PERSPECTIVES

How thin films wrinkle. Wrinkle formation of a thin film in response to a uniaxial compressive strain, ε , parallel to the interface. Similar wrinkles form in the experiments of Huang *et al.*, but in their case, wrinkle patterns radiate from the center of the load.

thicker, the number of wrinkles decreased, whereas their length increased. The authors used these results to develop two scaling relationships (one for the length and one for the number of wrinkles), adapting arguments made by Cerda and Mahadevan (6, 7). Combination of these two scaling relationships shows that if the length and number of wrinkles are known from experimental measurement, the elasticity and thickness of the film under study can be determined by a simple calculation.

To validate their method, Huang *et al.* monitored wrinkle formation in polystyrene films that contained different amounts of plasticizer and thus had different elastic properties. Their elasticity data are equivalent to, and



in some cases have higher precision than, previously reported data obtained with sophisticated, time-consuming, and expensive techniques, such as stress-induced buckling and nano-indentation (8). The authors also show that their calculated film thicknesses are comparable with those obtained from their x-ray reflectivity measurements.

Wrinkle formation, therefore, need not always be regarded as a nuisance. Invaluable information concerning the elasticity and thickness of ultrathin films can be determined simply by measuring the number and length of the wrinkles formed in response to a capillary force. The method developed by Huang *et al.* is not only simple; in contrast to existing techniques, it also allows both elasticity and film thickness to be determined in one easy, quick experiment. Moreover, measurements can be made directly at a fluid surface. The latter not only eliminates the introduction of artifacts but

also opens up the possibility of studying dynamical relaxation processes in thin films, a matter of crucial importance for advancing material design and understanding the viscoelastic behavior of numerous biological and soft materials.

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A protein in ovule cells of a flowering plant

recognizes the male pollen tube of the same species, ensuring successful fertilization.

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PLANT SCIENCE

Reproductive Dialog

Sheila McCormick

retilization in higher plants requires intricate signaling between the male and female. The molecular details underlying this communication are of great interest, not only to understand plant reproduction but also to guide efforts in crossing plant species to generate new hybrids. On page 656 of this issue, Escobar-Restrepo et al. (1) show that cells in the female ovule express a protein-a type of receptor that is widely known to mediate cell-cell communicationthat is required for fertilization. The unknown ligand(s) for the receptor may be present on or secreted by the pollen tube. Such a receptorligand interaction could control species-specific reproduction.

In flowering plants, the pollen grain (male gametophyte) contains three cells: a vegetative cell that will form the pollen tube, and two sperm cells. After release from the anther and landing on the stigma, the pollen grain extends a tube through the style, toward the ovule (see the figure). Within each ovule,

Pollen in anther Embryo sac Pollen tube Pollen tube enters Anther Pollen forms embryo sac Ovule Central cell Stigma Pollen tube Style Egg Sperm cells Vegetative nucleus Synergid cells ARARIDOPSIS THAI IANA **FERONIA** receptor Ligand? Fertilization communication. Synergid cells that attract pollen tubes express FERONIA protein. A ligand from the pollen tube may interact with FERONIA, causing Possible receptor-ligand the pollen tube to stop growing and Synergid cell interaction triggers release sperm cells. sperm release

there is an embryo sac (female gametophyte), typically composed of seven cells: an egg cell, a central cell, two synergid cells, and three antipodal cells. The pollen tube enters the ovule through an opening (the micropyle), penetrates one of the synergids, and bursts, thereby releasing the sperm cells. One sperm cell fuses with the egg cell to form a zygote, while the other sperm cell fuses with the central cell to form the primary endosperm cell.

A few years ago, two female gametophytic mutants, *feronia* (2) and *sirène* (3), were described in the flowering plant *Arabidopsis thaliana*. In these mutant plants, pollen tubes

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were attracted to ovules and entered the micropyle, but failed to burst and release sperm, continuing to grow instead. This phenotype suggested failed communication between the pollen tube and the embryo sac, but it was not known whether feronia and sirène affected the same or different components in this dialog. Escobar-Restrepo et al. now show that both mutants have lesions in the same gene and that the gene encodes an enzyme that phosphorylates proteins on serine and threonine residues. The enzyme, FERONIA, belongs to the previously uncharacterized CrRLK1L-1 group of receptor-like kinases (4), of which there are 15 members in A. thaliana. The authors determined that FERONIA is located in the plasma membrane of the synergid cells.

Because the pollen tube overgrowth phenotype resembled that seen after interspecies crosses in Rhododendron, Escobar-Restrepo et al. tested whether crosses with A. thaliana relatives would yield similar phenotypes and thereby implicate FERONIA in interspecies barriers. Indeed, crosses of A. thaliana females with Cardamine flexuosa pollen or with pollen of a more closely related species, Arabidopsis lyrata, yielded a pollen tube overgrowth phenotype. Recent studies suggest that synergid cells secrete a pollen tube attractant (5-7). In addition, an ovule already targeted by a pollen tube may produce a repellent to ward off additional pollen tubes (7). Moreover, these attractants and repellents exhibit some degree of species specificity (7, 8). In both sirène and feronia mutant plants, some ovules attracted more than one pollen tube (2, 3), perhaps because the attractant persists when the first pollen tube does not burst.

Proteins involved in sexual recognition can show amino acid diversification in regions that interact with a protein from the other sex (9) as the proteins evolve to match each other; that is, genes with increased rates of evolution increase the frequency with which incompatibilities evolve between closely related species. Among plants related to *A. thaliana*, the extracellular domain of FERONIA has more nonsynonymous nucleotide changes than the highly conserved kinase domain. This suggests that the presumed ligand-binding region was subject to positive selection and that coevolution between FERONIA and an equivalently diverging ligand could contribute to reproductive isolation.

Escobar-Restrepo *et al.* propose a signaling pathway wherein ligand from the pollen tube interacts with FERONIA, causing the synergid cell to send another signal back to the pollen tube to stop growing and burst (see the figure). Much more information is needed to test this intriguing model. The immediate challenge is to identify the FERONIA ligand. There is no way to guess a priori what it might be; even within the LRR (leucine-rich repeat) receptor kinase group—the best-studied such group in plants—the known ligands are diverse (10). Potential ligand-receptor pairs might be identified through screens of mutant plants for similar phenotypes (11) such as pollen tube overgrowth. Yeast two-hybrid screens (12) are another option, in which the extracellular domain of FERONIA can be used as bait for complementary DNA libraries prepared from germinated pollen tubes.

It will also be important to determine whether disruptions of *FERONIA* homologs in other species give similar phenotypes; if so, the pollen overgrowth phenotype may occur with interspecies crosses in other plant families. It is intriguing that in the cross with *A. lyrata*, 50% of the pollinated *A. thaliana* ovules showed the pollen overgrowth phenotype, whereas the other 50% showed normal fertilization (1). Indeed, interspecies crosses with *A. lyrata* are possible (13). Escobar-Restrepo *et al.* suggest that there might be different isoforms of the ligand in *A. lyrata*, with one allelic variant that recognizes the *A. thaliana* version of FERONIA.

FERONIA and its upstream and downstream signaling partners may be the key to successful sperm discharge. If so, then manipulating the components of this pathway might facilitate more promiscuous hybridizations than occur in nature.

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ASTRONOMY

Seeing Through Dark Matter

Stacy McGaugh

Dark matter was proposed to explain galaxy dynamics. A modification of Newton's law of gravitational force may offer a better explanation.

he universe appears to be dominated by invisible components that astronomers call dark matter and dark energy. The astronomical evidence implicating dark matter has been apparent for a generation (1): The rotational speeds of objects in extragalactic systems exceed what can be explained by the visible mass of stars and gas. This discrepancy has led to the inference that there is more mass than meets the eye. However, this inference requires that Newton's law of gravitational force be extrapolated well beyond where it was established. In addition, laboratory searches for dark matter have yet to bear fruit. This lack of corroboration, combined with the increasing complexity and "preposterous" nature of a once simple and elegant cosmology, leads one to wonder if perhaps instead gravity is to blame.

Simply changing the force law on some large length scale does not work (2). One

idea that has proven surprisingly resilient is the modified Newtonian dynamics (MOND) hypothesized by Milgrom (3) in 1983. Rather than change the force law at some large length scale, MOND subtly alters it at a tiny acceleration scale, around 10^{-10} m s⁻². In systems with gravitational accelerations above this scale (e.g., Earth, the solar system), everything behaves in a Newtonian sense. It is only when accelerations become tiny, as in the outskirts of galaxies, that the modification becomes apparent.

MOND has successfully described the rotation curves of spiral galaxies (see the figure) (4). In case after case, MOND correctly maps the observed mass to the observed dynamics. Why would such a direct mapping exist between visible and total mass if in fact dark matter dominates? Moreover, MOND's explicit predictions for low surface brightness galaxies have been realized (5). In contrast, the dark matter paradigm makes less precise predictions (6) for rotation curves that persistently disagree with the data (7).

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