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PLANT BIOLOGY

Abscisic acid in bloom

Julian I. Schroeder and Josef M. Kuhn

To survive environmental stresses, plants must respond to the hormone abscisic acid. The receptors for this hormone have remained elusive, but one receptor with unique functions in flowering has now been identified.

When plants experience drought or cold, they cannot get themselves a glass of water or move to a warmer place. Instead, their ability to survive lack of water, extreme temperatures and such stresses as high salt levels relies heavily on a plant hormone called abscisic acid (ABA). Despite their importance, the genes that encode the cellular receptors for this hormone have not been identified. On page 290 of this issue, however, Razem *et al.*¹ describe the characterization of a protein that binds to messenger RNA and that also binds ABA and controls ABA-dependent flowering in the model plant *Arabidopsis*.

The question of how plants cope with the recurring stresses of drought, cold and salinity not only engages plant scientists, agronomists, ecologists and climatologists. It also increasingly demands the attention of politicians, given that in arid regions across the globe more than 80% of the available fresh water is consumed by agriculture². Many avenues of research have shown that ABA is a key player in such stress resistance. Responses mediated by this hormone lead to the induction of complex tolerance mechanisms to drought, cold, salinity and wounding, including the control of closure of the stomatal pores in leaves to reduce water loss³.

Genetic screens with various twists have elucidated ABA signal-transduction mechanisms that act downstream of ABA sensing³. But genes that encode ABA-binding receptor proteins have remained unidentified. This might be because plant genomes have large numbers of homologous — closely related — genes that probably have overlapping functions, or because an ABA receptor is essential, such that plants with mutations in the receptor gene would not survive. Research on ABA signalling is also revealing the robustness of an intricate signal-transduction network. This can limit traditional 'forward' genetic approaches⁴, because a mutation in one pathway may be side-stepped to a degree by using another route that transmits the signal.

Razem and colleagues¹ have used an alternative, biochemical approach. They isolated a barley protein that has ABA-binding activity, named ABAP1 (ref. 5), and investigated whether a homologue of ABAP1 functions in an ABA response in *Arabidopsis*. Their work shows that an RNA-binding protein called FCA binds to ABA and is regulated by it, and that FCA is involved in a less well-studied function of ABA — the inhibition of flowering.

The *Arabidopsis* FCA protein is homologous to the barley ABAP1 protein in its carboxy-terminal half and, like ABAP1, it has a high affinity for active ABA analogues^{1,5}. (Its dissociation constant, K_d , is 19 nM.) The FCA protein is a component of the so-called autonomous flowering pathway, which reduces the activity of the flowering repressor *Flowering Locus C*, or *FLC* (Fig. 1, overleaf)^{6,7}. Two structural regions of the FCA protein are of particular relevance: a protein-interaction region known as a WW domain, and an RNA-recognition motif^{6,7}. The WW domain allows FCA to interact with the protein FY, which is an mRNA processing factor⁶.

The FCA-FY complex negatively regulates expression of the flowering repressor *FLC*. It also reduces the amount of functional FCA protein through a negative feedback loop by adding a premature polyadenylation tail to a truncated form of the *FCA* precursor mRNA^{6,7}. In this negative feedback loop, polyadenylation of the truncated *FCA* precursor mRNA results in a shortened mRNA, and thus in non-functional FCA protein (Fig. 1). Several reports have established a link between RNA-processing proteins and ABA signalling^{8–12}. But we don't yet know whether these mRNA-processing proteins, which affect ABA action, are components of an FCA-like ABA stress-response pathway.

In the new work, Razem *et al.*¹ report that the FCA-FY complex dissociates when ABA binds to FCA, making the complex non-functional (Fig. 1). As a result, premature polyadenylation of the truncated *FCA* precursor



50 YEARS AGO

"Benjamin Franklin's Purse"

— In connexion with the 250th anniversary of the birth of Benjamin Franklin (1706–90), the Department of Mineralogy of the British Museum (Natural History) is exhibiting the asbestos purse sold by Franklin to Sir Hans Sloane in 1725. The purse came into the collections of the British Museum at the time of its foundation in 1753, on the death of Sir Hans Sloane. It had lain unrecognized for many years and was identified in 1938. On his arrival in Britain, Franklin worked for some time as a compositor and sought to augment his income by the sale of some 'curiosities' which he had brought with him from America. One of these, the asbestos purse, is referred to by Franklin in his autobiography... The purse represents perhaps the earliest specimen of asbestos from North America to reach Great Britain. From *Nature* 21 January 1956.

100 YEARS AGO

The study of a few of our British stone monuments from an astronomical point of view [may give information on] the order of succession of the various swarms of immigrants who set out the various systems of alignments... I have evidence that the risings of stars, as well as of the sun, were observed in some of the circles... some circles used in the worship of the May year were in operation in 2000 B.C., and there was a change of cult about 1600 B.C., or shortly afterwards, in southern Britain, so definite that the changes in the chief orientation lines in the stone circles can be traced. To the worship of the sun in May, August, November, and February was added a solstitial worship in June and December. The easiest explanation is the advent of a new swarm of immigrants about that date. The associated phenomena are that the May–November Balder and Beltaine people made much of the rowan and maythorn. The June–December people brought the worship of the mistletoe. From *Nature* 18 January 1906.

50 & 100 YEARS AGO

mRNA is abolished. Thus, ABA causes accumulation of full-length *FCA* mRNA. Razem *et al.* show that ABA causes a dramatic increase in *FLC* mRNA, which in turn would delay the transition to flowering. Consistent with this model, the authors report that ABA causes a delay in flowering in *Arabidopsis*. As *Arabidopsis* plants can flower early in response to drought, which increases ABA production, the ABA–*FCA* response may be overridden during this response¹³. Possible modulation mechanisms during drought stress could be investigated by analysing the newly revealed direct ABA regulation of *FCA* mRNA (full-length versus truncated) and the strong ABA-induced increase in levels of *FLC* mRNA.

Interestingly, the RNA-recognition motif in *FCA* is absent in the barley ABAP1 protein⁵. Indeed, ABA-binding studies of *Arabidopsis* *FCA* in which the protein lacked specific structural regions show that ABA-binding activity lies in the carboxy-terminal half of *FCA*, which does share homology with ABAP1 (ref. 1).

Razem *et al.*¹ went on to show that in plants with a loss-of-function mutation in *FCA*, the ABA-induced closing of stomatal pores and inhibition of seed germination — two classical ABA responses — were not impaired. Furthermore, ABA inhibition of flowering was not affected in two dominant ABA-insensitive mutants, *abi1-1* and *abi2-1*, in which most of the stress-related ABA responses are impaired. Thus, other ABA receptors are needed to explain the classical ABA signalling responses to stress. The hunt could be on to characterize

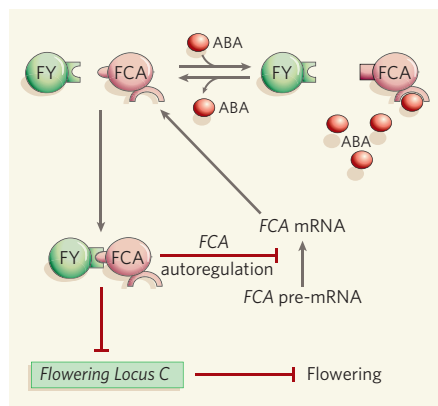


Figure 1 | Abscisic acid, RNA metabolism and control of flowering in plants. Binding of two proteins, *FCA* and *FY*, to one another results in a decrease in expression levels of *Flowering Locus C* (*FLC*), causing a transition from vegetative growth to flowering. The *FCA*–*FY* complex also causes synthesis of a truncated, non-functional *FCA* messenger RNA in a negative feedback loop that results in fewer full-length *FCA* mRNA transcripts and less *FCA* protein^{6,7}. Razem *et al.*¹ report that binding of abscisic acid (ABA) to *FCA* abolishes the interaction of *FCA* with *FY*, leading to an increase in full-length *FCA* transcripts and — through increased *FLC* activity — a delay in flowering. Red lines depict negative regulation. (Diagram modified from a figure provided by R. Hill.)

homologues to the ABA-binding carboxy terminus of *FCA*¹ and barley ABAP1. A simple search of protein databases reveals only one distant *FCA* homologue in the *Arabidopsis* genome. Alternatively, the *FCA* and ABAP1 proteins provide an opportunity to elucidate

the structure of an ABA-binding pocket, which may reveal important sub-domains and structural constraints for ABA binding.

A door to understanding ABA perception has been opened. The binding of ABA to *FCA* and ABAP1 is apparently a further example of which plant growth regulators mediate their responses. Further questions arise with each advance. Plant scientists will need to keep on trekking to illuminate how their immobile lab subjects perceive abscisic acid when faced with drought, cold and salinity.

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CHEMICAL ECOLOGY

In defence of maize

They can't run and they can't hide. But with those reactions denied to them, plants have evolved an extensive and varied repertoire for responding to threats to their well-being. Apart from the tolerance mechanisms discussed above by Schroeder and Kuhn, such responses can include calling upon insect allies to deal with pests that would otherwise damage or destroy the plant by eating it.

Christiane Schnee and colleagues have started to dissect one such signal system — that used by maize seedlings when they are attacked by caterpillars (*Proc. Natl Acad. Sci. USA* doi:10.1073/pnas.0508027103; 2005). The plant signals consist of volatile chemicals, which in the case investigated by Schnee *et al.* attract female wasps of the species *Cotesia marginiventris*. The wasps lay their eggs

in the caterpillars, with predictably unhappy results for the latter.

Maize emits a cocktail of volatile defence signals in response to an attack by herbivores, and the general difficulty in studying the process is identifying which constituent of these complex blends has which effect. From investigations of maize biosynthetic pathways, Schnee *et al.* first isolated an enzyme, a terpene synthase dubbed TPS10, that is responsible for producing most of the herbivore-induced volatiles.

But that was only an initial step. To look into the biological effects of these terpenes, the authors used genetic engineering to insert the gene that encodes TPS10 into *Arabidopsis*, the standard lab plant for biologists. The transgenic *Arabidopsis* plants were then used



in experiments in which female *C. marginiventris* could choose between the options offered in an 'olfactometer' (fresh air and untransformed *Arabidopsis* being the other choices).

The main result to emerge was that the wasps indeed showed a strong preference for the plant that produced the TPS-mediated terpene — but only after they had learned the association between the defence signal and the host by having previously

laid eggs in the caterpillar host.

This approach, say Schnee *et al.*, is an example of the value of using transgenic technology to study the effects of complex volatile compounds. Even when the compounds themselves or their constituents are not available, if the genes concerned have been identified, the ecological influences of these signals can nonetheless be investigated in genetically transformed plants.

Tim Lincoln