8. Wardill, T.J., Knowles, K., Barlow, L., Tapia, G., Nordström, K., Olberg, R.M., and Gonzalez-Bellido, P.T. (2015). The killer fly hunger games: target size and speed predict decision to pursuit. Brain. Behav. Evol. *86*, 28–37.

9. Reichardt, W., and Wenking, H. (1969). Optical detection and fixation of objects by fixed flying flies. Naturwissenschaften *56*, 424.

10. Heisenberg, M., and Wolf, R. (1979). On the fine structure of yaw torque in visual flight orientation of *Drosophila melanogaster*. J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol. *130*, 113–130.

11. Maimon, G., Straw, A.D., and Dickinson, M.H. (2008). A simple vision-based algorithm for decision making in flying *Drosophila*. Curr. Biol. *18*, 464–470.

12. Keesey, I.W., Grabe, V., Gruber, L., Koerte, S., Obiero, G.F., Bolton, G., Khallaf, M.A., Kunert, G., Lavista-Llanos, S., Valenzano, D.R., *et al*. (2019). Inverse resource allocation between vision and olfaction across the genus *Drosophila*. Nat. Commun. *10*, 1162.

13. Park, E.J., and Wasserman, S.M. (2018). Diversity of visuomotor reflexes in two *Drosophila* species. Curr. Biol. *28*, R865–R866.

14. Date, P., Crowley-Gall, A., Diefendorf, A.F., and Rollmann, S.M. (2017). Population differences in host plant preference and the importance of yeast and plant substrate to volatile composition. Ecol. Evol. *7*, 3815–3825.

15. van Breugel, F., Riffell, J., Fairhall, A., and Dickinson, M.H. (2015). Mosquitoes use vision to associate odor plumes with thermal targets. Curr. Biol. *25*, 2123–2129.

16. van Breugel, F., Huda, A., and Dickinson, M.H. (2018). Distinct activity-gated pathways mediate attraction and aversion to CO_2 in *Drosophila*. Nature *564*, 420.

17. Semmelhack, J.L., and Wang, J.W. (2009). Select *Drosophila* glomeruli mediate innate olfactory attraction and aversion. Nature *459*, 218–223.

18. Haberkern, H., and Jayaraman, V. (2016). Studying small brains to understand the building blocks of cognition. Curr. Opin. Neurobiol. *37*, 59–65.

19. Srinivasan, M.V. (2011). Honeybees as a model for the study of visually guided flight, navigation, and biologically inspired robotics. Physiol. Rev. *91*, 413–460.

Symbiosis: Fungi as Shrewd Trade Negotiators

John P. McCutcheon[1] and Ylva Lekberg[2,3]
[1]Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA
[2]MPG Ranch, Missoula, MT 59833, USA
[3]Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA
Correspondence: john.mccutcheon@mso.umt.edu (J.P.M.), ylekberg@mpgranch.com (Y.L.)
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Symbiotic fungi associated with plant roots can shuttle a key nutrient through their hyphal network in response to resource inequality. This need-based transport optimizes trade conditions for carbon with plants.

Microorganisms have cornered the market on metabolic diversity, innovation, and flexibility. Macroorganisms, though sometimes nice to look at, are comparatively dull from a metabolic point of view. But macroorganisms can be clever in their own ways. For example, many plants and animals have developed symbioses with microbes that exploit their vast metabolic potentials. The microbes in these associations can transform recalcitrant sources of energy into host-usable forms, concentrate limiting nutrients that hosts cannot access, produce protective compounds for their hosts, or even synthesize essential nutrients that macroorganisms are unable to make on their own [1]. One archetypal and ecologically vital symbiosis is the relationship formed between arbuscular mycorrhizal (AM) fungi and the roots of more than 70% of all vascular plants [2] (Figure 1). This symbiosis is often described as a mutualism, one in which plants deliver carbon to the fungi in exchange for nutrients — in particular phosphorus — and other services, including pathogen protection and drought tolerance [3]. In reality, however, the AM symbiosis seems to function along a continuum from parasitism to mutualism [4], and when interactions have been carefully examined they tend to resemble ruthless free markets more than groovy hippie hangouts. In this issue of *Current Biology*, Whiteside and colleagues [5] describe a clever, fluorescent-phosphorus labeling technique that allowed them to visualize phosphorus delivery from AM fungi to plants on microscopic scales. Using this technique, they discovered a novel fungal strategy that appears to increase resource delivery to plants while optimizing trade conditions for the fungal partner.

Unlike some endosymbioses, where symbionts can be carefully managed by restriction inside of host cells and faithful vertical transmission, symbiont specificity is low in the AM association. A single plant can host many AM fungal species, and a single continuous fungal mycelium can colonize multiple plants. Low host specificity, spatially separated carbon and phosphorus exchange sites, and many co-occurring AM fungal species within root segments could favor cheating — that is, selection at the symbiont level for AM fungi that would take host carbon but give less phosphorus — especially if being a better nutrient provider incurs additional cost to the symbiont [6]. Indeed, it has been elegantly demonstrated that carbon–phosphorus exchange rates can differ tremendously among fungal species [7].

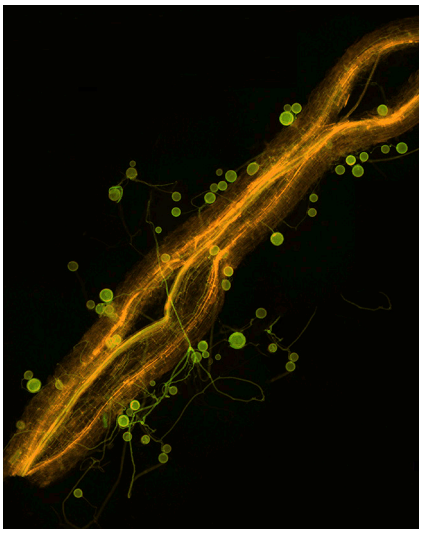

Figure 1. An underground nutrient-exchange network comes to light.
Autofluorescence micrograph of arbuscular mycorrhizal fungi (green) colonizing roots of its host plant (orange), *Medicago truncatula*. Plant and fungal partners form complex underground networks, trading nutrients in a market-like economy. Photo credit: Jan Jansa.

Given this complexity, researchers have spent decades trying to understand how the players in the AM symbiosis have remained stably associated for more than 400 million years. A biological 'market theory' has been proposed as a way around this conundrum, based on the hypothesis that both plants and fungi can detect and specifically reward better partners ([8], but see [9]). There is experimental evidence supporting this market-based strategy: plants tend to allocate more carbon to AM fungi that deliver more phosphorus, and more phosphorus is delivered to host plants that deliver more carbon [8,10,11]. Also, AM fungi seem to become better at providing phosphorus when they co-occur with fungi that are better phosphorus provisioners [12], perhaps as a way to avoid being sanctioned by the host plant. Although it is tempting to think that AM fungi, having lost the ability to gain carbon through environmental absorption, should just be grateful for whatever carbon they can manage to get from their host plant(s), they still manage to drive a tough bargain by delivering less phosphorus to hosts (that is, by hoarding phosphorus) when hosts deliver less carbon [13]. Whiteside *et al.* [5] show us that AM fungi have yet another bargaining strategy in their arsenal.

In contrast to aquatic systems, where nutrients can be relatively well mixed due to diffusion, environmental heterogeneity in terrestrial systems can be high, even at very short distances. Given that host plants reward fungi that provide more phosphorus with more carbon, Whiteside *et al.* were interested in how AM fungi would deal with extreme phosphorus inequality over the length of their hyphal networks [5]. By labeling two resource patches with phosphorus-coated nanoparticles that fluoresced at different wavelengths, they could trace which patch the phosphorus came from. They showed that when phosphorus inequality between the two patches became greater, AM fungi redistributed phosphorus from areas of excess to areas of scarcity, resulting in more phosphorus than expected being delivered to the host plant from the fungal tissue in the low-quality phosphorus-patch. It is still unclear whether this phosphorus redistribution results in a better phosphorus–carbon exchange rate or simply allows the low-phosphorus regions of fungus to continue to be paid in host carbon. Excitingly, this nanoparticle approach provides a possible way to address this question in the future. Carbon-tagged nanoparticles could also be used to determine whether carbon is delivered to the fungus via the arbuscule, the site at which the fungus delivers phosphorus to the plant, and if so, how much can be transferred via this route. The potential for this was recently shown using genetics [14,15] and a direct carbon–phosphorus exchange might offer another mechanism by which cheaters could be sanctioned. Regardless of phosphorus and carbon exchange rates, the findings by Whiteside *et al.* [5] highlight another strategy that AM fungi have to obtain as much carbon from their hosts for as long as possible — an arrangement that also, incidentally, results in a less nutritionally heterogeneous environment for the plant.

The presence of AM fungi has been shown to promote plant diversity and productivity under controlled conditions [16]. However, we still know very little about its actual function in natural and managed ecosystems [17]. One main obstacle has been a lack of suitable methods. Previously, tracking phosphorus movement required radioactive isotopes, which are often restricted in field conditions. The quantum-dot technology developed by Whiteside *et al.* offers a great opportunity to trace phosphorus in complex real-world systems, especially if the phosphorus uptake and translocation pathways are similar (or similar enough) between quantum dot-bound phosphorus and phosphate. If it is, these fluorescent nanoparticles offer a great new tool to answer many questions, some of which are as basic as knowing whether the most abundant AM fungus in a community is the best mutualist or the best competitor. The future for mycorrhizal research might be even 'brighter' than we previously thought.

REFERENCES

1. McFall-Ngai, M., Hadfield, M.G., Bosch, T.C., Carey, H.V., Domazet-Lošo, T., Douglas, A.E., Dubilier, N., Eberl, G., Fukami, T., Gilbert, S.F., *et al*. (2013). Animals in a bacterial world, a new imperative for the life sciences. Proc. Natl. Acad. Sci. USA *110*, 3229–3236.

2. Brundrett, M.C., and Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. *220*, 1108–1115.

3. Delavaux, C.S., Smith-Ramesh, L.M., and Keubbing, S.K. (2017). Beyond nutrients: a meta-analysis of the diverse effects of arbuscular mycorrhizal fungi on plants and soils. Ecology *98*, 2111–2119.

4. Johnson, N.C., Graham, J.H., and Smith, F.A. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. New Phytol. *135*, 575–585.

5. Whiteside, M.D., Werner, G.D.A., Caldas, V.E.A., van 't Padje, A., Dupin, S.E., Elbers, B., Bakker, M., Wyatt, G.A.K., Klein, M., Hink, M.A., *et al*. (2019). Mycorrhizal fungi respond to resource inequality by moving phosphorus from rich to poor patches across networks. Curr. Biol. *29*, 2043–2050.

6. Bever, J.D., Richardson, S.C., Lawrence, B.M., Holmes, J., and Watson, M. (2009). Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol. Lett. *12*, 13–21.

7. Pearson, J.N., and Jakobsen, I. (1993). Symbiotic exchange of carbon and phosphorus between cucumber and three arbuscular mycorrhizal fungi. New Phytol. *124*, 481–488.

8. Kiers, E.T., Duhamel, M., Beesetty, Y., Mensah, J.A., Franken, O., Verbruggen, E., Fellbaum, C.R., Kowalchuk, G.A., Hart, M.M., Bago, A., *et al*. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science *333*, 880–882.

9. Walder, F., and van der Heijden, G.A. (2015). Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. Nat. Plants *1*, 15159.

10. Bücking, H., and Hill, Y.S. (2005). Phosphate uptake, transport and transfer by the arbuscular mycorrhizal fungus *Glomus intraradices* is stimulated by increased carbohydrate availability. New Phytol. *165*, 899–912.

11. Lekberg, Y., Hammer, E.C., and Olsson, P.A. (2010). Plants as resource islands and storage units – adopting the mycocentric view of arbuscular mycorrhizal networks. FEMS Microbiol. Ecol. *74*, 336–345.

12. Argüello, A., O'Brien, M.J., van der Heijden, M.G., Wiemken, A., Schmid, B., and Niklaus, P.A. (2016). Options of partners improve carbon for phosphorus trade in the arbuscular mycorrhizal mutualism. Ecol. Lett. *19*, 648–656.

13. Hammer, E., Pallon, J., Wallander, H., and Olsson, P.A. (2011). Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability. FEMS Microbiol. Ecol. *76*, 236–244.

14. Keymer, A., Pimprikar, P., Wewer, V., Huber, C., Brands, M., Bucerius, S.L., Delaux, P.M., Klingl, V., Röpenack-Lahaye, E.V., Wang, T.L., *et al*. (2017). Lipid transfer from plants to arbuscular mycorrhiza fungi. Elife *6*, e29107.

15. Luginbuehl, L.H., Menard, G.N., Kurup, S., Van Erp, H., Radhakrishnan, G.V., Breakspear, A., Oldroyd, G.E., and Eastmond, P.J. (2017). Fatty acids in arbuscular mycorrhizal fungi are synthesized by the host plant. Science *356*, 1175–1178.

16. van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., and Sanders, I.R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature *396*, 69–72.

17. Lekberg, Y., and Helgason, T. (2018). *In situ* mycorrhizal function – knowledge gaps and future directions. New Phytol. *220*, 957–962.

Bodily Awareness: How Flies Learn Their Own Body Size

Hiromu Tanimoto
Graduate School of Life Sciences, Tohoku University, Katahira 2-1-1, 980-8577 Sendai, Japan
Correspondence: hiromut@m.tohoku.ac.jp
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Animals need to perceive their own body size to apprehend their relationship to the environment. A new study shows that the fruit fly *Drosophila* acquires the requisite information on its body size from visual feedback during walking, and has further identified a subset of neurons responsible for maintenance of body-size memory.

Accurate estimation of one's own bodily properties is important for the successful execution of many motor programs, such as those used in sports like rock climbing, and even for avoiding body collision in a narrow corridor. Animals in their natural environments use the knowledge of their own body size in a variety of different contexts, for example when deciding if they should fight a competitor or not [1]. An individual's body size depends on many genetic and environmental factors, and so its perception of its body size needs to be flexible enough to take these changes into account [2]. Despite all the evidence for its behavioral importance, the neuronal underpinnings of self-body-size awareness are poorly understood. As they reported in a recent issue of *Current Biology*, Krause *et al*. [3] have now discovered that knowledge of its own body size is crucial for the fruit fly *Drosophila melanogaster* to avoid futile trials in crossing an insurmountable gap. They further showed that flies acquire body size memory through visual experience of stripes during walking — that is, by parallax motion vision — and, using the techniques of *Drosophila* genetics, they have identified part of the underlying neural circuit [3].

When a walking *Drosophila* is challenged by a cleft in its path, the fly has to make a prediction on whether the gap is manageable to cross or not [4]. Integration of awareness of their own body reach and the actual gap width is thus critical for the decision of the gap-crossing behavior (Figure 1). When facing a gap wider than their step size, flies have several behavioral options: they may try climbing down or turning around, but more motivated flies on the edge typically flail their forelegs, or more specifically make overhead leg swings (Figure 1). The percentage of flies showing these foreleg flails is a reliable measure of an attempt at gap crossing. Flies avoid making futile attempts when facing a gap that seems impossible for them to cross [4,5]: in other words, they make an effort to cross a gap only if it looks manageable.

The Krause *et al.* [3] paper starts with an interesting observation: the gap distances where a fly will initiate a crossing attempt vary with its body size. When confronted with a wide gap that a larger fly would usually attempt to cross, a smaller fly is more likely to give up and switch to other behavioral options. The implication is that a fly has some previously acquired knowledge about its body size and reach.

How might a fly know its own body size? Given the varying gap-size threshold which correlates with a fly's own body length, it is unlikely that the body size information is genetically programmed. Rather, Krause *et al.* [3] hypothesized that each individual fly acquires information on its own body size through visual experience. Indeed, flies reared in total darkness made more