

eXtra Botany

Insight

Take your sunscreen: plant photoreceptor systems in *Serritaenia testaceovaginata*

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This article comments on:

Busch A, Gerbracht JV, Davies K, Hoecker U, Hess S. 2024. Comparative transcriptomics elucidates the cellular responses of an aeroterrestrial zygnematophyte to UV radiation. *Journal of Experimental Botany* **75**, 3624–3642.

Light is undoubtedly the most important physical resource for plant life. As light in the environment always comes in the form of sunlight, its spectrum also includes a certain amount of potentially harmful UV light. Based on a comparative transcriptome analysis, Busch *et al.* (2024) investigated how gene expression in the green alga *Serritaenia testaceovaginata* responds to moderate UV radiation. The results revealed the presence of a conserved, plant-like system for UV perception and signal transduction, and components of all major plant photoreceptor systems. This suggests that embryophyte adaptations to light conditions on land may not so much rely on fundamentally new components but rather on the adaptation of the core system that was present in the last common ancestor of today's land plants and streptophyte algae.

Plants have evolved sophisticated systems for sensing the intensity and spectral composition of light (Fig. 1). Plant light signalling systems include the red/far-red light sensing phytochromes, the blue-light sensing phototropins, cryptochromes, and ZEITLUPE family proteins, and the UV-sensing UV RESISTANCE LOCUS 8 (UVR8) (Galvão and Fankhauser, 2015).

The work by Busch *et al.* (2024) relates to the question of which evolutionary innovations enabled the progenitors of

land plants to survive and then to thrive on land, a process called terrestrialization. There is substantial evidence suggesting that the first representatives of the land plants, the *Embryophyta*, appeared approximately half a billion years ago (Morris *et al.*, 2018; Strother and Foster, 2021). This step definitely has shaped the surface of our planet, but which genetic, developmental, and physiological changes needed to occur, and in which order, to make this accomplishment possible is still not clear.

Sensing the quality and quantity of ambient light and the physiological responses to it are clearly important elements of the water-to-land transition. A type of phytochrome containing the photosensory core module known from plant phytochromes already exists in cyanobacteria, the bacteria that are ancestral to plant chloroplasts and contributed considerably to the plant gene pool (Wang *et al.*, 2020). Networks for light sensing and signalling, and for integration of light and other environmental cues are widespread in plants. Yet, it is a matter of debate in which taxonomic groups these networks have evolved. Furthermore, did these systems only evolve in land plants—after terrestrialization—or had they evolved beforehand in an aquatic environment? Also if they evolved before, probably in green algae, in which groups, and did this happen in multicellular or in unicellular species and why?

While most insight into plant light signalling has essentially been obtained in a very limited number of species, in particular seed plants, the research highlighted here was performed on *Serritaenia testaceovaginata*, a species most readers might not be familiar with.

What is *Serritaenia testaceovaginata*?

There is widespread consensus now that the first land plants emerged from progenitors within the streptophyte green

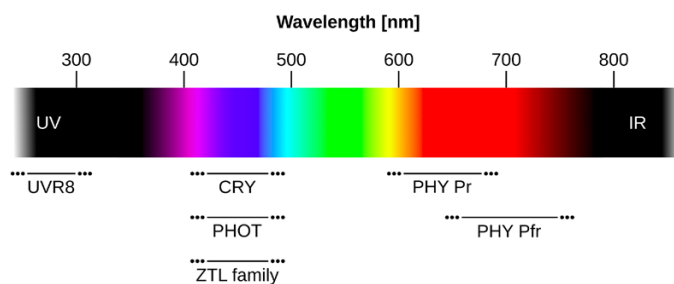


Fig. 1. Photoreceptors in plants. The approximate spectral range in which different plant photoreceptors absorb are indicated. For phytochromes (PHYs), absorption of the Pr and Pfr state is shown. UV, UV light; IR, infrared light; CRY, cryptochrome; PHOT, phototropin; ZTL, ZEITLUPE.

algae, and that the *Zygnematophyceae* represent the closest extant algal relatives of land plants (Wodniok *et al.*, 2011; Wickett *et al.*, 2014; de Vries and Archibald, 2018; Hess *et al.*, 2022). *Zygnematophyceae* are a class of freshwater and, interestingly, semi-terrestrial algae. These algae have adaptations to cope with stress factors typically associated with the life on land, such as desiccation or UV (Busch and Hess, 2022). There is evidence that the evolution of important stress responses predated plant terrestrialization (Dadras *et al.*, 2023). For all these reasons, the molecular mechanisms underlying stress responses in *Zygnematophyceae* deserve attention.

Serritaenia testaceovaginata is a unicellular species, belongs to the *Zygnematophyceae*, and can be cultivated in the laboratory. Further advantageous for research related to light signalling, and especially UV-related signalling, is that *Serritaenia* produces an easily observable extracellular pigmentation in response to illumination by UV light (Busch and Hess, 2022). It is, however, less helpful that there is no reference genome sequence for this alga.

How do we study responses to UV at the molecular level if a reference genome sequence is lacking?

Because there was no reference genome sequence available, the authors decided on a *de novo* transcriptome analysis. Following exposure to UV on three consecutive days for 4 h each, RNA was extracted and, following cDNA library construction, it was sequenced. The experiment was performed in triplicate; the controls were cultivated under identical conditions except that UV was filtered out. Processed reads from all conditions were pooled (267 756 958 reads in total) and assembled into contigs which were used for annotation and differential gene expression analysis.

The annotated *de novo* transcriptome led to 39 988 complete, 20 701 partial, and 4671 likely internal gene fragments. At first glance, the number of possibly >60 000 predicted different coding sequences might seem high. For instance, 11 080 and 27 137 genes were modelled with high confidence for

two other species of *Zygnematophyceae* (*Mesotaenium endlicherianum* and *Spirotaenia muscicola*) (Cheng *et al.*, 2019). However, between 27 822 and 52 529 annotated genes together with substantial genome size variation were reported for four unicellular *Zygnematophyceae* in the *Closterium peracerosum–strigosum–littorale* complex (Kawaguchi *et al.*, 2023). Therefore, this number of genes is not as out of range as it may seem. Moreover, the number of individual coding sequences from a *de novo* assembled transcriptome cannot be directly compared with the gene content determined by total genome analysis. Even though some genes will not have been transcribed at all under the conditions studied, the *de novo* transcriptome established here still provided a fairly sound basis for differential gene expression analysis of *S. testaceovaginata*.

Light signalling systems in *Serritaenia testaceovaginata*

Differential expression analysis of *S. testaceovaginata* revealed that genes encoding enzymes involved in the production of aromatic amino acids, for phenylpropanoid biosynthesis, and suitable transport systems were up-regulated under UV irradiance, suggesting a polyphenolic origin of the *Serritaenia* sun-screen pigment.

The authors identified components of the phytochrome, phototropin, cryptochrome, and ZEITLUPE systems, as well as the UV-sensing UVR8 system in *Serritaenia* (i.e. components of all major plant photoreceptor systems; Galvão and Fankhauser, 2015). With the exception of the phototropins, expressional changes upon UVB treatment were found for components of all photoreceptor systems.

The authors looked more closely into the UV-related signalling system. In addition to UVR8, *Serritaenia* also contains potential homologues of key components required for UVR8 downstream signalling in seed plants, including CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1), REPRESSOR OF UV-B PHOTOMORPHOGENESIS (RUP), and ELONGATED HYPOCOTYL 5 (HY5) (Podolec *et al.*, 2021). UVR8 contains three tryptophan residues that serve as a chromophore for UV light; regions containing these residues are also conserved in UVR8 from *Serritaenia*. In Arabidopsis, monomerization of the UVR8 dimer in response to UV radiation and binding to the substrate-binding site of the E3 ubiquitin ligase COP1 prevents targeting for degradation of the transcription factor HY5 and thereby controls gene expression. RUP acts as a negative regulator of UV radiation signalling in Arabidopsis by promoting re-dimerization of UVR8 (Podolec *et al.*, 2021). The chlorophyte alga *Chlamydomonas reinhardtii* is more distantly related to land plants than *Serritaenia*. However, even *Chlamydomonas* contains homologues of key components of UV sensing and signalling, and a previous study has shown that basic principles of UVR8 action are functionally conserved between *Chlamydomonas* and

Arabidopsis (Tilbrook *et al.*, 2016). Sensing non-damaging levels of UV radiation to anticipate and prepare for potentially damaging levels may therefore be a strategy shared by land plants, streptophyte algae, and the more distantly related chlorophyte algae that at least partially also relies on a common mechanism. However, lessons learned from evo-devo studies, such as on hormone signalling pathways in plants, should remind us that homologues identified on the basis of sequence similarity are not necessarily functional homologues and that molecular mechanisms predicted based on the presence of a set of components need to be confirmed experimentally (Blázquez *et al.*, 2020). The lack of established and easy-to-use standard protocols for the generation of transgenic lines and targeted mutants for streptophyte algae is an important limitation in this regard. Another important limitation is that the search for photoreceptors and downstream signalling components in non-seed plants has so far been mainly based on testing the role of sequence homologues of components identified in seed plants. This is certainly a valid approach, but we should be aware that non-seed plants may well have components that are not present in seed plants and that can only be identified in unbiased approaches such as mutant screens or proteome-wide interaction studies.

The study by Busch *et al.* provides important insights into the conservation of key components of light signalling and highlights the urgent need for studies in non-seed plant species.

Conflict of interest

The authors declare no conflict of interest.

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