

Spotlight

Plant Colonization of Land: Mining Genes from Bacteria

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Although it is known that novel genes facilitated plant colonization of land, the evolutionary origin of these genes remains largely unclear. A recent study by Cheng *et al.* suggests that some key genes related to plant development and stress responses were acquired from soil bacteria during the early evolution of land plants.

Moving onto Land and the Challenges for Plants

Land plants evolved from charophyte green algae, a paraphyletic group that primarily inhabits freshwater environments. The movement from water to land presumably was a repeated and continuing effort by plants. This effort is clearly documented by the fact that the ability to live in drier or subaerial habitats evolved independently in several algal lineages [1]. Ultimately, one charophyte alga successfully evolved into the most dominant eukaryotic group on earth, the embryophytes, that are now commonly known as land plants. The prevailing view based on genome analyses is that Zygnematophyceae, a group with coccoid or filamentous cells, are the extant charophyte algae that are most closely related to land plants [1].

Living on land allows plants to access abundant atmospheric carbon dioxide and sunlight, which means significantly more efficient photosynthesis. These benefits for a terrestrial lifestyle, however, do not come without daunting challenges, notably desiccation, fluctuating temperatures, osmotic pressure, UV irradiation,

and pathogens. To overcome these challenges, early land plants went through a cascade of major physiological and developmental changes. For instance, their often flat and undifferentiated thalli (e.g., in liverworts) enabled efficient water and nutrient absorption, whereas rhizoids (hair-like structures that are also found in some charophyte algae) provided better anchorage for plants, which in turn led to loss of motility. This transition to a sessile lifestyle had major implications for land plants: when facing environmental stresses, land plants must either tolerate these stresses or resist them by regulating their own development and physiology instead of escaping from stresses as animals do. To a large extent, these physiological and developmental changes are under genetic control, sometimes through the functions of novel genes. However, where did these novel genes come from? A recent study by Cheng *et al.* suggests that some key genes related to development and stress responses might have been acquired from environmental bacteria, which in turn aided the settlement of pioneering land plants [2].

Innovations of Bacterial Origin: Insights from Zygnematophyceae Genomes

Novel genes may evolve by *de novo* generation, gene duplication followed by neofunctionalization, transposition, horizontal gene transfer (HGT), or other mechanisms. Among these mechanisms, HGT does not involve the evolution of new genes from existing genetic material within the genome, but instead represents a process of gene sharing among distantly related organisms. Some beneficial genes may be shared between species: this may provide new genes or phenotypes to recipient organisms, allowing them to access niches or resources that were previously inaccessible [3]. Therefore, HGT is a rapid and efficient way to spread evolutionary success.

Given the sister relationship between Zygnematophyceae and land plants, Cheng *et al.* first identified gene family innovations in the most recent common ancestor of the two groups [2]. Notable among these gene families are those related to phytohormone signaling, cell-wall formation, and transcription factors (*GRAS*, *KNOX2*, and *BBR/BPC*). This comes as no surprise not only because plant physiological and developmental changes are regulated through phytohormone signaling, but also because the expression of the genes involved is controlled through actions of transcription factors. For two families, including abscisic acid (ABA) receptor *PYR/PYL/RCAR*-like and *GRAS* genes, their homologs, however, appear to be restricted to bacteria, Zygnematophyceae, and land plants. ABA is a vital phytohormone involved in plant responses to environmental stresses such as drought and desiccation; *GRAS* proteins are known for their regulatory roles as transcriptional factors, but are also involved in symbiotic interactions and stress responses. Phylogenetic analyses showed that each of the two gene families present in both Zygnematophyceae and land plants formed a monophyletic group, suggestive of a common origin. Cheng *et al.* concluded that these two families were most likely acquired from soil bacteria, followed by duplication and functional differentiation [2] (Figure 1).

HGT in Plant Colonization of Land: A Common Theme or Rare Exceptions?

The findings by Cheng *et al.* lead to another interesting question: how frequent and important was HGT during the transition of green plants from water to land? Although HGT is often considered to be a driving force in prokaryotic evolution, it was historically controversial and largely remains so in eukaryotes [4,5]. In particular, in complex multicellular eukaryotes such as animals and plants, the differentiation between somatic and reproductive cells is often suggested to be a significant

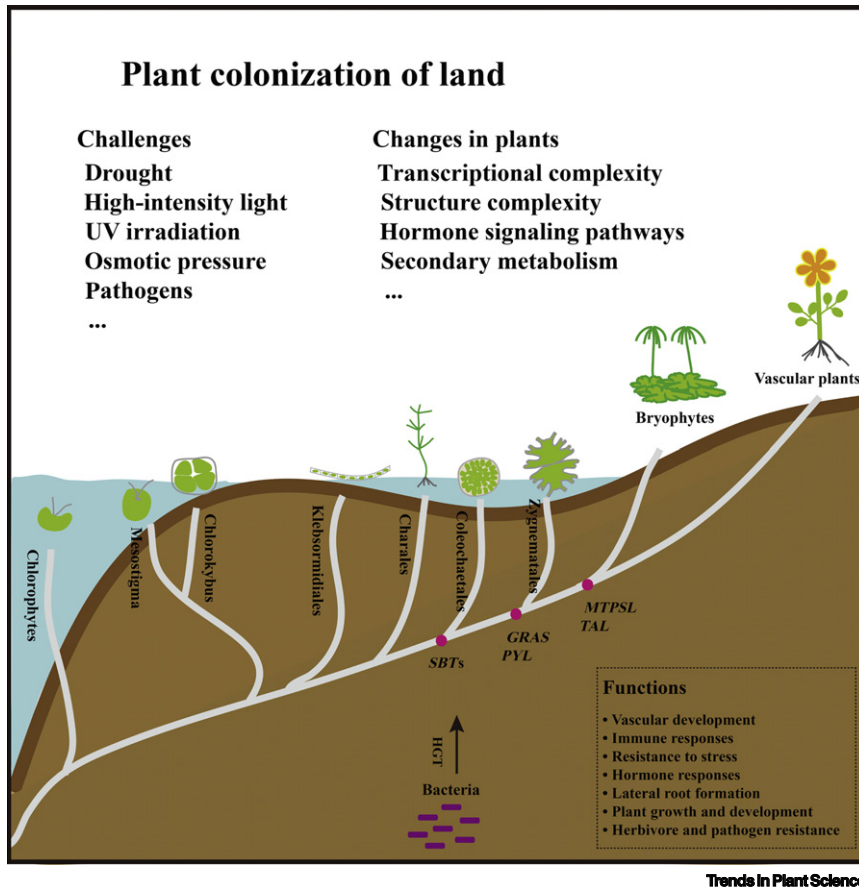


Figure 1. Role of Horizontal Gene Transfer (HGT) in Plant Colonization of Land. The movement of plants from water onto land was a complex process, starting gradually from ocean to freshwater and then to land [1]. Major challenges for plants during colonization and their corresponding changes are listed. Phylogenetic relationships within green plants are based on previous analyses [1,2]. Red dots indicate several genes that were acquired from bacteria during the evolution of streptophytes (land plants and charophyte algae). The role of HGT in plant colonization of land is summarized in the dotted box (lower right). Key genes: *SBTs*, encoding plant subtilases that are commonly involved in plant development and immune responses; *GRAS*, encoding transcription factors related to plant development and stress response; *PYL*, pyrabactin resistance 1-like genes, encoding abscisic acid (ABA) receptors that are involved in biotic and abiotic stress responses; *MTPSL*, microbial terpene synthase-like genes acquired from bacteria and fungi that are commonly involved in defense against herbivores and pathogens; and *TAL*, transaldolase-like genes that have been experimentally demonstrated in flowering plants to participate in vascular development [11].

barrier to HGT: for an acquired gene to be transmitted to the next generation, it must pass through reproductive cells. This suggestion has been challenged recently because all multicellular eukaryotes have unicellular or early developmental stages that are often exposed to environmental microbes and are thus prone to HGT [6]. Indeed, HGT not only takes place frequently for mitochondrial genes and in parasitic plants, but is also documented in bryophytes and ferns [7–9]. In the

moss *Physcomitrella patens*, the best-studied model species of early-diverging land plants, genes were reportedly acquired from miscellaneous sources, including viruses, bacteria, archaea, fungi, and animals [7,10]. The genes acquired by land plants are involved in a variety of important processes including stress resistance, auxin biosynthesis, and vascular development [7,10,11] (Figure 1). The majority of these genes were identified through analyses of bryophytes, which

are more structurally complex than charophytes. In charophytes, other than the two families documented by Cheng *et al.* [2], some other gene families also are reportedly of bacterial origin, including the large family of *SBT* genes encoding subtilases that are commonly involved in plant development and immune responses [12]. Because organisms with simpler structures are more prone to HGT, it is possible that more genes of foreign origin are present in charophytes. Nevertheless, systematic investigations of acquired genes in charophytes are still rare and, as such, knowledge about the role of HGT in plant colonization of land remains fragmented.

Concluding Remarks and Future Perspectives

Despite the possibly important role of HGT in the early evolution of land plants [2,3,7,8], many issues remain to be addressed. Key questions concern the scope of HGT and the number of acquired genes in charophytes and early-diverging land plants. These issues are often complicated by the controversies surrounding HGT in eukaryotes [4,5], and are also constrained by the amount of genome sequence data available and the quality of the data. The vast majority of the acquired genes in both prokaryotes and eukaryotes are so-called dispensable genes or peripheral genes. These genes are frequently involved in organismal adaptation to specific niches and are therefore short-lived. Conceivably, such genes could have facilitated the transition of plants from water to land, but they might have been lost subsequently once plants became fully settled in terrestrial environments. As more genome data from charophytes and early-diverging land plants become available, it will be important to perform further detailed investigations, including re-examination of acquired genes identified in earlier analyses. Such detailed analyses should provide a better understanding of the role of HGT in plant colonization of land.

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