INSTITUT DE FRANCE
Académie des sciences

Séance solennelle de l'Académie des sciences / 15 juin 2010
Réception des nouveaux Associés étrangers sous la coupole de l'Institut de France

How plants know when to grow and when not to grow

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Twenty-five years ago, we knew very little about the mechanisms of plant growth. There were the five classical plant "growth regulators": auxin, cytokinins, gibberellins, abscisic acid, and ethylene gas. We knew the effects of applying these hormones to plants and we also knew that auxins and cytokinins were required to make plants regenerate. But the age of molecular mechanism had not yet reached the plant science community. There were a few exceptions, of course: much was beginning to be learned about the rhizobium/legume symbiosis, the first maize transposons had just been cloned, and stable transformation of solanaceous plants led to hopes of modernizing the field.

Almost nothing was known of signaling pathways that affect growth within the plant, or how these developmental programs were altered by the local environment. One thing that was beginning to become clear, though, was that plant biologists needed to adopt a model organism. Thus, *Arabidopsis thaliana* became the plant of choice and has remained so until this day. *Arabidopsis* is a small, prolific weed, with a rapid life cycle, good genetics, and a very small genome. For a brand new postdoc, such as myself, just entering the field from outside, the possibilities for using molecular genetics to dissect complex signaling pathways were immense and very exciting.

Because knowledge was scant, our first research questions were not very sophisticated. In my case, one such question was, "Do you think it is possible to find a mutant plant that thinks it is in the light, even though it has never seen light?" I was lucky enough to find such mutants, which we called, *de-etiolated*, because they did not have the usual "etiolated" or pale sprout phenotype. Further genetic studies told us that these genes played a negative regulatory role downstream of multiple photoreceptors. We now know that the proteins encoded by some of these genes are involved in the turnover of key transcription factors that initiate the light response of seedlings as they emerge from the soil. These genes are conserved in all multicellular eukaryotes where they play important roles in regulated turnover of key signaling proteins. Their initial discovery in plants underscores the power of plant genetics for new gene identification.

From these first genetic screens, we also found a subclass of *de-etiolated* mutants that were dark-green dwarf plants, with reduced male fertility, delayed senescence, and decreased apical dominance. We went on to show that these loci defined genes involved in the biosynthesis or response to a steroid made and utilized by plants, called brassinosteroids. Although these steroids had been purified from *Brassica* pollen in the 1970's, most felt that there was not a compelling case that they acted as hormones. Knowing the phenotype of biosynthesis and receptor mutants for brassinosteroids ultimately convinced the plant science world that there were more than just 5 plant hormones. We also learned that plants, like animals, utilize steroids to regulate gene expression that controls growth, development, and homeostasis. The pathways of synthesis and turnover of steroids are remarkably conserved between the 2 kingdoms, despite their divergence from a common ancestor over 1 billion years ago. In contrast, steroid receptors appear to have evolved independently in plants and animals. This may be due to the unique predator/prey relationship of animals and plants, which may have influenced the evolution of signaling pathways in humans as a result of our diet.

Other genetic screens followed. Because of the power of *Arabidopsis* genetics, we currently know that *Arabidopsis* contains at least 3 major photoreceptor classes, comprising about 10 photoreceptors: the red/far-red absorbing phytochromes, and the blue-UV-A-absorbing cryptochromes and phototropins. Together these photoreceptors regulate all the major developmental transitions of plants, from germination to flowering to senescence. They are also the interface of plants with their light environment, from which plants obtain such information as the time of day, the time of year, their geographic location, and whether or not they are being shaded by other plants. Likewise, multiple new plant hormones have been discovered, including the brassinosteroids, jasmonic acid, and strigolactones, and the receptors for most of these small molecule plant hormones are known. Today, we want to know how the action of multiple plant hormones is integrated to give a growth response, and how this growth response is modulated by the action of many photoreceptors.

Studies of photoreceptor signaling and plant hormones have had a major impact on our understanding of the most basic mechanisms of how plants decide whether to grow or not to grow. I am confident that the next 25 years will bring the translation of this knowledge to the design of new crop varieties and cleaner, more environmental-friendly biofuels.