experiments capable of disproving them. However, whatever their merits, all models are ephemeral, state-of-the-art creations destined to be ultimately replaced by those models of another sort that we call structures, because they were obtained by crystallography or nuclear magnetic resonance and usually can claim a much greater accuracy. Although modeling of RNA is most efficient and rigorous when performed at the atomic level, where full use can be made of stereochemical constraints, the accuracy of the final product is still inevitably much lower than the apparent resolution.

The architecture of the model for the group I intron core was derived on the basis of sequence comparisons, with limited experimental data, whereas the HDV ribozyme model rested more on chemical probing and mutagenesis experiments. As was already known for secondary structure prediction, the superiority of comparative sequence analysis, which looks for coordinated events in sequence evolution to infer spatial relationships, is again clearly established for three-dimensional modeling. However, the recent development of "chemogenetic" methods (*12*), which allow the binding partners of individual RNA chemical groups to be readily identified in a single experiment, could soon tip the balance in favor of hard-core biochemistry—that is, unless technical advances in RNA crystallography should make all other structural approaches accessory.

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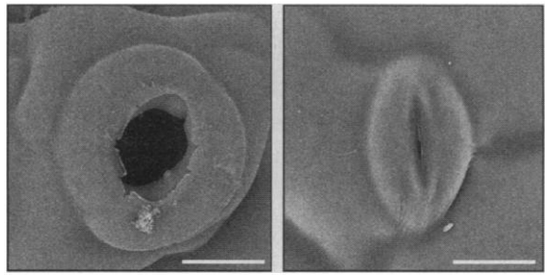
PERSPECTIVES: BOTANY

A Plant's Dilemma

Erwin Grill and Hubert Ziegler

According to a recent United Nations resolution, water will become an increasingly scarce resource for humankind in the next century. Plants have faced this same problem ever since they conquered land some 450 million years ago. To protect themselves from excess water loss they have adopted several strategies, including a waxy cuticula that coats the plant, and closable stomata, specialized cells within the epidermis that form pores for gas exchange (*1*). Now a report by Pei *et al.* (*2*) on page 287 of this issue points to a way in which plants can be assisted in conserving water, by harnessing the molecular mechanism that closes the stomata.

The stomatal aperture is controlled by osmotic adjustment in the surrounding cells. In a sophisticated regulatory mechanism, light, the carbon dioxide required for photosynthesis, and the water status of the plant are integrated to regulate stomatal aperture for optimization of the plant's growth and performance. In most plants, the stomatal pore is formed by two parallel, longitudinal guard cells whose flanking sides are physically linked just at the ends of the cells (see the figure at right). Opening of the stomata is brought about through swelling of the guard cells by solute and water uptake, which are then stored in the vacuole. Solute uptake—primarily ions such as potassium and chloride—from the apoplast of the 15-carbon group is driven by proton pumping and by the generation of osmolytes such as malate and sucrose within the cell. Closure of the stomata is mediated by solute efflux and is triggered by the plant hormone abscisic acid (ABA). Environmental cues such as drought, heat, and cold stress trigger the ABA-induced stomatal response, which is then executed by the orchestration of several ion channels located at the plasmalemma and the tonoplast of the guard cells (*3*). Several components of this signaling pathway have been identified, including cADP ribose (cADPR), Ca^{2+}, pH, two homologous type 2C protein phosphatases (PP2C) ABI1 and ABI2, as well as several ion channels (*3*, *4*).



Stomata, open and closed. Scanning electron micrographs of stomata from hydrated leaves of *Arabidopsis thaliana*, fully open (left) and largely closed (right). Bar, 10 μm.

Pei and his colleagues add another facet to ABA signal transduction by demonstrating control of stomatal aperture by farnesylation (*2*), enzymatic addition of the 1-carbon group farnesyl to a protein. In mammalian cells, farnesylation of the small G protein (GTP-binding protein) Ras is required for activation of the mitogenic response, which Ras accomplishes by recruiting the protein Raf to the membrane (*5*). In plants, the role of farnesylations is less well defined, but it has been linked to the control of cell division and ABA signaling (*6*, *7*).

Pei *et al.* now show that a farnesyltransferase negatively regulates the S-type (slow) anion channel activity in guard cells of *Arabidopsis*. When this channel—located in the plasmalemma—opens, the concomitant loss of cytoplasmic anions leads to a sustained decline in the membrane potential that subsequently activates outward-rectifying K^+ channels, a necessary step in stomata closure (*8*).

The analysis of a mutant strain of *Arabidopsis* defective in its ABA response paved the way for this achievement. The mutant *era1-2* is hypersensitive to inhibition of seed germination by ABA, owing to the deletion of a gene that encodes the essential β subunit and may signal through ERA1 by inhibiting the farnesyltransferase (*7*). Guard cells from *era1* mutants are hypersensitive to ABA in the stomatal response as well. The conductance of the S-type anion channel is enhanced in the presence of ABA in guard cells of the mutant or after farnesyltransferase inhibition (*2*). Genetic analyses with double mutants placed the action of the farnesyltransferase downstream of or parallel to the PP2C phosphatases ABI1 and ABI2.

A picture of ABA signal transduction in guard cells is beginning to emerge (see the figure on next page). Although it is not exactly clear where and how ABA is per-

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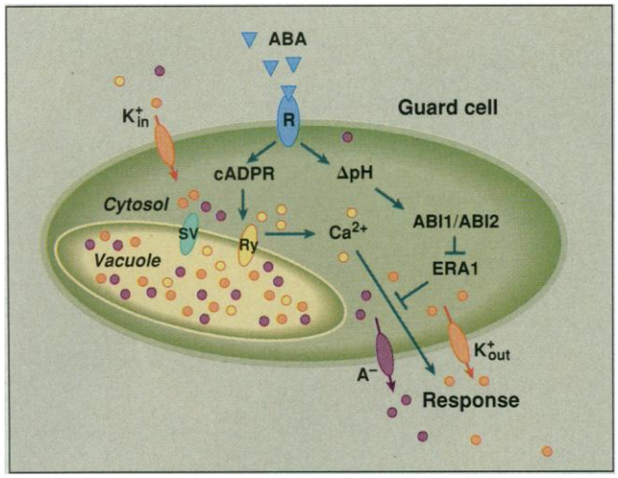

ABA signal transduction in guard cells. R, ABA receptor; cADPR, cyclic adenosine 5′-diphosphate ribose; K_{in}, K_{out}, potassium channels; A, S-type channel; Ry, ryanodine-sensitive Ca^{2+} channel; SV, nonspecific slow vacuolar channel.

ceived by the cell, specific ABA-binding sites have been detected in plant membrane preparations (*9*). ABA subsequently induces an initial depolarization of the membrane potential, an increase in cytosolic pH, and, probably, the generation of cADPR (*4*). cADPR and inositoltrisphosphate can induce stomatal closure by increasing the cytosolic free Ca^{2+} concentration ($[Ca^{2+}]_i$) (*10*). [cADPR acts through its action on ryanodine-sensitive Ca^{2+}-release channels (*4*, *11*).] $[Ca^{2+}]_i$ and the pH signal inhibit the inward-rectifying K_{in}^+ channel, which is responsible for K^+ uptake and is required for stomatal opening, and by stimulating ion efflux (*3*). Although Ca^{2+} indirectly stimulates the S-type channel, the pH signal in ABA activates the K_{out}^+ channel. In addition, the pH shift activates the partially redundant PP2Cs ABI1 and ABI2 that constitute part of a negative control mechanism of ABA signal progression (*12*). The PP2Cs act downstream of or parallel to cADPR and Ca^{2+} (*13*) and may signal through ERA1-dependent farnesyltransferase. The downstream control of channel activities is exerted by distinct but unresolved pathways of reversible phosphorylation events consisting of staurosporin-sensitive protein kinases, possibly an ABA-activated protein kinase, and type 1, 2A, or 2B protein phosphatases (*14*).

Water loss from terrestrial plants occurs primarily through the stomata that cover the leaf surface at a density of several thousand per square centimeter. If one were able to manipulate the ABA signaling pathway to enhance stomatal closure, it might be possible to reduce water transpiration in plants. This strategy could then be used to reduce water usage in crop plants cultivated in areas of water shortage, an economic benefit.

Here, however, is the dilemma. Faced with water shortage a plant can close its stomata, but then other essential functions would become impaired. Plants need open stomata to allow gas exchange for net photosynthesis: carbon dioxide uptake and oxygen emission. In addition, transpiration (as emission of water vapor) drives transport in the xylem tissue of the vascular system and can cool leaf surfaces. Some plants have evolved strategies to ameliorate the problem: high-affinity carbon fixation by phosphoenolpyruvate carboxylase in C_4 plants like maize or the temporal separation of photosynthesis (day) and carbon fixation (night), as in cacti.

Greening up. The *Myrothamnus* shrub from the Namib Desert in Namibia, dormant during drought (left), becomes green within a day of watering (right).

PHOTOS: P. WALTHER (*18*)

Nevertheless, with abundant water, plants consume more water than is necessary for optimal yield (*1*). Thus, reducing stomatal opening by application of ABA and ABA analogs can lower water consumption by ~30%, while yield is only marginally lower or even identical (*15*). Hence, the ABA-hypersensitive *era1* plants transpired, by a factor of 3, less than wild-type plants with a limited water supply (*2*). The new findings offer a molecular strategy to manipulate the water-use efficiency of plants by specifically down-regulating the farnesyltransferase activity in stomata.

Although most plants are irreversibly injured by severe water stress, several "resurrection" plants can tolerate a residual water content of ~1% and survive for years in a dormant state (*16*). For example, the dormant resurrection plant *Myrothamnus flabellifolia* turns green and actively photosynthesizes within a day of water application (see the photographs below). ABA administration to resurrection plants can induce the desiccation-tolerant state, and several genes involved in the process have been identified (*17*). The molecular mechanisms and energetic tradeoffs of desiccation tolerance in these specialized plant species are as yet poorly understood. A combined effort to elucidate the evolved strategies of plants to cope with water shortage and the biotechnological implementation of the results promise a rich harvest for the future.

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