detected in *Zygnum cumcarinatum* (de Vries et al., 2018a). The presence of *PYR/PYL/R/CAR* homologs in Zygnematophyceae was recently corroborated by the publication of the first two genomes of Zygnematophyceae (Cheng et al., 2019). Cheng et al. (2019) found *PYR/PYL/R/CAR* homologs in one (*Mesotaenium endlicherianum*) of the two zygnematophycean genomes. Interestingly, in the second zygnematophycean genome the authors analyzed, that of the newly described alga *Spirigloca muscicolia* (Cheng et al., 2019), no *PYR/PYL/R/CAR* homolog was found; the same applied to an independent genome study of another Zygnematophyceae, *Penium marginatum* (Jiao et al., 2019, Preprint). Hence, the genes of the *PYR/PYL/R/CAR* family were probably gained at the base of the monophyletic group of Zygnematophyceae and land plants (see also the excellent discussion in Cuming, 2019). Functional studies of the protein encoded by the homologous PYL gene found in *Z. cumcarinatum* have shown that *ZcPYL* does interact with the downstream PP2Cs—but that it does so in an ABA-independent manner (Sun et al., 2019). The exact regulatory function of *PYL:PP2C:SnRK* is thus an open question (see also discussions in the last section of this manuscript). It is, however, clear that the presence of these genes has offered fertile ground for the evolution of the canonical ABA signaling cascade that we know from land plants.

### Carrying out the essential work downstream of the signal transduction cascades: streptophytic stress responses

Chemodiversity in secondary metabolites is a keytrait of land plants. It has been speculated that such a breadth of secondary metabolites has been critical for the success of embryophytes in the challenging environment of *terra firma* (Weng, 2014). A prime source from which a plethora of embryophytic secondary metabolites emerges is the phenylpropanoid pathway, which is the backbone for a range of compounds that can be associated with any abiotic (terrestrial) stressor imaginable (Dixon and Paiva, 1995; Vogt, 2010). All land plants—bryophytes and tracheophytes—use the phenylpropanoid pathway when challenged with stressors (Wolf et al., 2010; Oliva et al., 2015; Albert et al., 2018; Clayton et al., 2018; Carella et al., 2019). Indeed, the phenylpropanoid pathway was thought to have emerged at the base of the clad of embryophytes, thus being an early adaption of embryophytes (Emiliani et al., 2009; Weng, 2014). However, a homologous genetic framework for many components of the core phenylpropanoid pathway was found in many streptophyte algal species when several transcriptomic data sets and one genome were cumulatively investigated (de Vries et al., 2017). This suggests that streptophyte algae could in general be able to synthesize phenylpropanoids—and possibly downstream derivatives, which have been previously reported as a land plant invention (de Vries et al., 2017). Indeed, biochemical and histochemical data accumulated over the years indicate that lignin-like components are present in the cell walls of several streptophyte algae—most prominently in the genus *Coleochaete* (Delwiche et al., 1989; Sørensen et al., 2011). In land plants, the production of lignins can be considered a route that is distal to—but hinging on—the core part of the phenylpropanoid pathway (Vanholme et al., 2012). Together with the genes found in many streptophyte algae, this suggests that the capacity to use core and peripheral routes of the phenylpropanoid pathway arose before phragmoplastophytes emerged. Interestingly, Jiao et al. (2019, Preprint) detected flavonoids in the Zygnematophyceae *Penium marginatum* despite the absence of homologous genes that might code for the two required upstream enzymes of the core phenylpropanoid pathway in its genome. Altogether, it is likely that the phenylpropanoid pathway was already present—in some fashion—in the earliest land plants. There, it might have acted in the production of compounds that warded off terrestrial stressors. Further, this provided fertile genetic ground for likely gene duplication-based diversification of the pathway routes and the chemodiversity it yields (see Niklas et al., 2017 for an erudite explanation).
High irradiances are a prime challenge in the terrestrial environments. What do extant streptophyte algae tell us about how the earliest land plants might have overcome these? UV irradiances could have been shielded by phenolic compounds produced by the phenylpropanoid pathway (Popper et al., 2004; LHCSR, Peers et al., 2009), whereas land plants used another protein of the LHC superfamily, PSBS (Li et al., 2000). Yet, this view was changed by two findings: (i) the chlorophyte *Chlamydomonas reinhardtii* PSBS protein was found to be light induced—an induction that correlates with NPQ (Correa-Galvis et al., 2016); and (ii) mosses also have an NPQ that depends on the action of LHCSR proteins (Peers et al., 2009), whereas land plants used another protein of the LHC superfamily, PSBS (Li et al., 2000). This means that the differences in PSBS detection along the trajectory of streptophyte algal evolution (see Gerotto and Morosinotto, 2013) must be seen in a new light—possibly reflecting the notorious difficulties in detecting algal PSBS. Nonetheless, this means that the conclusion of Alboresi et al. (2010) holds: the earliest land plants probably had a photoprotection mechanism that included the action of both LHCSR and PSBS.

Streptophyte algae that live in terrestrial habitats have remarkable photoprotection capacities. For example, terrestrial *Klebsormidium* can tolerate astonishingly high intensities of light without suffering photoinhibition (Karsten et al., 2016; Pierangelini et al., 2017). Yet, these ecophysiological traits differ when considering multiple representatives of Klebsormidiphyceae (Herburger et al., 2016). Hence, it is likely that such photoprotection mechanisms are particularly moldable by environmental factors, hampering inferences over long evolutionary timescales.

Next to high light, desiccation is a major stressor for streptophyte algae that live in terrestrial habitats (Pierangelini et al., 2019). Indeed, tolerance to both often goes hand in hand. Upon water deficiency, carbon fixation is limited but electron flow continues, leading to possible triplet chlorophyll (\(^3\)Chl\(^*\)) formation which in turn contributes to the formation of the ROS singlet oxygen (\(^1\)O\(_2\)) (Frankel, 1984; Müller et al., 2001). Also, under limited carbon fixation, the biosynthesis of photoprotective molecules is impaired, leading to even more ROS formation (Takahashi and Murata, 2008). Terrestrial streptophyte algae such as *Klebsormidium* and *Zygmena* have a remarkable desiccation tolerance (e.g. Pierangelini et al., 2017; Rippin et al., 2017; Herburger et al., 2019). Their tolerance is based on a range of mechanisms such as protective substance production, cell wall remodeling, formation of specialized cells, and many more (for an excellent overview, see Holzinger and Pichrtová, 2016; for more on cell walls and plant terrestrialization, see also Harholt et al., 2016). Even streptophyte algae that are not considered terrestrial, such as *Coleochaete*, can tolerate desiccation when challenged with it in the lab (Graham et al., 2012). Finding the ability to overcome terrestrial stressors in extant streptophyte algae has important implications: it is likely that streptophyte algae have equally found their way onto land multiple times independently (see also Figs 1, 2). Among terrestrial streptophyte algae, there is a mix of completely independent as well as convergent solutions (many of which we illustrate in the next section) to dealing with terrestrial stressors. An example for divergent solutions is that terrestrial *Klebsormidium* deposits callose under desiccation stress while *Zygmena* does not (Herburger and Holzinger, 2015). However, these differences and independent solutions also highlight that streptophyte algae have a moldable genetic framework for molecular stress responses. Molding this framework eventually formed the network that was also put to use by the earliest land plants.

During the course of evolution, various photosynthetic eukaryotes have found their way onto land. This includes various members of the green lineage that made the wet to dry transition multiple times independently (Lewis and McCourt, 2004). Yet, for example, some diatoms and even cyanobacteria are also terrestrial: photosynthetic organisms that are as distantly related to land plants as can be. These convergently terrestrial organisms must also have found solutions to the challenges of UV, desiccation, high light, etc. In the following we will outline a few of their strategies.
Is the physiology of streptophytes unique?

Photosynthetic organisms from various lineages have settled on land. Only one became the ancestor of the land plants. In an evolutionary context, it is assumed that there were photosynthesizing eukaryotes and prokaryotes on land long before the origin of embryophytes (Raven and Edwards, 2014). How did they overcome the stressors discussed above in the context of plant terrestrialization? Here, again, the diversity of extant photosynthesizing life on land holds illuminating clues.

Desiccation stress responses in green algae can be divided into different categories depending on their function within the organism (Holzinger and Karsten, 2013). One way of responding to desiccation stress is to avoid it. A prime example for desiccation stress avoidance in extreme environmental conditions are desert biological soil crusts (BSCs). Formation of BSCs is a phenomenon that is well known from chlorophytic and streptophytic green algae (e.g. Belnap and Lange, 2001; Flechtner, 2007; Holzlinger and Karsten, 2013). Cyanobacteria form BSCs, too. These BSCs are a mixture of sand particles and polysaccharides which are excreted by the cyanobacteria and are able to withstand extreme environmental desiccation, temperature changes, and very high irradiance (Mager and Thomas, 2011; Ferrenberg et al., 2015). Particularly noteworthy is the cyanobacterium Leptolyngbya ohadii that is native to deserts (Raanen et al., 2016; Oren et al., 2019).

Leptolyngbya ohadii employs a range of physiological mechanisms to go through cycles of dehydration and recovery during rewetting: before dehydration, phytochromes and cryptochromes act as signal transmitters, sensing dawn illumination. Genes of *L. ohadii* involved in photoprotection—such as OCP (Leverenz et al., 2015)—were up-regulated during dehydration while genes involved in biosynthesis of photosynthetic components were down-regulated (Oren et al., 2019). Cellular activity (photosynthesis) in *L. ohadii* and other cyanobacteria was measured a short time after rewetting: the results suggested a complex gene regulatory network that is highly adapted to dehydration/rewetting cycles being reflected in swift modulation of the photosynthetic machinery (Bar-Eyal et al., 2015; Oren et al., 2019). It was proposed that intrinsically disordered proteins (IDPs) play a possible role in protecting and stabilizing RNA during desiccation (Oren et al., 2019). IDPs have been studied regarding their role in desiccation tolerance of tardi-grades (Milnesium tardigradum; Boothby et al., 2017) and might have a similar role in Chloroplastida, too (Sun et al., 2013; Y. Zhang et al., 2018; see also Niklas et al., 2018). Hence, even in terrestrial cyanobacteria—which reside in another domain of life—mechanisms that function similarly in terrestrial chlorophytes and streptophytes can be found.

Protective responses to desiccation stress include formation of a modified cell wall. Some Trebouxiophyceae do so palpably. *Prasiola crispa* subsp. *antarctica* grows, as the name implies, in the supralittoral of Antarctica and possesses a very thick cell wall that protects the alga from osmotic stress during desiccation (Jacob et al., 1992). The cell wall in *Prasiola* contains a large amount of pectin (Jacob et al., 1992). Pectins are important components of the cell wall of land plants and streptophyte algae (Ridley et al., 2001; Sorensen et al., 2011) but have also been shown to be involved in desiccation stress responses in the ulvophyte Ulva compressa by providing a flexible cell wall (Holzinger and Karsten, 2015). Under hypoosmotic conditions, the flexible nature of the cell wall prevents the algal cells from swelling excessively, while under hyperosmotic conditions it prevents plasmolysis—a feature that is beneficial not only under desiccation stress but also under salinity stress which is a frequent stressor considering the habitat of *P. crispa* subsp. *antarctica* (Jacob et al., 1992). Hence, both chlorophytes and streptophytes have evolved mechanisms for cell wall modification under desiccation stress.

The ability of algae to form symbiotic interactions is assumed to have been key in the conquest of land by plants (Delaux et al., 2013; Field et al., 2015). While land plants have unique beneficial symbionts (foremost the arbuscular mycorrhiza), other green organisms are not without friends. For example, many species of Trebouxiophyceae are lichen-forming. Lichens are highly resistant to desiccation and are thus able to stay in a dehydrated state for an extended amount of time until rehydration. In order for a lichen to survive under such extreme conditions, the underlying molecular regulatory network must be extremely fine-tuned and adapted to dehydration/rehydration cycles. For example, dehydration of DNA resulting in strand breaks would mean death for the lichen (Dose et al., 1992). Carniel et al. (2016) provide a good example for transcriptomic regulation in the lichen photobiont Trebouxia gelatinosa; their data reveal a different gene regulatory set-up in various categories such as cell wall modifications, photosynthetic apparatus, or oxidative stress response during dehydration/rehydration cycles (Carniel et al., 2016). In this context, photoprotective processes are crucial because in desiccated photosynthetic tissues there is a high risk of excessive ROS formation (Smirnoff, 1993; Scheibe and Beck, 2011). Rapid adjustments of the antioxidant homeostasis appear to be a mechanism that lichens employ under desiccation stress (Calatayud et al., 1997; Zorn et al., 2001; Kramer et al., 2003); such antioxidants include zeaxanthin, which can deactivate excited chlorophylls (Jahns and Holzwarth, 2012) —thusthe substances that are found conserved across plastid-bearing eukaryotes (Dautermann and Lohr, 2017).

The aforementioned PSBS and LHCSR are LHC-like proteins that are key for the response to high light. An additional important group of LHC-like proteins are the early light-induced proteins (ELIPs), which are swiftly up-regulated in response to high light stress as well as also being up-regulated in response to dehydration stress and byABA (Bartels et al., 1992; Pötter and Klopstech, 1993; Zeng et al., 2002; Dinakar and Bartels, 2013). ELIPs are hallmark stress-responsive proteins in a variety of oxygenic photosynthetic organisms from cyanobacteria, to algae, to land plants (Heddad and Adamska, 2002). Hutin et al. (2003) demonstrated that ELIPs have an essential photoprotective role by using the *A. thaliana* mutant *chaos,*
which is not able to translocate LHC-type proteins such as ELIP via the chloroplast signal recognition particle (CpSRP) pathway to the thylakoid membranes (see also Hutin et al., 2002). The authors observed leaf bleaching and phototoxic oxidative damage in chaos mutants challenged with high-light cues. The data of Hutin et al. (2003) thus revealed the photoprotective role of ELIPs. It was further suggested that ELIPs have an influence on chlorophyll biosynthesis, thus indirectly preventing chlorophyll accumulation under high light conditions and thereby also preventing ROS formation (Hutin et al., 2003; Tzvetkova-Chevolleau et al., 2007).

The formation of sunscreens is a powerful protection against UV irradiance. Above, we illustrated how the biosynthesis of phenylpropanoid-derived metabolites is involved in this mechanism in streptophytes—and discussed how such metabolites might have been critical for streptophyte terrestrialization. Yet, other terrestrial organisms have sunscreens, too. In some cyanobacteria, scytotenin acts as a very potent UVA sunscreen that protects the cells from near UV and blue radiation (Gao and Garcia-Pichel, 2011). It accumulates as a stable pigment in extracellular polysaccharide sheaths of cyanobacteria and possesses various convenient characteristics. Scytotenin changes dependent on the redox status, stays active even under physiological inactive conditions, and is capable in performing strong absorption in the UVA range due to its ring structure with conjugated double bonds (Garcia-Pichel and Castenholz, 1991; Proteau et al., 1993; Gao and Garcia-Pichel, 2011). The pigment is typically found in biological soil crusts or epilithic biofilms (Gao and Garcia-Pichel, 2011). While many questions regarding its biosynthesis and regulation remain, the exposure of cyanobacterial cells to UVA irradiance, however, appears to be correlated with scytotenin production (Garcia-Pichel and Castenholz, 1991; see also Ehling-Schulz et al., 1997).

In chlorophyte algae, mycosporine-like amino acids (MAAs) act as sunscreens when exposed to solar UV radiation. For example, an accumulation of MAAs was found to be advantageous against UV irradiance in the aeroterrestrial green algae Stichococcus sp. and Chlorella luteoviridis when compared with two green algae from soil with a different MAA setup (Karsten et al., 2007). Such aeroterrestrial species possess a unique type of MAA (324 nm MAA) which is only found in Trebouxia-like algae—including the alga P. crispa (Hoyer et al., 2001; Karsten et al., 2005). In the streptophyte algal class of Klebsormidiophyceae, we also find the production of 324 nm MAA—yet, despite their similar absorption spectrum, these are different substances (Kitzing and Karsten, 2015). This provides yet another intriguing example of convergent evolution.

So, what makes streptophytes special? There are multiple lineages of algae that made their way onto land by mastering its stressors. Post-hoc, we see that only the progenitors of the last common ancestor of embryophytes gave rise to a lineage that globally conquered land. Why do only they dominate the terrestrial flora? A specific (embryophyte-like) physiology that aided them in dealing with stressors will not be the only reason. However, it has to be part of the answer. Dealing with terrestrial stressors was not only under selection in the earliest land plants but is under selection still. Like the core processes in energy metabolism (such as the citrate cycle) that are essential, core response mechanisms to stressors are continually tested by adverse terrestrial conditions and are essential for survival in the terrestrial habitat. The question is which building blocks of that core were present in the earliest land plants.

**Rewiring of an ancient molecular physiology was a likely facilitator of the success of land plants**

The responses of land plants to stressors hinges on complex regulatory networks. In such stress-relevant networks, nodes are genes/proteins that are connected by edges that circumscribe an interaction—such as phosphorylation and transcriptional activation—that are triggered and/or modulated by environmental stimuli. Dissecting ancient pathways and setting them into context with land plant data enables us to trace the evolution of such networks across the streptophyte tree of life. Correlative data, such as genomes, have indicated the presence of many genes (the nodes) that could act in stress-relevant regulatory networks—but what about the wires that connect them (the edges)? To understand these, more involved functional analyses are required.

ABA is a key modulator of stress responses. Above, we outlined that streptophyte algae have most—and Zygnematomophyceae all—homologous genes of the canonical cascade that land plants use for ABA signaling (de Vries et al., 2018a; Cheng et al., 2019; Sun et al., 2019). What does this mean for the evolution of the laying of the wires that underpin ABA signaling? Although Klebsormidium completely lacks a gene for the ABA receptor, Holzinger et al. (2014) found the other components (PP2C, SnRK2s, and AREBs) to be responsive to drought (see also Holzinger and Becker, 2015). Furthermore, the genes of Klebsormidium that are homologous to ABA signaling components complement the respective mutants of A. thaliana and P. patens in heterologous experiments (Lind et al., 2015; Shinozawa et al., 2019); for example, expressing Klebsormidium nitens SnRK2.6 in A. thaliana protoplasts that are deficient in SnRK2.2, 2.3, and 2.6 (snrk2.2/2.3/2.6 triple mutants) rescues the transduction of ABA-induced gene expression (Lind et al., 2015). Hence, the specific wires of the interaction required for the ABA signaling cascade that are downstream of the ABA–PYL interaction appear to be conserved between Klebsormidium and land plants. This means that the cascade is probably hundreds of millions of years older than its bona fide ABA dependency mediated by PYLs. Recently, another piece was added to the puzzle of the evolution of the ABA signaling cascade: through *in vitro* and heterologous work, Sun et al. (2019) showed that the PYL homolog found in *Z. circumcarinatum* does regulate its downstream target—the PP2Cs. Yet, their data also show that this regulation happens in an ABA-independent manner. What this means is that the bona fide ABA signaling cascade, which consists of PYLs:PP2Cs:SnRKs, has evolved in a modular fashion—with components being successively plugged in. The ABA dependency of the cascade—another addition—has probably evolved along the trajectory from the earliest land plants to the last
common ancestor of land plants (see also the discussion on this topic in Sun et al., 2019). Whether there is nonetheless an ABA dependency of parts of the signaling cascade in algae mediated through other means—such as the ABA NON-RESPONSIVE kinases that are only present in non-flowering plants (Stevenson et al., 2016)—remains to be investigated. However, it offers an explanation for how conserved stress tolerance-conferring mechanisms such as LEA accumulation can be part of the same cascade that we now think of as ABA mediated: they might have been part of the downstream response triggered by the same regulatory cascade conserved for hundreds of millions of years, in which they have been functional and riding along since before the signal transduction chain was under the control of ABA.

The signaling network that mediates the action of the growth phytohormone auxin has a similar story to tell. A series of recent studies [Flores-Sandoval et al. (2018); Mutte et al. (2018); Martin-Arevalillo et al. (2019)] proposed an evolutionary history that features a modular build-up for the nuclear auxin response pathway that is mediated by AUXIN RESPONSE FACTORS (ARFs), the TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALLING F-BOX (TIR/AFB), AUXIN/INDOLE-3-ACETIC PROTEIN (AUX/IAA) system: class C ARFs are present in streptophyte algae—and perhaps were even present in the last common ancestor of streptophytes (see also Wang et al., 2019); the common ancestor of Coleochaetophyceae, Zygnematophyceae, and land plants gained the single co-ortholog (A/B ARF) of the classes of A and B ARFs known from land plants. In the absence of TIR/AFB and AUX/IAA, these algal ARFs act in an auxin-independent manner (Martin-Arevalillo et al., 2019; see also Mutte et al., 2018). In land plants, the A/B ARF diverged into the class A and class B ARFs (Flores-Sandoval et al., 2018; Mutte et al., 2018; Martin-Arevalillo et al., 2019). Onto this diversified system, the TIR/AFB and AUX/IAA were plugged, rendering the whole system auxin dependent (Flores-Sandoval et al., 2018; Mutte et al., 2018; Martin-Arevalillo et al., 2019).

Thus, adding one regulatory mechanism upstream was sufficient to turn a conserved gene regulatory cascade into a phytohormone-dependent cascade. Similar to the aforementioned case of ABA-mediated signaling, gaining such phytohormone dependency probably occurred along the trajectory between the earliest land plants and the last common ancestor of land plants.

Recent functional studies on the liverwort model system M. polymorpha have illustrated how a different type of modular evolution of a phytohormone pathway can occur—in this case not concerning a protein that is plugged in, but a different effector molecule. Of course, such changes ultimately hinge on differences on the protein level, too; that is, in the binding pocket for the input molecule. Monte et al. (2018) investigated the origin of jasmonic acid (JA) perception by focusing on the COI1 receptor. Instead of sensing JA–Ile, the COI1 protein of M. polymorpha senses dinor–12-oxo–phytadienoic acid (dinin–OPDA), which emerges from an earlier branching point in the JA biosynthesis pathway (Monte et al., 2018). Hence, while the entire pathway for the canonical, JA–Ile–based, perception of JA is present in the bryophyte M. polymorpha, it does not work in the same way as we know it from angiosperms. Plugging in a different molecule at the uppermost layer of the signaling cascade hence has the ability to change the entire co-evolutionary relationship between phytohormone biosynthesis and its perception. Even more extreme cases of rewiring can be expected to have taken place in streptophyte algae, which are hundreds of millions of years divergent from land plants. Thus, the gain of a specific phytohormone dependency can also entail shifts in input signal. Illuminating whether such shifts in input signal underpinned the evolution of other phytohormone signaling cascades (such as ABA) is an exciting avenue for future research.

Rewiring is not limited to signaling pathways. Secondary metabolites of land plants are known for their chemodiverse and lineage-specific—sometimes species-specific—secondary metabolic fingerprints (see, for example, Dudareva et al., 2004). During the course of evolution, the same building block-producing backbone pathways have been rewired to give rise to tens of thousands of different secondary metabolites. For example, Berland et al. (2019) recently showed that the liverwort model system M. polymorpha produces a novel class of anthocyanins, which they termed auronidins. Auronidins appear to be derived from anthocyanin but emerge from a novel route via auronos (Berland et al., 2019). This highlights the complexities one has to tackle when inferring the secondary metabolism of the earliest land plants. Since the genes for the phenylpropanoid biosynthesis pathway are present in streptophyte algae (de Vries et al., 2017) and building blocks have been detected even in chlorophytes (Goiris et al., 2014), we can expect that the earliest land plants used a plethora of secondary metabolites derived from these routes. Inferring the routing of the pathways, however, requires more than the mere knowledge of the presence of some genes or some metabolites. A functional dissection of the biosynthetic pathways across the streptophyte tree of life—especially in the streptophyte algae—is needed.

**Conclusion**

The lineage of embryophytes has conquered land. Only through a fortuitous combination of traits did they succeed in this conquest. These traits include complex networks for stress response that are, in their elaboration, probably limited to land plants. Yet, often, the integral components and/or decisive nodes and wires of these networks were already present—they represent complete and functioning building blocks ready for co-option. Moreover, as of yet, we do not know how most of these components function in their own environment; that is, how are they wired in streptophyte algae? It may very well be that the present components have the same functions as in land plants, yet their interactors may be different in streptophyte algae (e.g. different receptor specificity or different downstream components). Likewise, a completely different function for the streptophyte algal components underlying a network is also entirely possible. One thing, however, is very clear; these conserved proteins that participate in the stress signaling networks in land plants will not be without a function in streptophyte algae. Comparative studies that dissect the routing of upstream (e.g. signaling) and downstream (e.g.
biosynthesis of stress protectants) stress response pathways across streptophytes will illuminate how their co-options were realized in the earliest land plants.

Acknowledgements

This project has received funding from the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (grant agreement no. 852725), supporting work in the lab of JDV through the ERC Starting Grant ‘TerreStriAL’. We thank Debbie Maiels (Zoobotanica Scientific Illustration: www.scientific-art.com) for her marvelous work on Figs 1 and 2.

References

Adl SM, Bass D, Lane CE, et al. 2019. Revisions to the classification, nomenclature, and diversity of eukaryotes. Journal of Eukaryotic Microbiology 66, 4–119.

Adl SM, Simpson AG, Farmer MA, et al. 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. Journal of Eukaryotic Microbiology 52, 399–451.

Albert NW, Thrimawithana AH, McGhee TK, Clayton WA, Deroles SC, Schwinn KE, Bowman JL, Jordan BR, Davies KM. 2018. Genetic analysis of the liverwort Marchantia polymorpha reveals that R2R3MYB activation of flavonoid production in response to abiotic stress is an ancient character in land plants. New Phytologist 218, 554–566.

Alboresi A, Gerotto C, Giacometti GM, Bassi R, Morosinotto T. 2010. Physcomitrella patens mutants affected on heat dissipation clarify the evolution of photoprotection mechanisms upon land colonization. Proceedings of the National Academy of Sciences, USA 107, 11128–11133.

Archibald JM. 2015. Genomic perspectives on the birth and spread of plastids. Proceedings of the National Academy of Sciences, USA 112, 10147–10153.

Aro EM, Virgin I, Andersson B. 1993. Photoinhibition of photosystem II. Inactivation, protein damage and turnover. Biochimica et Biophysica Acta 1143, 113–134.

Arrighi JE, Barre A, Ben Amor B, et al. 2006. The Medicago truncatula lysin [corrected] motif-receptor-like kinase gene family includes NFP and new nodule-expressed genes. Plant Physiology 142, 265–279.

Bar-Eyal L, Eisenberg I, Faust A, et al. 2015. An easily reversible structural change underlies mechanisms enabling desert crust cyanobacteria to survive desiccation. Biochimica et Biophysica Acta 1847, 1267–1273.

Bartels D, Hanke C, Schneider K, Michel D, Salamin F. 1992. A desiccation-related Elip-like gene from the resurrection plant Craterostigma plantagineum is regulated by light and ABA. The EMBO Journal 11, 2771–2778.

Becker B, Marin B. 2009. Streptophyte algae and the origin of embryophytes. Annals of Botany 103, 999–1004.

Belnap J, Lange OL. 2001. Biological soil crusts: structure, function and management. 7 Berlin Heidelberg: Springer-Verlag.

Bengtson S, Sallstedt T, Belivanova V, Whitehouse M. 2017. Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae. PLoS Biology 15, e2000735.

Berbee ML, James TY, Strullu-Derrien C. 2017. Early diverging fungi: diversity and impact at the dawn of terrestrial life. Annual Review of Microbiology 71, 41–60.

Berland H, Albert NW, Stavliand A, et al. 2019. Auronidins are a previously unreported class of flavonoid pigments that challenges when anthocyanin biosynthesis evolved in plants. Proceedings of the National Academy of Sciences, USA 116, 20232–20239.

Blakeslee JJ, Spatola Rossi T, Krichebaum V. 2019. Auxin biosynthesis: spatial regulation and adaptation to stress. Journal of Experimental Botany 70, 5041–5049.

Bonente G, Ballottari M, Truong TB, Morosinotto T, Ahn TK, Fleming GR, Niyogi KK, Bassi R. 2011. Analysis of LhcaSR3, a protein essential for feedback de-excitation in the green alga Chlamydomonas reinhardtii. PLoS Biology 9, e1000577.

Boot KJ, Libbenga KR, Hille SC, Offringa R, van Duijn B. 2012. Polar auxin transport: an early invention. Journal of Experimental Botany 63, 4213–4218.

Boothby TC, Tapia H, Brozena AH, Piszczewicz S, Smith AE, Giovannini I, Rebecchi L, Pielak GJ, Koshland D, Goldstein B. 2017. Tardigrades use intrinsically disordered proteins to survive desiccation. Molecular Cell 65, 975–984.e5.

Bowman JL, Sakakibara K, Furumizu C, Dierschke T. 2016. Evolution in the cycles of life. Annual Review of Genetics 50, 133–154.

Bressendorff S, Azevedo R, Kenchappa CS, Ponce de León I, Olsen JV, Rasmussen MW, Erbs G, Newman MA, Petersen M, Mundy J. 2016. An innate immunity pathway in the moss Physcomitrella patens. The Plant Cell 28, 1328–1342.

Breuninger H, Thamm A, Streubel S, Sakayama H, Nishiyama T, Dolan L. 2016. Diversification of a transcription factor family led to the evolution of antagonistically acting genetic regulators of root hair growth. Current Biology 26, 1622–1628.

Butterfield NJ. 2000. Bangiophora pubescens n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. Paleobiology 26, 386–404.

Calatayud A, Deltoro VI, Barreno E, Del Valle-Tascon S. 1997. Changes in vivo chlorophyll fluorescence quenching in lichen thalli as a function of water content and suggestion of zeaxanthin-associated photoprotection. Physiologia Plantarum 101, 93–102.

Carella P, Gogleva A, Hoey DJ, Bridgen AJ, Stolze SC, Nakagami H, Schornack S. 2019. Conserved biochemical defenses underpin host responses to oomycete infection in an early-divergent land plant lineage. Current Biology 29, 2282–2294.e5.

Carniel FC, Gerdol M, Montagner A, Banchi E, De Moro G, Manfrin C, Muggia L, Pallavicini A, Tretiach M. 2016. New features of desiccation tolerance in the lichen photobiont Trebouxia gelatinae are revealed by a transcriptomic approach. Plant Molecular Biology 91, 319–339.

Catarino B, Hetherington AJ, Emms DM, Kelly S, Dolan L. 2016. The stepwise increase in the number of transcription factor families in the pre-cambrian predated the diversification of plants on land. Molecular Biology and Evolution 33, 2815–2819.

Chan KK, Phua SY, Crisp P, McQuinn R, Pogson BJ. 2016. Learning the language of the chloroplast: retrograde signaling and beyond. Annual Review of Plant Biology 67, 25–53.

Chater CCC, Caine RS, Fleming AJ, Gray JE. 2017. Origins and evolution of stomatal development. Plant Physiology 174, 624–638.

Cheng S, Xian W, Fu Y, et al. 2019. Genomes of subaerial zygnematophyceae provide insights into land plant evolution. Cell 179, 1057–1067.e14.

Christa G, Cruz S, Jahns P, de Vries J, Cartaxana P, Estoves AC, Seródio J, Gould SB. 2017. Photoprotection in a monophyletic branch of chlorophyte algae is independent of energy-dependent quenching (qE). New Phytologist 214, 1132–1144.

Clayton WA, Albert NW, Thrimawithana AH, et al. 2018. UVB-mediated induction of flavonoid biosynthesis for UVB tolerance is conserved between the liverwort Marchantia polymorpha and flowering plants. The Plant Journal 96, 503–517.

Cooke TJ, Poli D, Sztein AE, Cohen JD. 2002. Evolutionary patterns in auxin action. Plant Molecular Biology 49, 319–339.

Correa-Galvis V, Redekop P, Guan K, Griess A, Truong TB, Wakao S, Niyogi KK, Jahns P. 2016. Photosystem II subunit PsbS is involved in the induction of LHCSR protein-dependent energy dissipation in Chlamydomonas reinhardtii. Journal of Biological Chemistry 291, 17478–17487.

Cuming AC, Cho SH, Kamisugi Y, Graham H, Quatrano RS. 2015. An easily reversible structural change underlies mechanisms enabling desert crust cyanobacteria to survive desiccation. Biochimica et Biophysica Acta 1847, 1267–1273.

Dautermann O, Lohr M. 2017. A functional zeaxanthin epoxidase from red algae shedding light on the evolution of light-harvesting carotenoids and the xanthophyll cycle in photosynthetic eukaryotes. The Plant Journal 92, 879–891.

Downloaded from https://academic.oup.com/jxb/article/71/11/3254/5699832 by guest on 31 March 2022
Delaux PM, Hetherington AJ, Coudert Y, et al. 2019. Reconstructing trait evolution in plant evo-devo studies. Current Biology 29, R1105–R1121.

Delaux PM, Radhakrishnan GV, Jayaraman D, et al. 2015. Algal ancestor of land plants was preadapted for symbiosis. Proceedings of the National Academy of Sciences, USA 112, 13990–13995.

Delaux PM, Séjalon-Delmas N, Bécard G, Ané JM. 2013. Evolution of the plant-microbe symbiotic ‘toolkit’. Trends in Plant Science 18, 298–304.

Delaux PM, Varala K, Edger PP, Coruzzi GM, Pires JC, Ané JM. 2014. Comparative phylogenomics uncovers the impact of symbiotic associations on host genome evolution. PLoS Genetics 10, e1004487.

Delaux PM, Xie X, Timme RE, Puech-Pages V, Dunand C, Lecompte E, Delwiche CF, Yoneyama K, Bécard G, Séjalon-Delmas N. 2012. Origin of strigolactones in the green lineage. New Phytologist 195, 857–871.

Delwiche CF, Cooper ED. 2015. The evolutionary origin of a terrestrial flora. Current Biology 25, R899–R910.

Delwiche CF, Graham LE, Thomson N. 1989. Lignin-like compounds and sporopollenin Coleochaete, an algal model for land plant ancestry. Science 245, 399–401.

Delwiche CF, Karol KG, Cimino MT, Sysma TS. 2002. Phylogeny of the genus Coleochaete (Coleochaetales, charophyta) and related taxa inferred by analysis of the chloroplast gene rbcL. Journal of Phycology 38, 394–403.

de Vries J, Archibald JM. 2017. Endosymbiosis: did plastids evolve from a freshwater cyanobacterium? Current Biology 27, R103–R105.

de Vries J, Archibald JM. 2018. Plant evolution: landmarks on the path to terrestrial life. New Phytologist 217, 1428–1494.

de Vries J, Curtis BA, Gould SB, Archibald JM. 2018a. Embryophyte stress signaling evolved in the algal progenitors of land plants. Proceedings of the National Academy of Sciences, USA 115, E3471–E3480.

de Vries J, de Vries S, Slamovits CH, Rose LE, Archibald JM. 2017. How embryophyte is the biosynthesis of phenylpropanoids and their derivatives in streptophyte algae? Plant & Cell Physiology 58, 934–945.

de Vries J, Gould SB. 2018. The monoplastidic bottleneck in algae and plant evolution. Journal of Cell Science 131, jcs203411.

de Vries J, Stanton A, Archibald JM, Gould SB. 2016. Streptophyte terrestrialization in light of plastid evolution. Trends in Plant Science 21, 467–476.

de Vries S, de Vries J, von Dahlen JK, Gould SB, Archibald JM, Rose LE, Slamovits CH. 2018b. On plant defense signaling networks and early land plant evolution. Communicative & Integrative Biology 11, 1–14.

Dinakar C, Bartels D. 2013. Desiccation tolerance in resurrection plants: new insights from transcriptome, proteome and metabolome analysis. Frontiers in Plant Science 4, 482.

Dixon RA, Paiva NL. 1995. Stress-induced phenylpropanoid metabolism. The Plant Cell 7, 1985–1997.

Dose K, Bieger-Dose A, Labusch M, Gill M. 1992. Survival in extreme dryness and DNA-single-strand breaks. Advances in Space Research 12, 1085–1097.

Dudareva N, Pichersky E, Gershenzon J. 2001. Evolution of volatiles. Plant Physiology 126, 1893–1902.

Dupuy L, Mackenzie J, Hasleff J. 2010. Coordination of plant cell division and expansion in a simple morphogenetic system. Proceedings of the National Academy of Sciences, USA 107, 2711–2716.

Dure L3rd, Greenway SC, Galau GA. 1981. Developmental biochemistry of cottonseed embryogenesis and germination: changing messenger ribonucleic acid populations as shown by in vitro and in vivo protein synthesis. Biochemistry 20, 4162–4168.

Ehleng-Schulz M, Bilger W, Scherer S. 1997. UV-B-induced synthesis of photoprotective pigments and extracellular polysaccharides in the terrestrial cyanobacterium Nostoc commune. Journal of Bacteriology 179, 1940–1945.

Eklund DM, Kanei M, Flores-Sandoval E, Ishizaki K, Nishihama R, Kohchi T, Lagercrantz U, Blaheraro RP, Sakata Y, Bowman JL. 2018. An evolutionarily conserved abscisic acid signaling pathway regulates dormancy in the liverwort Marchantia polymorpha. Current Biology 28, 3891–3899.

Emilianni G, Frati F, Fani R, Gribaldo S. 2009. A horizontal gene transfer at the origin of phenylpropanoid metabolism: a key adaptation of plants to land. Biology Direct 4, 7.

Fahad S, Hussain S, Malloob A, et al. 2015. Phytohormones and plant responses to salinity stress: a review. Plant Growth Regulation 75, 391–404.

Ferrenberg S, Reed SC, Belnap J. 2015. Climate change and physical disturbance cause similar community shifts in biological soil crusts. Proceedings of the National Academy of Sciences, USA 112, 12116–12121.

Field KJ, Pressel S. 2018. Unity in diversity: structural and functional insights into the ancient partnerships between plants and fungi. New Phytologist 220, 996–1011.

Field KJ, Pressel S, Duckett JG, Rimage WR, Bidartondo MI. 2015. Symbiotic options for the conquest of land. Trends in Ecology & Evolution 30, 477–486.

Flechtner VR. 2007. North American desert microbiotic soil crust communities: diversity despite challenge. In: Seckbach J, ed. Algae and cyanobacteria in extreme environments. Berlin: Springer, 537–551.

Flores-Sandoval E, Eklund DM, Hong SF, et al. 2018. Class C ARFs evolved before the origin of land plants and antagonize differentiation and developmental transitions in Marchantia polymorpha. New Phytologist 218, 1612–1630.

Frankel EN. 1984. Chemistry of free radical and singlet oxidation of lipids. Progress in Lipid Research 23, 197–221.

Friml J, Vietaen A, Sauer M, Weijers D, Schwarz H, Tamann H, Offerfie R, Jürgens G. 2003. Efflux-dependent auxin gradients establish the apical–basal axis of Arabidopsis. Nature 426, 147–153.

Furuhata T, Maruyama K, Fujita Y, Umezawa T, Yoshida R, Shinozaki K, Yamaguchi-Shinozaki K. 2006. Abscisic acid-dependent multisite phosphorylation regulates the activity of a transcription activator AREB1. Proceedings of the National Academy of Sciences, USA 103, 1989–1993.

Gao Q, García-Pichel F. 2011. Microbial ultraviolet sunscreens. Nature Reviews, Microbiology 9, 791–802.

Gao Y, Wang W, Zhang T, Gong Z, Zhao H, Han GZ. 2018. Out of water: the origin and early diversification of plant R-genes. Plant Physiology 177, 82–89.

Garcia-Pichel F, Castenholz RW. 1991. Characterization and biological implications of scytocinorm, a cyanobacterial sheath pigment. Journal of Phycology 27, 395–409.

Geiger D, Scherzer S, Mumm P, et al. 2009. Activity of guard cell anion channel SLAC1 is controlled by drought-stress signaling kinase–phosphatase pair. Proceedings of the National Academy of Sciences, USA 106, 21425–21430.

Gerotto C, Alboresi A, Giacometti GM, Bassi R, Morosinotto T. 2012. Coexistence of plant and algal energy dispensation mechanisms in the moss Physcomitrella patens. New Phytologist 196, 763–773.

Gerotto C, Morosinotto T. 2013. Evolution of photoprotection mechanisms upon land colonization: evidence of PSBS-dependent NPQ in late Streptophyte algae. Physiologica Plantarum 149, 583–598.

Goiris K, Muyaert K, Voorspoels S, Noten B, De Paep E, De Baart GJ, De Cooman L. 2014. Detection of flavonoids in microalgae from different evolutionary lineages. Journal of Phycolology 50, 483–492.

Gómez-Gómez L, Boller T. 2000. FLS2: an LRR receptor-like kinase involved in the perception of the bacterial elicitor flagellin in Arabidopsis. Cell 101, 197–205.

Harbor Perspectives in Biology 6, 1. 2015. Algal annect: evaluating evidence from fossils and molecular clocks. Cold Spring Harbor Perspectives in Biology 6, a016139.

Harrison CJ. 2017. Development and genetics in the evolution of land plant body plans. Philosophical Transactions of the Royal Society B: Biological Sciences 372, 20150490.
Heddam M, Adamska I. 2002. The evolution of light stress proteins in photosynthetic organisms. Comparative and Functional Genomics 3, 504–510.

Herburger K, Holzinger A. 2015. Localization and quantification of callose in the streptophyte green algae Zygnema and Klebsormidium: correlation with desiccation tolerance. Plant & Cell Physiology 56, 2259–2270.

Herburger K, Karsten U, Holzinger A. 2016. Entranisia and Hornidiella, sister lineages of Klebsormidium (Streptophyta), respond differently to light, temperature, and desiccation stress. Protoplasma 253, 1309–1323.

Herburger K, Xin A, Holzinger A. 2019. Homogalacturonan accumulation in cell walls of the green alga Zygnema sp. (Charophyta) increases desiccation resistance. Frontiers in Plant Science 10, 540.

Hetherington AJ, Dolan L. 2017. The evolution of lycopod rooting structures: conservatism and disparity. New Phytologist 215, 538–544.

Hirschi S, Oldroyd GE. 2009. GRAS-domain transcription factors that regulate plant development. Plant Signaling & Behavior 4, 698–700.

Hoffmann L. 1989. Algae of terrestrial habitats. Botanical Review 55, 77–105.

Holdsworth MJ, Bentsink L, Soppe WJ. 2008. Molecular networks regulating Arabidopsis seed maturation, after-ripening, dormancy and germination. New Phytologist 179, 33–54.

Holzinger A, Becker B. 2015. Desiccation tolerance in the streptophyte green alga Klebsormidium: the role of phytohormones. Communicative & Integrative Biology 8, e1059978.

Holzinger A, Herburger K, Kaplan F, Lewis LA. 2015. Desiccation tolerance in the chlorophyte green alga Ulva compressa: does cell wall architecture contribute to ecological success? Planta 242, 477–492.

Holzinger A, Kaplan F, Blaas K, Zechmann B, Komsic-Buchmann K, Becker B. 2014. Transcriptionomics of desiccation tolerance in the streptophyte green alga Klebsormidium reveal a land plant-like defense response. PLoS One 9, e110630.

Holzinger A, Karsten U. 2013. Desiccation stress and tolerance in green algae: consequences for ultrastructure, physiological and molecular mechanisms. Frontiers in Plant Science 4, 327.

Holzinger A, Pichrtová M. 2016. Abiotic stress tolerance of charophyte green algae: new challenges for omics techniques. Frontiers in Plant Science 5, 3978.

Horst NA, Katz A, Pereman I, Decker EL, Ohad N, Reski R. 2016. A single homeobox gene triggers phase transition, embryogenesis and axesexual reproduction. Nature Plants 2, 15209.

Horton P, Ruban AV, Wentworth M. 2000. Allosteric regulation of the assexual reproduction. Nature Plants 2, 182–193.

Jiao DL, Sorensen I, Sun X, et al. 2019. The genome of the charophyte algae Prasinum margaritaceum bears footprints of the evolutionary origins of land plants. bioRxiv doi: 10.1101/835561. [Preprint].

John RP. 1942. An ecological and taxonomic study of the algae of British soils: I. The distribution of the surface-growing algae. Annals of Botany 6, 323–349.

Jones VA, Dolan L. 2012. The evolution of root hairs and rhizoids. Annals of Botany 110, 205–212.

Ju C, Van de Poel B, Cooper ED, Thierer JH, Gibbons TR, Delwiche CF, Chang C. 2015. Conservation of ethylene as a plant hormone over 450 million years of evolution. Nature Plants 1, 14004.

Kaku H, Nishizawa Y, Ishii-Minami N, Akimoto-Tomiyama C, Dozhmae N, Takio K, Minami E, Shibuya N. 2006. Plant cells recognize chitin fragments for defense signaling through a plasma membrane receptor. Proceedings of the National Academy of Sciences, USA 103, 11086–11091.

Karsten U, Friedl T, Schumann R, Hoyer K, Lembcke S. 2005. Mycosporine-like amino acids and phylogenies in green algae: Praisidia and its relatives from the Trebouxioideae (Chlorophyta). Journal of Phycolgy 41, 557–566.

Karsten U, Herburger K, Holzinger A. 2016. Living in biological soil crust communities of African deserts—physiological traits of green algal Klebsormidium species (Streptophyta) to cope with desiccation, light and temperature gradients. Journal of Plant Physiology 194, 2–12.

Karsten U, Lembcke S, Schumann R. 2007. The effects of ultraviolet radiation on photosynthetic performance, growth and sunscreen compounds in aeroterrestrial biofilm algae isolated from building facades. Planta 225, 991–1000.

Keeling PJ. 2013. The number, specie, and impact of plastid endosymbioses in eukaryotic evolution. Annual Review of Plant Biology 64, 583–607.

Kenrick P, Strullu-Derrien C. 2014. The origin and early evolution of roots. Plant Physiology 166, 570–580.

Kitzing C, Karsten U. 2015. Effects of UV radiation on optimum quantum yield and sunscence contents in members of the genera Interfilum, Klebsormidium, Hornidiella and Entranzia (Klebsormidiaceae, Streptophyta). European Journal of Phytology 50, 279–287.

Knack JJ, Wilcox LW, Dellaux PM, Ané JM, Piotrowski MJ, Cook ME, Graham JM, Graham LE. 2015. Microbiomes of streptophyte algae and bryophytes suggest that a functional suite of microbiota fostered plant colonization of land. International Journal of Plant Sciences 176, 405–420.

Knopp M, Garg SG, Handrich M, Gould SB. 2019. Major changes in plastid protein import and the origin of the Chloroplastida. bioRxiv doi: 10.1101/799577. [Preprint].

Kohli A, Sreenivasulu N, Lakshmanan P, Kumar PP. 2013. The phytohormone crosstalk paradigm takes center stage in understanding how plants respond to abiotic stresses. Plant Cell Reports 32, 945–957.

Kraner I, Minibayeva FV, Beckett RP, Seal CE. 2010. What is stress? Concepts, definitions and applications in seed science. New Phytologist 188, 655–673.

Kraner I, Zorn M,urb K, Wornik S, Beckett RP, Batic F. 2003. Biochemical traits of lichens differing in relative desiccation tolerance. New Phytologist 160, 167–176.

Lang D, Weibe C, Timmerhaus G, Richardt S, Riaño-Pachón DM, Corrêa LG, Reski R, Mueller-Roeber B, Rensing SA. 2010. Genome-wide phylogenetic comparative analysis of plant transcriptional regulation: a timeline of loss, gain, expansion, and correlation with complexity. Genome Biology and Evolution 2, 488–503.

Leebens-Mack JH, Barker MS, Carpenter EJ, et al. 2019. One thousand million years of evolution of land plants. bioRxiv doi: 10.1101/835561. [Preprint].

Downloaded from https://academic.oup.com/jxb/article/71/11/3254/5699832 by guest on 31 March 2022
Rensing SA. 2018. Great moments in evolution: the conquest of land by plants. Current Opinion in Plant Biology 42, 49–54.

Ridley BL, O’Neill MA, Mohnen D. 2001. Pectins: structure, biosynthesis, and oligogalacturonide-related signaling. Phytochemistry 57, 929–967.

Rippin M, Becker B, Holzinger A. 2017. Enhanced desiccation tolerance in mature cultures of the streptophytic green alga Zygnema circinnaratum revealed by transcriptomics. Plant & Cell Physiology 58, 2067–2084.

Sánchez-Baracaldo P, Raven JA, Pisani D, Knoll AH. 2017. Early photosynthetic eukaryotes inhabited low-salinity habitats. Proceedings of the National Academy of Sciences, USA 114, E7737–E7745.

Scheibe R, Beck E. 2011. Drought, desiccation, and oxidative stress. In: Lütte U, Beck E, Bartels D, eds. Plant desiccation tolerance. Vol. 215. Ecological Studies. Heidelberg: Springer, 209–232.

Scheres B, van der Putten WH. 2017. The plant perception connects environment to development. Nature 543, 337–345.

Shinozaki K, Yamaguchi-Shinozaki K, Seki M. 2003. Regulatory network of gene expression in the drought and cold stress responses. Current Opinion in Plant Biology 6, 410–417.

Shinozawa A, Otake R, Takezawa D, et al. 2019. SnRK2 protein kinases represent an ancient system in plants for adaptation to a terrestrial environment. Communications Biology 2, 30.

Skogen R, Medvecká E, Viane T, et al. 2019. PIN-driven auxin transport emerged early in streptophyte evolution. Nature Plants 5, 1114–1119.

Smirnoff N. 1993. The role of active oxygen in the response of plants to water deficit and desiccation. New Phytologist 125, 27–58.

Smit P, Limpens E, Geurts R, Fedorova E, Dolgikh E, Gough C, et al. 2017. Enhanced desiccation tolerance of resting cells of freshwater and terrestrial benthic diatoms to experimental desiccation and freezing is habitat-dependent. Phycologia 56, 246–255.

Souffreau C, Vanormelingen P, Sabbe K, Vyverman W. 2013. Tolerance of resting cells of freshwater and terrestrial benthic diatoms to experimental desiccation and freezing is habitat-dependent. Phycology 52, 246–255.

Stancheva R, Hall JD, Herburger K, Lewis LA, McCourt RM, Sheath RH, Holzinger A. 2014. Phylogeographic position of Zygogonium ericetorum (zygnematophyceae, charophyta) from a high alpine habitat and ultrastructural characterization of unusual aplanosporic. Journal of Phycology 50, 790–803.

Stenson SR, Kamisugi Y, Trinh CH, Stevenson SR, et al. 2016. Genetic analysis of Physcomitrella patens identifies ABCB10 as a regulator of ABA responses unique to basal land plants and required for desiccation tolerance. The Plant Cell 28, 1310–1327.

Sun J, Miller JB, Granquist E, et al. 2015. Activation of symbiosis signaling by arbuscular mycorrhizal fungi in legumes and rice. The Plant Cell 27, 893–907.

Sun X, Rikkerink EH, Jones WT, Uversky VN. 2013. Multifarious roles of intrinsically disordered proteins in plants illustrate its broad impact on plant biology. The Plant Cell 25, 38–55.

Sun Y, Harpazi B, Wijerathna-Yapa A, Merilo E, de Vries J, Michaeli D, Gal M, Cuming AC, Kollist H, Mosgau A. 2019. A lignin-independent origin of abscisic acid perception. Proceedings of the National Academy of Sciences, USA 116, 24892–24899.

Takahashi S, Murata N. 2008. How do environmental stresses accelerate photoinhibition? Trends in Plant Science 3, 178–182.

Tzvetkova-Chevolleau T, Franck F, Alawady AE, Dall’Osto L, Carrière F, Bassi R, Grimm B, Nussaume L, Havaux M. 2007. The light stress-induced protein ELIP2 is a regulator of chlorophyll synthesis in Arabidopsis thaliana. The Plant Journal 50, 795–809.

Umezawa T, Nakashima K, Miyakawa T, Kuromori T, Tanokura M, Shinozaki K, Yamaguchi-Shinozaki K. 2010. Molecular basis of the core regulatory network in ABA responses: sensing, signaling and transport. Plant & Cell Physiology 51, 1821–1839.

Van de Poel B, Cooper ED, Van Der Straeten D, Chang C, Delwiche CF. 2016. Transcriptome profiling of the green alga Spirogyra platensis (Charophyta) suggests an ancestral role for ethylene in cell wall metabolism, photosynthesis, and abiotic stress responses. Plant Physiology 172, 532–545.

Vanholme R, Storme V, Vanholme B, Sundin L, Christensen JH, Geomiene G, Halpin C, Rohde A, Morreel K, Boerjan W. 2012. A systems biology view of responses to lignin biosynthesis perturbations in Arabidopsis. The Plant Cell 24, 3506–3529.

Vogt T. 2010. Phenylpropanoid biosynthesis. Molecular Plant 3, 2–20.

Wang S, Li L, Sahu SK, et al. 2019. Genomes of early-diverging streptophyte algae shed light on plant terrestrialization. Nature Plants doi:10.1038/s41477-019-0560-3.

Weijers D, Wagner D. 2016. Transcriptional responses to the auxin hormone. Annual Review of Plant Biology 67, 539–574.

Weng JK. 2014. The evolutionary paths towards complexity: a metabolic perspective. New Phytologist 201, 1114–1149.

Wickett NJ, Mirarab S, Nguyen N, et al. 2014. Phylogenetic analysis of the origin and early diversification of land plants. Proceedings of the National Academy of Sciences, USA 111, E4859–E4868.

Wilhelmsson PKI, Mühlich C, Ulrich KK, Rensing SA. 2017. Comprehensive genome-wide classification reveals that many plant-specific transcription factors evolved in streptophyte algae. Genome Biology and Evolution 9, 3384–3397.

Wolf L, Rizzini L, Stracke R, Ulm R, Rensing SA. 2010. The molecular and physiological responses of Physcomitrella patens to ultraviolet-B radiati. Plant Physiology 153, 1123–1134.

Xu B, Ohtani M, Yamaguchi M, et al. 2014. Contribution of NAC transcription factors to plant adaptation to land. Science 343, 1505–1508.

Xu D, Duan X, Wang B, Hong B, Ho T, Wu R. 1996. Expression of a late embryogenesis abundant protein gene, HVA1, from barley confers tolerance to water deficit and salt stress in transgenic rice. Plant Physiology 110, 249–257.

Yoshida K, Inoue N, Sonobe S, Shimmenn T. 2003. Involvement of microtubules in the redox differentiation of Spirogyra species. Protoplasma 221, 227–235.

Yoshida K, Shimmenn T. 2009. Involvement of actin filaments in rhizoid morphogenesis of Spirogyra. Physiologia Plantarum 135, 98–107.

Yoshida T, Mogami J, Yamaguchi-Shinozaki K. 2014.ABA-dependent and ABA-independent signaling in response to osmotic stress in plants. Current Opinion in Plant Biology 21, 133–139.

Zakka A, Polit JT, Winicki K, Paciorek P, Justczak J, Nowak M, Maszewska J. 2016. PIN2-like proteins may contribute to the regulation of morphogenetic processes during spermatogenesis in Chara vulgaris. Plant Cell Reports 35, 1655–1669.

Zeng Q, Chen X, Wood AJ. 2002. Two early light-inducible protein (ELIP) cDNAs from the resurrection plant Tortula ruralis are differentially expressed cDNAs from the resurrection plant Tortula ruralis. Cell Reports 1, 929–967.

Zhang Y, Launay H, Schramm A, Lebrun R, Gontero B. 2018. Exploring intrinsically disordered proteins in Chlamydomonas reinhardtii. Scientific Reports 8, 1–11.

Zhang B, Liu J, Yang ZE, Chen EY, Zhang CJ, Zhang XY, Li FG. 2018. Genome-wide analysis of GRAS transcription factor gene family in rice. Plant Physiology 201, 2465–2476.

Zielinski K, Rensing SA, Wilhelmsson PKI, Mühlich C, Ulrich KK, Rensing SA. 2017. Enhanced desiccation tolerance of resting cells of freshwater and terrestrial benthic diatoms to experimental desiccation and freezing is habitat-dependent. Phycologia 56, 246–255.

Zimmer A, Lang D, Richardt S, Frank W, Reski R, Rensing SA. 2007. Dating the early evolution of plants: detection and molecular clock analyses of orthologs. Molecular Genetics and Genomics 278, 393–402.

Zorn M, Pfeifer HW, Grill D, Kraner I. 2001. Responses of plastid pigments to desiccation and rehydration in the desert lichen Ramalina maciformis. Symbiosis 31, 201–211.