EDITORIAL: REFLECTIONS ON THE PLANT CELL CLASSICS

Put on Your Sunscreen: The Birth of Arabidopsis Abiotic Stress Genetics

Why do plants make so many small-molecule metabolites? Today the standard answer is that specialized metabolites are produced “to protect from enemies and attract friends”, and there are many elegant examples in the literature (e.g., Peters, et al., 1986, Schemske and Bradshaw, 1999, Wittstock et al., 2003, Dudareva and Pichersky, 2006, Weinhold and Baldwin, 2011). However, the view of plants as master biochemists is relatively new in the history of plant biology, ecology and evolutionary biology. The broad range of taxonomically- and cell type-limited molecules that we now know as specialized metabolites were long known as “secondary metabolites”, reflecting a belief that they are evolutionary oddities or waste products.

Due to the reduction in the stratospheric ozone layer caused by widespread use of halocarbon refrigerants and other industrial chemicals, in the 1980’s concern arose about the possibility of widespread increases in terrestrial ultraviolet-B (UV-B; ~280-320 nm). UV-B was known to damage DNA, RNA, and proteins and reduce productivity of crops and natural ecosystems (Caldwell, 1971). This led to studies of plant UV-B sensitivity, and searches for correlated molecular mechanisms that might protect plants from excessive UV-B, mainly related to flavonoid sunscreens.

These studies tended to be of two general types: 1. Subject plants to stress known to induce flavonoid sunscreens and ask whether these pretreatments increase UV-B tolerance; 2. Compare the UV-B tolerance of different crop cultivars or plants collected from nature—for example, from an altitudinal cline (where UV-B naturally increases with higher altitude)—and look for correlations with sunscreens. A major problem with both approaches was that neither “treatment” specifically influences sunscreens. For example, high light pretreatment causes induction of many physiological changes in addition to the targeted flavonoid increases, and accessions from an altitudinal cline evolve in the presence of innumerable other factors beyond UV-B.

Geneticists take for granted the notion that gene product function is always best evaluated by comparing the biology of a mutant to its isogenic wild-type strain; or as I recall master yeast geneticist Gerry Fink succinctly saying “it is always better to have a mutant”. This approach—which seems obvious these days—was uncommon in the 1980’s, perhaps because our collective isogenic mutant collection was limited. However, collaborators at the Boyce Thompson Institute in the early 1990’s took this philosophy to heart, using Mendelian mutants to evaluate the importance of phenylalanine-derived specialized metabolites as sunscreens in Arabidopsis thaliana (Li et al., 1993).

The experimental design is now familiar, but this may have been the first published use of the now tried and true approach to study abiotic stress tolerance mechanisms. We compared the impacts of varied UV-B fluences on wild type and two mutants blocked early in flavonoid biosynthesis: transparent testa 4 (tt4; defective in the committing enzyme chalcone synthase) and tt5 (blocked in the second enzyme, chalcone isomerase). In a sense, the expected results were obtained: the flavonoid deficient mutants showed enhanced sensitivity compared with the isogenic wild type. However, the study revealed an unexpected gift: the tt5 mutant was far more UV-B sensitive than tt4.

Biochemical pathway and HPLC analysis of UV-absorbing compounds from wild-type, tt4, and tt5 Arabidopsis plants. (Adapted from Li et al., [1993], Figure 3).
The general reason for the difference was deciphered through analysis of leaf UV absorptive compounds by high-performance liquid chromatography (see figure). While both mutants lacked detectable kaempferol flavonol glycosides (peaks 7-10), they had differences in sinapate esters, which were the other major UV absorptive leaf epidermal sunscreens that we identified (peaks 5-6).

It only took a couple of sentences to describe here, but getting to that level of understanding took hard work and luck. Jiayang Li showed that hydrolyzed purified peak 10 had the absorbance properties of kaempferol aglycone (i.e., lacking sugar decorations), and it fragmented in a mass spectrometer to yield the same products as authentic kaempferol standard. Luck ran high in that Clint Chapple was early in his beautiful work on the biochemical genetics of peaks 5-6, characterizing the FAH1 ferulate hydroxyxylase gene and mutants of A. thaliana as a postdoc with Chris Somerville at Michigan State (Chapple et al., 1992). Clint generously provided expertise, standards, and mutants that sped up the work tremendously.

Even simple Mendelian mutants can defy your expectations, and in doing so lead you in interesting directions. While the differences in tt mutant UV-B sensitivity were later verified to be due to variation in sinapate esters (Landry et al., 1995) the question still remains: why do the sinapate esters vary in mutants of flavonoid biosynthesis? The increase in tt4 mutants of flavonoid biosynthesis? The increase in sinapate esters (Landry et al., 1995) the mutants that sped up the work tremendously.


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REFERENCES


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