

EVOLUTION

The Plant-Fungal Marketplace

Plant-fungal symbiosis is stabilized by the extent of reciprocal nutrient supply.

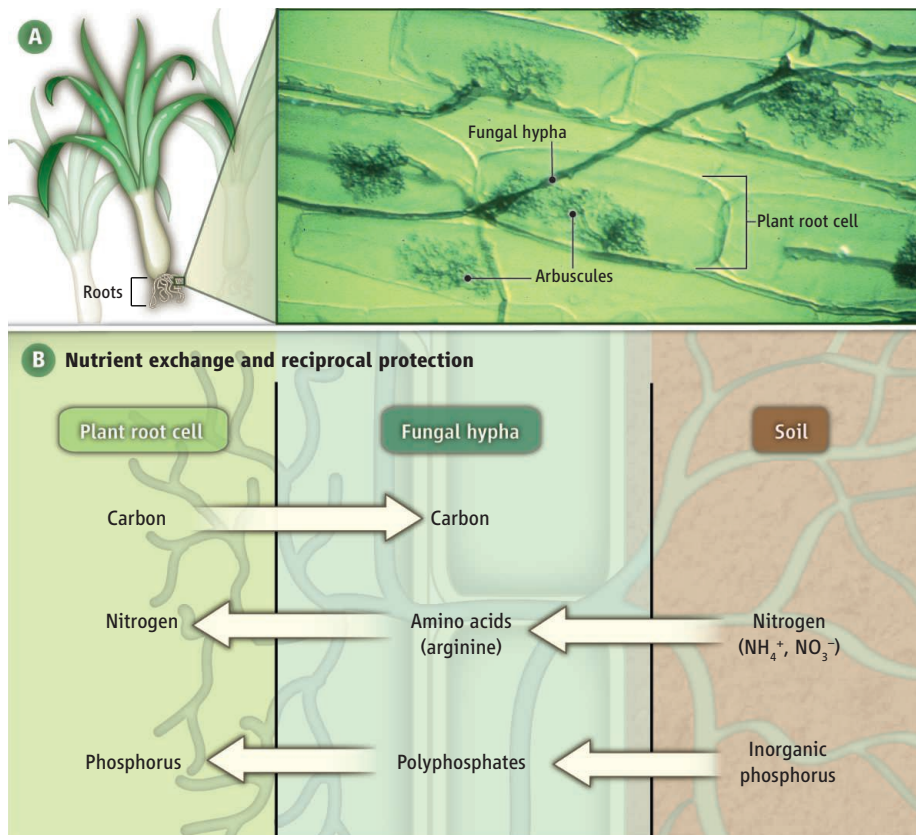
Marc-André Selosse¹ and François Rousset²

The transition of plants to land, 470 million years ago, relied on the emergence of cooperation between plants and soil microbes (1). Both fossil records and the conserved mechanism for fungal recognition among plants (2) support the ancestral nature of this relationship. Today, in over 80% of land plants, roots associate with the soil fungi Glomeromycetes, forming chimeric organs called mycorrhizae (3). Plants depend on Glomeromycetes for mineral resources, especially phosphorus, which is limiting in many soils. Reciprocally, Glomeromycetes depend on nutrients produced by plants during photosynthesis (see the figure). On page 880 of this issue, Kiers *et al.* (4) unravel mechanisms that stabilize this ancient symbiotic relationship.

Cooperation between different species is intrinsically unstable. As Darwin stated in *The Origin of Species*, “natural selection cannot possibly produce any modification in any one species exclusively for the good of another species.” Because cooperation entails costs, any mutant that enhances its fitness (i.e., the ability to produce more offspring) by defecting from cooperation will be favored, even if this destabilizes the relationship. However, various stabilizing mechanisms exist (5). If the reward has no cost for one partner, then there is no benefit to defecting; or if both partners reproduce together in a common structure (vertical transmission, in zygotes or asexual propagules), harm to one partner also harms the other. For mycorrhizal partners, nutrient exchange is costly (vertical transmission never evolved, as mycorrhizal fungi cannot colonize seeds). Moreover, each fungus interacts with several plants, and vice versa (3). When plants are offered different fungal partners, the outcomes for the plant range from beneficial to deleterious (6). Here, another mechanism might act: restricting cooperation to partners that reciprocate.

Kiers *et al.* investigated plants colonized by up to three Glomeromycete species. By tracking the incorporation of carbon from plants into fungal RNAs, the authors show that the most cooperative fungi receive more carbon than the other species. That plants

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Perfect partners. (A) Glomeromycete fungi produce structures called arbuscules within root cells to exchange nutrients. Inset photo shows roots of *Allium porrum* colonized by *Glomus mosseae* [reproduced from (15) with permission from NRC Research Press]. (B) The symbiotic benefits include reciprocal nutrient exchange and protection against abiotic and biotic stress in the soil environment.

sanction noncooperative root microbial symbionts is already reported (7, 8), but Kiers *et al.* now show that plants discriminate fungi at fine scale, even when multiple fungi colonize a root. They inoculated a single root with two different fungi, which were allowed to simultaneously grow into separate environmental compartments. Then, they enforced each fungus to be cooperative (or not) by adding some (or no) phosphorus to its own compartment. The more cooperative fungus received more carbon from root cells. Likewise, Kiers *et al.* manipulated plant cooperation by exposing roots to variable amounts of sucrose as a carbon source (which Glomeromycetes only use after plants hydrolyze it to glucose). The fungi made more phosphorus available to the roots that offered more carbon. Thus, both partners choose more rewarding symbionts, and control cooperation based on bidirectional exchange of nutrients.

The study by Kiers *et al.* should direct more empirical and theoretical attention to “biological markets.” The market metaphor describes iterated interactions wherein an individual can change a partner on the basis of the services supplied by the other partner, comparable to an ideal human market economy. The ability to switch partners is a simple mechanism that favors cooperation both within and between species (4, 9). Beyond classic examples of biological markets [e.g., fish cleaning parasites off fish of another species (9)], market processes have not always received sufficient attention. In particular, much research on reciprocal cooperation has assumed that an individual has the opportunity to terminate cooperation with a partner that has defected, but not to seek another partner. The outcome of interactions without partner choice is highly sensitive to the strategies available to each partner, raising doubts

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about explanations that do not allow partner choice (10). Another investigated process is the interaction between relatives of the same species, which is relevant in interactions between members of different species insofar as relatives of one partner (e.g., a bacterial clone) receive the benefits of the reciprocating host, but partner choice may still be required for the stability of cooperation. Biological markets are often markedly asymmetric in that one partner has more control than the other (11). For example, nitrogen-fixing rhizobia associated with legumes have no opportunity to change partners once entering a host plant's roots (7). By contrast, Kiers *et al.* show that both plants and their fungal symbionts can switch partners, allowing cooperation enforcement on both sides.

Many plant lineages, including Ericaceae, orchids, and temperate forest trees, among others, abandoned Glomeromycetes and shifted to mycorrhizal interaction with different fungal lineages (1, 3). These convergent evolutions offer opportunities to examine bidirectional control in phylogenetically

independent replicates of the mycorrhizal interaction. And indeed, nutrient flux from temperate tree roots to mycorrhizal fungi depends on nutrient delivery in the opposite direction (12). Moreover, mycorrhizal interactions involve diverse rewards such as other nutrients [e.g., water or nitrogen for plants, perhaps vitamins for fungi (3)] and protection against abiotic and biotic stress. Protection may be the main benefit for plants in some ecosystems (13). Future investigations may test whether these other rewards are also used for controlling cooperation.

The story may be even more complex. In several plant families, some nonphotosynthetic plants receive both mineral nutrients and carbon from mycorrhizal Glomeromycetes (3, 14). Fungi associated with such heterotrophic plants do not control for the exchange of phosphorus against carbon. What drives this apparent lack of reciprocity? Do these heterotrophic plants confer other benefits, or do they manipulate the partner's ability to discriminate, and thus successfully parasitize the mycorrhizal symbiosis? On the fun-

gal side, less-cooperative species successfully persist, as shown by Kiers *et al.* Thus, bidirectional control may not alone explain the persistence of the mycorrhizal symbiosis over 470 million years.

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DEVELOPMENT

Determining Sexual Identity

Mark Van Doren

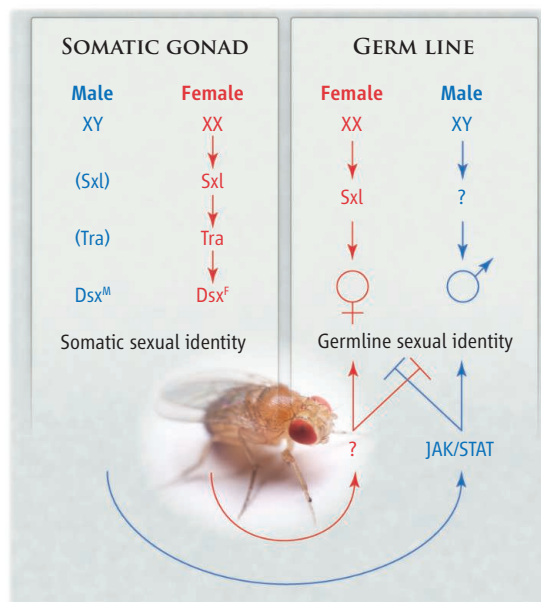
Back when we were embryos, a genetic “switch” was thrown, providing us with a male or female identity that had profound influence on the development of our bodies and our minds. The effects of sex determination are particularly important in the germ cells, which must form either the sperm or eggs necessary for sexual reproduction. The mechanism that determines sex in the germ line can be very different from the mechanism that determines sex for the rest of the body, the soma. On page 885 of this issue, Hashiyama *et al.* describe a critical aspect of how germline sex determination is regulated in fruit flies (1), bringing us a step closer to understanding how sexual identity is regulated in humans and other animals.

Germ cells usually develop in close contact with specialized somatic cells in the gonads. These somatic cells are essential to regulate germ cell development, germline stem cell function, and gametogenesis (formation of sperm or egg). The somatic gonad also plays an important role in influencing

germline sex determination. In some species, the sex of the soma is sufficient to determine the sex of the germ cells, and the germ line will follow along with whatever sex the soma happens to be—even switching from making

In *Drosophila*, expression of the *Sex lethal* gene feminizes male germ cells.

sperm to making eggs, or vice versa, in those animals that can naturally change their sex. However, in other species such as fruit flies, mice, and humans, the sex chromosome constitution of the germ cells is also important



Determining sexual identity. In the *Drosophila* gonad (left), the presence of two X chromosomes activates an RNA binding protein (Sxl) and gene expression via alternative splicing (involving Tra and Tra-2) (14) to produce the female form of a transcription factor (Doublesex, Dsx) that initiates female identity. In males (blue), the absence of Sxl leads to the male form of Dsx by default. Sexual identity of the somatic gonad regulates sex-specific signaling to the germ line (lower right) via the Janus kinase/signal transducer and activator of transcription (JAK/STAT) pathway (blue arrows) in males (15), and an unknown pathway (red arrows) in females. In the germ line (right), the presence of two X chromosomes also leads to Sxl expression, but its activation process and downstream targets are different than in the soma.