cade regulating the expression of antimicrobial peptide genes in exposed tissues such as the trachea and the gut (*4, 5*). Second, it has been established that the Toll and Imd pathways are differentially activated by different microbes. Therefore, the presence of recognition proteins with PGRP domains in both pathways suggests that the PGRP domain may exhibit multiple binding specificities (like the extracellular leucine-rich repeat domain found in all TLRs). The existence of distinct recognition properties could explain the large number of *PGRP* genes in the fly genome, although it is probable that some of them control other immune reactions like the prophenoloxidase cascade, which has been described in *Bombyx* (*7*).

That PGRPs work in both the Toll and Imd pathways also highlights several aspects of insect immunity that are not understood. Foremost is the nature of the microbial compounds that are recognized by the insect immune system. Direct injection of LPS into flies does not induce a strong immune response or any toxic shock–like reaction, which suggests that the fly immune system is less sensitive to LPS than is the mammalian innate immune system. The ability of PGRP-LC to recognize Gram-negative bacteria also suggests that Gram-negative bacteria are not recognized because of their LPS but perhaps through another molecular pattern such as a specific form of peptidoglycan. Alternatively, as suggested by Choe *et al.*, PGRP-LC might bind to both peptidoglycan and LPS, or cooperate with other proteins as part of a recognition complex. Further studies will have to reconcile these apparent contradictions and identify the precise microbial compounds recognized by these pattern recognition receptors.

The growing appreciation of the conservation of some immune responses in insects and mammals has produced an exchange of ideas and results that has invigorated the field of innate immunity. The discovery of the involvement of NF-κB in *Drosophila* antimicrobial gene expression was stimulated by the recognized importance of NF-κB in mammalian immunity. The identification of the Toll receptor as a mediator of insect immunity directed attention to the mammalian TLR proteins. Now, the identification of PGRPs as pattern recognition receptors in insects points to the importance of these proteins in mammalian immunity (*12*). Mechanisms of host defense shared by insects and mammals highlight the value of genetics to the study of immunity. Several years ago, it was generally felt that, in contrast to developmental processes that are tightly regulated, genetic analyses of immune systems would be hampered by functional redundancies among protein components of immune pathways. Mutations in *Drosophila* and mouse proteins, however, reveal that disrupting genes that belong to large families, such as those encoding TLRs and PGRPs, can generate specific immune defects. Such results validate this approach in the ongoing dissection of the battle between pathogens and their hosts.

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PERSPECTIVES: PLANT BIOLOGY

MADS-Box Genes Reach Maturity

Barry Causier, Martin Kieffer, Brendan Davies

Since Adam's first visit to the fruiteress in the Garden of Eden, humankind has been totally dependent upon the angiosperm flower and the fruit it bears. Much of our food and clothing is derived from flowers and their fruits. Unraveling the pathways that regulate how flowers, fruits, and seeds develop has significant implications for agriculture. Ripening is a vital aspect of fruit production. For many fruits to be palatable they must be fully ripe, and ripening is essential for propagation of the species. In terms of shipping, storage, and shelf life, we need to know how to control the ripening of edible fruits. On page 343 of this issue, Vrebalov *et al.* (*1*) reveal that a tomato plant whose fruit cannot ripen, called *ripening-inhibitor* (*rin*), carries a mutation in a gene encoding a MADS-box transcription factor. This work not only establishes the involvement of MADS-box factors in fruit ripening, but also has important agricultural implications.

In today's world of global distribution, the control of fruit ripening is of strategic importance. Unfortunately, our understanding of the genetic regulation of ripening is limited, reducing our ability to manipulate this process. In the tomato and many other fruits, early ripening events involve an increase in biosynthesis of the plant hormone ethylene accompanied by a burst of respiration. The fruit then undergoes a complex and coordinated transformation (*2*). Cell wall structure is modified, improving texture and inducing softening (see the figure). The production of compounds conferring flavor and aroma increases. Starch is converted into sugars, adding sweetness, and red pigments (such as carotene and lycopene) begin to replace the green chlorophyll. Ethylene signaling is one of the best known plant hormone regulatory pathways (*3*) and is a key factor in the control of ripening. However, developmental pathways also influence ripening, and many types of fruit do not require increased ethylene biosynthesis to ripen. So far, an overall developmental regulatory pathway, common to all fruit, has remained elusive.

Successful attempts to manipulate ripening have centered on either reducing ethylene production to slow down the process, or decreasing the rate of fruit softening (*4*). Fruit with reduced ethylene production can be ripened by artificial exposure to ethylene. Unfortunately, fruits that do not depend on increased ethylene production for ripening are not amenable to this approach. Reduced softening has been achieved by altering the expression of genes involved in cell wall modification. The best known example is the "Flavr Savr" tomato, in which shelf life was increased by reducing the level of the enzyme polygalacturonase. One limitation of this approach is that different genes will need to be altered to reduce softening in different fruits (*5*). Discovering a presumptive developmental pathway that is conserved between all types of fruits would create new opportunities for controlling fruit ripening.

Characterization of the *rin* mutation by Vrebalov and colleagues (*1*) could mark a turning point. Tomato plants carrying the *rin* mutation are blocked at an early stage in the ripening process, before the respiratory burst, and do not ripen in response to ethylene. The *rin* tomato plant also has enlarged sepals and an altered inflorescence architecture. Vrebalov *et al.* show that the *rin* mutation is caused by a deletion of approximately 3 kilobases of DNA from the

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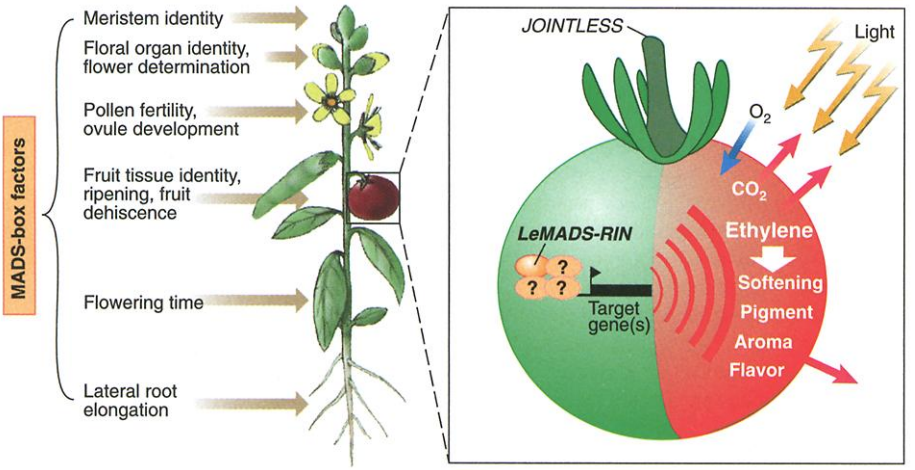

A MAD pathway from root to fruit. (Left) MADS-box transcription factors are involved in numerous steps in plant development (*6*). **(Right)** The LeMADS-RIN transcription factor directs ripening of the tomato fruit. LeMADS-RIN is depicted acting together with other unknown MADS-box factors. Members of the MADS-box family bind to DNA as dimers, heterodimers, or heteromultimers (*7*) to regulate the expression of target genes.

tomato genome, resulting in the fusion and inactivation of two adjacent genes. Remarkably, both genes belong to the MADS-box family of transcription factors. Loss of one of these transcription factors, *LeMADS-MC*, results in altered sepals and inflorescence, whereas loss of the other, *LeMADS-RIN*, results in a failure to produce ripe fruit. *LeMADS-RIN* is particularly interesting because it appears to act upstream of the earliest known steps in fruit ripening. This raises the possibility that a related gene might also regulate ripening in fruits such as the strawberry, which do not require the ethylene pathway to ripen. Indeed, these authors demonstrate the existence of such a gene in the strawberry. The possibility that these genes act as global regulators of fruit development can now be tested.

MADS-box factors are involved in many other aspects of plant development including the regulation of flowering time, fertility, organ and meristem identity, and even root architecture (see the figure), providing further opportunities for crop improvement. However, we still do not know what many MADS-box factors do. Functional analysis of this gene family will undoubtedly reveal additional targets for crop improvement and further insights into the control of plant development. Although the control of many developmental steps has been assigned to plant MADS-box factors, very little is known about the genes that are targeted by these transcriptional regulators. The way that MADS-box factors work to regulate plant development is still a mystery. In the case of *LeMADS-RIN* we have the first example of a MADS-box factor whose extensive biochemical and physiological downstream effects on ripening are already well documented (see the figure). Perhaps fruit ripening will provide an opportunity to forge the elusive connections between the regulator and the regulated.

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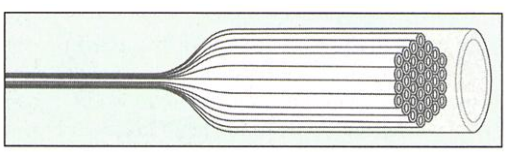
PERSPECTIVES: APPLIED OPTICS

New Ways to Guide Light

J. C. Knight and P. St. J. Russell

Silica-based optical fibers have been one of the engineering triumphs of the last few decades. Yet after an initial period of intense development that revolutionized telecommunications by massively increasing the information-carrying capability of cables, the rate of innovation in fiber design slowed to a crawl in the early 1980s as performance approached the fundamental limitations of the technology. Then, in the early 1990s, a new idea was formulated: Could an optical fiber be created that would guide light through a two-dimensional microstructure running along its length? Such a design would greatly extend the boundaries of fiber optics.

We now know that the answer is indeed yes. Around the world, the result has been a renaissance of fundamental research and development on optical fibers. The new fibers—variously called photonic crystal fibers or "holey" or microstructured fibers—have been used to demonstrate several useful effects and are approaching the performance levels required to be commercially viable.



How to draw a photonoic fiber.

Historically, optical fibers have been made from two materials with different refractive indices. The higher index material forms the fiber core, which "carries" the light. It is surrounded by a lower index cladding, which confines the light to the core by total internal reflection. Despite their remarkable transparency and low losses, such fibers are limited by the small refractive index contrasts attainable between the core and cladding materials (which need to be thermally compatible). Furthermore, the nonlinear optical response of the solid silica core limits the amount of light that the fiber can carry.

A conventional optical fiber is drawn from a macroscopic glass rod with the same transverse profile as the final, hair-thin fiber. Photonic crystal fibers are made in a similar way, but with one important difference: the preform contains a close-packed stack of silica capillaries (see the first figure) (*1*). A two-dimensional "crystal" of tiny air holes runs down the entire length of the fiber, reproducing the arrangement of the capillaries in the stack. By leaving out some capillaries or replacing them with solid canes, one can form a core that is embedded within the photonic crystal material. Light can be trapped in this core and guided along the fiber, producing unusual optical properties.

Because of their micrometer-scale regularity, the fibers can be modeled as "photonic crystals": composite materials that have a regular structure with a length scale of the order of optical wavelengths. Work on photonic crystal fibers was stimulated in part by the interest in photonic crystal ma-

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