Biology in pictures

Mutant meristems

As anyone who has looked at a petunia or a pansy can testify, plants generate flowers with characteristic numbers and patterns of organs. The floral organs are derived from a pool of stem cells called the floral meristem. In wild-type *Arabidopsis thaliana* flowers (shown at lower left) the meristem gives rise to four sepals that enclose the bud, four white petals, six pollen-bearing stamens and a central gynoecium comprised of two fused, ovule-containing carpels.

The other flowers shown above have mutations in genes that control floral organ number. The *wiggum* mutant flower at the top has extra organs of all types, mainly sepals and petals. These mutants have wider floral meristems than the wild type, which allows formation of more organs in the outer regions of the flower.

The *clavata3* mutant flower (lower centre) has extra organs of all types, mainly stamens and carpels. These mutants have taller floral meristems than the wild type, allowing formation of more organs in the inner region of the flower. The *perianthia* mutant flower (lower right) has five each of sepals, petals and stamens. In these mutants the size of the floral meristem is not affected; instead, the distance between floral organ initiation events is altered. (For more details, see Running MP, Fletcher JC, Meyerowitz EM, *Development* 1998, **125:**1545-2553. Images provided by Jenn Fletcher, Division of Biology, California Institute of Technology, Pasadena, California 91125, USA.)

Quick guide

Hydrophobicity

A.D.J. Haymet

What is it? Hydrophobic means 'water-hating' (although no-one has yet defined an SI unit of 'hate').

Why is it important in biological systems? An impressive example of the effect of hydrophobicity in nature is the stabilization of the interior of phospholipid membranes — the fluid-like phase that separates the 'inside' from the 'outside' of every animal cell. Other oft-quoted examples include binding of substrates to enzymes, conformational changes to biopolymers, and association of subunits to form enzymes. To date, it is not clear whether all these effects are due to hydrophobicity, or to some other weird property of water, such as hydrogen bonding.

How do I know if it's hydrophobicity? Hard to say. It's certainly a candidate for the most over-used and least well-understood word in biology. According to some, if it behaves unusually and it's in water (… or 'remembers' water…), it must be the hydrophobic effect.

So, how do I know if it's really hydrophobicity? The characteristic feature of hydrophobicity is the heat capacity of transfer of a solute molecule from the gas phase to water, which is large and positive over a wide range of temperature. This implies that although the transfer is opposed by entropy at room temperature, it is opposed by enthalpy at much higher temperatures. The magnitude and temperature dependence of this curve is characteristic of the hydrophobic effect and its integral is the magnitude of the entropy penalty. Well, you did ask.

Who discovered hydrophobicity? Who knows? In 1729 Hermann Boerhave "exposed beer, wine, vinegar and brine … to the frost," and speculated about the temperature dependence of the "dissolving power" of water, but he did not publish his results until three years later. (History doesn't relate whether or not he kept his funding.)

What causes it? Oil and water don't mix. Conventional wisdom has it that the oil 'hates' the water. In fact, oil quite likes water (as shown by the high solubility of water in liquid hydrocarbons). It's the water that hates the oil. At room temperature and pressure, a simple hydrocarbon such as methane is more than 100 times less soluble in water than it is in hexane. One often reads that proteins fold so that oily residues escape from water. Not true. In fact, the water tells the protein: 'get those oily residues out of my structure, or precipitate'.

Why does water hate oil? Under ambient conditions, the water has to pay a huge entropy penalty to incorporate the oily solute into the water's liquid structure. In other words, the (water + oil) mixture is more 'ordered' than water alone, hence the entropy penalty and the low solubility of the oil. But although the thermodynamic facts are well known, the exact location and spatial extent of the entropy is still debated hotly. Some researchers using neutron scattering and nuclear magnetic resonance (NMR) might have their sleep disturbed by the fact that the solubility of oily molecules in H_2O and in deuterium is different.

Most misleading concept … The notion of hydrophobic interactions as attractive interactions between oily objects that can be measured as energies and are independent of temperature. Nothing is further from the truth. Such rough models can only possibly work at one temperature, as the real hydrophobic effect is the minimization of the entropy penalty incurred by the water, which is highly temperature dependent. The existence of more than 15 different relative hydrophobicity scales for the amino acids at room temperature is evidence of the confusion caused by such rough models. For example, in these scales, the ranking of histidine varies from 2 to 20 (out of 20); it is 12th in one of the more popular scales.

Will we ever understand hydrophobicity? Computer simulations will soon unravel the facts for simple mixtures of oil and water, and eventually for lipids and proteins. For in-depth understanding, you'll need to get to grips with several competing candidate theories: mixture models, which try to model subsets of water molecules with different hydrogen-bonding characteristics; models that estimate the free energy needed to form a 'cavity' in the water solvent; and, perhaps, polarization theories.

Where can I find out more?

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Introns

German artist Jim Avignon is best known on the thriving Berlin art scene for his irreverent advertising campaigns and live performance art (which mixes painting and music). Avignon has never studied biology but this doesn't stop him from taking a sideways look at the subject; he often uses biological themes as an allegory for human society.

This example of Avignon's work is from the collection *Popbones* (1996).