



Figure 2. Lignification in *Brachypodium distachyon* and *Arabidopsis thaliana* stems. (A) A 30- μ m cross-section of *Brachypodium distachyon* internode, with lignins stained red with phloroglucinol-HCl. Inset: enlargement of boxed area corresponding to developing sclerenchyma fiber cells. Black arrows point out the middle lamella overstained in red. White arrows show cell corners, were nucleation points for lignification are localized. (B) Cross-section of *Arabidopsis thaliana* inflorescence stem stained with Maüle staining. Red color corresponds to S units in secondary cell walls. The middle lamella (black arrows) is not stained.

How is ferulic acid transported into the Golgi apparatus? Lignin polymerization is also influenced by the cell wall polysaccharide composition — for instance, in grasses, arabinose residues on arabinoxylans can be enzymatically feruloylated in the Golgi apparatus before deposition in

the cell wall [17]. These ferulic acid residues are thought to initiate lignin polymerization. It is not known how ferulic acid crosses the Golgi membrane, and it will be interesting to see whether or not Golgi-associated ABC transporters are involved in this process.

In conclusion, this work not only opens up new research avenues in the cell wall field, but also creates novel opportunities for the manipulation of lignin in crop plants.

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Institute Jean-Pierre Bourgin, UMR1318 INRA/AgroParisTech, Saclay Plant Science, INRA Centre de Versailles-Grignon, Route de St-Cyr (RD10), 78026, Versailles, Cedex, France.
*E-mail: herman.hofte@versailles.inra.fr

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Seed Dispersal: The Blind Bomb Maker

A recent study shows that a desert shrub uses a ‘mustard oil bomb’ to regulate the behaviour of seed-predating rodents — transforming these predators into mutualistic seed dispersers.

K.C. Burns

Seed dispersal sets the stage for everything that happens to a plant during its lifetime — after germination,

plants will never again be able to travel across the landscape. Seeds can’t move very far on their own, though, so they rely on wind, water or animals to get the job done. For example,

coconuts float on water to reach their destination. Maple seeds fly through the air using auto-rotating wings that operate similarly to helicopter blades. Dandelion seeds use feathery plumes that function like parachutes. Another common mechanism of seed dispersal is to enlist the help of animals. Many plants surround their seeds with fleshy pulp to strike up mutualistic partnerships with fruit-consuming animals, who swallow seeds whole and defecate them intact in new locations. Animal-assisted

seed dispersal can be a highly effective means of seed transportation, but it is often fraught with difficulty. In a new study in this issue of *Current Biology*, Samuni-Blank *et al.* [1] demonstrate that a desert plant has taken an ingenious step towards solving the problems associated with animal-mediated seed dispersal.

In addition to attracting mutualistic seed dispersers, brightly coloured, fleshy fruits can also attract seed predators, who destroy seeds for the energy they contain, rather than dispersing them intact. Seeds contained in fleshy fruits are freely available to all, generating an evolutionary conundrum for plants, which would benefit from attracting seed dispersers, while repelling seed predators.

On the surface of things, there doesn't appear to be much a plant can do to deter seed predators and to attract mutualistic seed dispersers simultaneously. However, pioneering work conducted a decade ago in South-western Arizona revealed that a desert shrub had solved this problem using a widely known chemical, capsaicin [2].

Wild chilli peppers (*Capsicum annuum*) produce capsaicin in their fruit pulp, affecting consumers in a distinctive way — capsaicin triggers receptors located in mammalian mouths that have been designed by evolution to respond to excessive heat. Many people enjoy the sensation caused by capsaicin, so domesticated chilli peppers have found their way into the diets of people living in nearly every corner of the world. Others, however, avoid eating chillies, due to the fiery sensation caused by capsaicin.

Seed-predating rodents have to chew through the fruit pulp to get to the seeds, so they leave chilli peppers off their menu. On the other hand, seed-dispersing birds, who swallow fruits whole and disperse seeds intact, never taste the pepper's simulated 'fire'. Therefore, the production of capsaicin by wild chilli peppers is a directed deterrent — it wards off seed-predating rodents, but has little or no effect on mutualistic, seed-dispersing birds.

In the new study by Samuni-Blank *et al.* [1], the authors demonstrate that a different desert plant has taken an additional step towards solving this

problem. *Ochradenus baccatus*, a common shrub in the deserts of the Middle East, produces fleshy fruits that superficially appear to be rather ordinary. However, within the seeds is a special suite of chemicals, which, when combined with a similarly special but entirely different suite of chemicals in the fruit pulp, produce a toxic 'mustard oil bomb'. Many explosives developed by man are based on the same principle: a chemical reaction that occurs when two reactive chemicals are mixed. In this case, though, rather than exploding, the chemical cocktail contained in the mustard oil bomb produces a behavioural change in its victims — it profoundly influences the actions of desert rodents, converting them from seed predators into mutualistic seed dispersers.

Rather than avoid *O. baccatus* fruits, desert rodents have learned how to 'diffuse' the mustard oil bomb. Rodents collect fruits and bring them to rocky areas before beginning to consume them, because they themselves are less susceptible to being eaten by predators in rocky habitats. Once there, the rodents consume the fruit pulp, and instead of crushing the seeds as they do with most other desert plants, they spit the seeds out whole without damaging them. Voiding the seeds intact ensures that the mustard oil bomb is never detonated, to the net benefit of both the rodents, who harvest the energy contained in the fruit pulp, and of the plant, whose seeds get dispersed without harm. Samuni-Blank *et al.* [1] also suggest that the rodents' preferred places to consume fruits safely (rocky areas) are also the best places in the landscape for young *O. baccatus* plants to germinate, grow and survive.

We can relate to the rodents' plight. Watermelons (*Citrullus lanatus*) are filled with large seeds, and most of us spit them out before swallowing the juicy pulp, largely because the seeds have a sour taste. This sour taste is our bodies' way of telling us that the seeds are defended chemically. By listening to our taste buds and spitting the seeds out, we avoid investing the energy to metabolise these defensive chemicals and avoid any harmful effect they might have after ingestion. However, in the case of *O. baccatus*, it is the combination of

chemicals stored separately in the fruit pulp and in the seeds that creates the chemical deterrent, not just the seeds themselves.

Like chilli peppers, the mustard oil bomb appears to be a directed deterrent, as it affects only would-be seed predators. Because mutualistic seed dispersers only consume the fruit pulp, and do not break open the seeds, the bomb never detonates — the potentially toxic chemicals stay separated and harmless.

Samuni-Blank *et al.*'s [1] study is important for several reasons. First, it is an eloquent example of a unique solution derived by natural selection to cope with a complicated ecological problem. Second, and perhaps more importantly, this study might help to point the way forward for future studies of seed dispersal ecology.

Seed dispersal ecology emerged as a discipline approximately forty years ago, when inaugural work suggested that fruit-consuming animals and fleshy-fruited plants were coevolved tightly [3]. Plants produce fleshy fruits that suit the behaviour of fruit consumers, who in turn deposit seeds in locations preferred by plants. However, three decades of subsequent work have failed to substantiate much evidence for this paradigm [4]. Instead, seed-dispersal mutualisms appeared to be stochastic systems, with many fruit-consuming animal species interacting more or less interchangeably with many fleshy-fruited plant species, few of which were tightly coevolved with one another [5].

In conjunction with earlier work on chilli peppers, Samuni-Blank *et al.*'s [1] pioneering work suggests that we may be looking in the wrong place. Rather than searching for patterns at higher levels of ecological organisation, for example, within networks of interacting plant and animal species, which typify most ecological work on animal seed dispersal, evidence for tighter coupling between fruits and fruit consumers may occur at smaller spatial and temporal scales — inside animal digestive tracts at the molecular level. Future work that continues from where Samuni-Blank *et al.* [1] left off is now needed to ascertain whether blind bomb makers [6] are at work in the chemistry of other fleshy fruits.

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Victoria University of Wellington, Wellington, New Zealand.

E-mail: kevin.burns@vuw.ac.nz

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Axis Formation: Microtubules Push in the Right Direction

Live imaging reveals that the *Drosophila* oocyte nucleus is pushed by growing microtubules to break the radial symmetry of the oocyte and establish dorsoventral polarity.

Siegfried Roth* and Jeremy Lynch

One of the attractions of studying dorsoventral axis formation in *Drosophila melanogaster* is the completeness with which the entire process has been analyzed starting from the first symmetry-breaking event in the ovary, up to the specification of particular cell types within the embryo [1,2]. There are not many cases in developmental biology where such a continuous causal chain can be constructed. In a recent paper, Daniel St. Johnston and colleagues [3] shed new light on the initial step of dorsoventral axis polarisation, the asymmetric positioning of the oocyte nucleus, which defines the dorsal side of the egg chamber and future embryo.

The importance of the oocyte nucleus' asymmetric position for dorsoventral axis formation in *Drosophila* has been recognized for a long time [4]. Even older, however, are similar observations for other insects: in the 1960s, for instance, Netzel [5] observed that oocyte nucleus migration in crickets breaks the rotational symmetry of the egg chamber and defines the plane of bilateral symmetry of the future embryo. Netzel also saw that follicle cells adjacent to the asymmetrically localized oocyte nucleus changed their morphology, and concluded that a signal emanating from the vicinity of the nucleus is received by the overlying follicle cells.

This idea has later been confirmed by studies of EGF signalling in *Drosophila* ovaries [6]. The mRNA of the TGF α -like ligand Gurken is concentrated within *Drosophila* oocytes close to the asymmetrically positioned oocyte nucleus. Gurken protein resulting from locally translated mRNA is secreted and activates the EGF receptor in the overlying follicle cells, thus providing spatial information to the follicle cells in relation to their distance from the oocyte nucleus. This patterning process results in the deposition of asymmetric cues in the eggshell, which is secreted by the follicular epithelium. These cues later orient formation of the dorsoventral axis in the embryo [7]. Recent comparative molecular and functional studies indicate that EGF signalling from the asymmetrically localized oocyte nucleus indeed represents an ancient mode of dorsoventral axis formation in insects [8]. However, the cell-biological mechanisms of asymmetric migration of the oocyte nucleus have, until recently, remained elusive.

In *Drosophila*, the early oocyte nucleus is located in a posterior position that is symmetric with respect to the short axis of the egg chamber (Figure 1). At mid-oogenesis, the nucleus migrates to the anterior, where it occupies an eccentric position along the perimeter of the anterior face of the oocyte, thereby breaking the radial symmetry of the egg chamber [9,10]. There is no indication that the final position of the oocyte nucleus is

predetermined by any pre-existing asymmetry in the ovary, or by any external cues, such as gravity or the dorsoventral axis of the female abdomen. Thus, nuclear migration appears to be a genuine symmetry-breaking event [11].

In the past, two models have been suggested [2] for how the oocyte nucleus migrates. Both models incorporate the fact that the posterior follicle cells send a 'signal back' to the oocyte during mid-oogenesis, which initiates nuclear movement and the repolarisation of the microtubule network along the anterior-posterior axis [9,10]. In the first model, the oocyte nucleus is passive. Upon repolarisation of the network, the nucleus is then pulled to the anterior pole by dynein motors [12–17]. The other model is based on the observation that the nucleus migrates together with centrosomes and that the nucleus-centrosomal complex nucleates microtubules. Upon asymmetric nuclear positioning, the microtubules emanating from the nucleus were suggested to repolarize the microtubule cytoskeleton of the oocyte [18]. While the forces moving the nucleus were not specified in this model, one speculation was that microtubules growing from the nucleus-centrosomal complex could push the nucleus [2].

In the new study by Zhao, St. Johnston and colleagues [3], live imaging of oocyte nucleus migration, together with centrosome and microtubule dynamics, is used to rigorously test, for the first time, the different models of nuclear migration. In particular, the new results suggest that asymmetric nuclear positioning is neither dependent on, nor required for, the anterior-posterior polarisation of the oocyte. The main conclusions are based on the careful observation of the