

The other sexual revolution: hormonal control of family planning in plants

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The development of hormonal contraceptives stands out as a key contribution of biochemistry to the 20th century, part of the wider 'sexual revolution' that dramatically changed society in many Western countries. But unbeknown to them, the pioneers of the contraceptive pill had been beaten to the idea by a few hundred million years, by a rather unlikely group of organisms that have been using hormones as contraceptives since their own sexual revolutions back in the swinging Palaeozoic. Since their successful conquest of land in the Ordovician, land plants had been restricted in the genetic mixing and expansion of populations by their relative immobility. A series of key innovations in the seed plant group, and in particular in flowering plants, enabled plants to mate and to disperse their offspring over much longer distances, by harnessing the wind or animals to provide mobility. However, all this 'outsourcing' created new challenges; coordinating and optimizing reproductive effort is not straightforward when it depends on a third party. Here, I discuss some of the key signalling molecules – sex hormones, as it were – that plants use to plan their families and manage their fertility, and why this matters to us, now more than ever.

A riot of careless descendants

For many people, being interminably stuck at home has been one of the unpleasant novelties of the last year. Spare a thought then for plants, for whom being stuck at home is a permanent state of affairs and one they complain about a good deal less than us. Admittedly, given that plants earn their living through the everyday photosynthetic miracle of turning water and carbon dioxide into sugar, staying still – with their roots deep in the soil and leaves in the wind – is a pretty good strategy. But it's a strategy that tends to make plant families close-knit, because finding a mate and dispersing your offspring is pretty tricky when you can't move. Stuck at home with the kids; what a nightmare.

Free love, seed plant style

Plants though are nothing if not adaptable. Even if staying still creates some major headaches, these are nothing that plants haven't been able to find elegant solutions to down the aeons. The first major sexual revolution in land plants could be described as the 'pollen revolution'. The more ancient groups of land plants, including mosses and ferns, have mobile zoosperm that 'swim' to a mate, a hangover from their aquatic ancestors, and one of several features that tend to limit these plants to damp environments. However,

in the more anatomically modern 'seed plants'ⁱ, the male gametes are packaged into the tiny, weightless pollen grains that torment people each summer. By releasing pollen into the breeze, it became possible for seed plants to mate over great distances, significantly increasing genetic dispersal and outbreeding – key goals for any successful population. But as anyone who has seen Yew trees dumping improbably dense clouds of pollen into the air will testify, it's a pretty scattershot approach to reproduction (Figure 1).

Flower power

The second key sexual revolution in plants – the one that really changed the game – was therefore undoubtedly the 'floral revolution'. With their showy petals and sugary bribes (Figure 2), flowers have one basic function: outsourcing the hard labour of reproduction to animals, and particularly insects.ⁱⁱ Now *that's* a sexual revolution. By harnessing the

ⁱAs the name suggests, pollen isn't the only key feature of the seed plants – seeds are too. The packaging of embryos in desiccation-resistant seeds was another huge leap forward in freeing plants from damp environments, but didn't have a major effect on the sexual conduct of plants.

ⁱⁱAnd also birds, most obviously humming birds. Some mammals (e.g., bats) and reptiles can act as pollinators, but insects and birds account for the vast majority of animal pollinators. Some groups of flowering plants have reverted to wind



Figure 1. Scattershot reproduction. In spring, Yew trees release clouds of pollen – no different from other wind-pollinated plants, except that the pollen is unusually large and hence visible.

motility of animals, flowering plants (a subset of seed plants) dramatically increase the chances that their pollen will reach its intended destination, without decreasing the distance (relative to wind pollination) over which outbreeding can occur. Indeed, so successful has this innovation been that the flowering plants are – by some distance – the most successful and diverse group of land plants.

Feeling fruity

Having subtly manipulated animals into doing their work once, flowering plants soon repeated the trick. Because if insects could be bribed into transferring their pollen to initiate reproduction, there was no reason that larger animals couldn't be bribed into dispersing the offspring arising from that reproduction. Thus, the third key sexual revolution

pollination, particular the grasses (including maize, wheat and rice).



Figure 2. Top row: flowers of tomato and pea, which are specialized for pollination by different groups of insects. Bottom row: fruits of tomato and pea; the tomato fruit is specialized for animal dispersal, whereas the pea fruit is not, and lacks 'flesh'.

was the 'fruit revolution', in which the protective tissues containing the seeds of many flowering plantsⁱⁱⁱ evolved into a fleshy inducement to promote long-range seed dispersal^{iv} (Figure 2). Again, this greatly enhances genetic mixing in the population, but also means that plants are less likely to be competing with their own parents and siblings for resources, a key factor when you can't move.

A time to flower

It must be confessed that all this outsourcing wasn't without side effects. For a start, it became particularly important for flowering plants to synchronize reproduction to the

ⁱⁱⁱIndeed, the scientific name for flowering plants, 'angiosperms', means 'enclosed seed' and draws a contrast with the remaining seed plants, which are known as 'gymnosperms' ('naked seed'). In the interests of fairness, some gymnosperms have convergently evolved fleshy fruit-like structures to promote seed dispersal, most obviously juniper (whose berries are used to make gin) and yew. In yew, the 'aril' is the only part of the plant that is not exceptionally poisonous.

^{iv}After pollination, all flowering plants form a protective case from the female reproductive organs that encompasses their seeds. This protective case is confusingly called a 'fruit', which is a culinary term recycled as a botanical term. All flowering plants make a fruit (botanical sense), but not all flowering plants make a fleshy fruit for the purpose of seed dispersal (culinary sense). Many flowering plants use wind to disperse seeds over long distance, while others may use explosive dispersal. Many other flowering plants don't bother with the expense of seed dispersal at all, particularly in 'monocarpic' species in which the mother plant dies immediately after reproduction, thereby avoiding competing with its offspring.

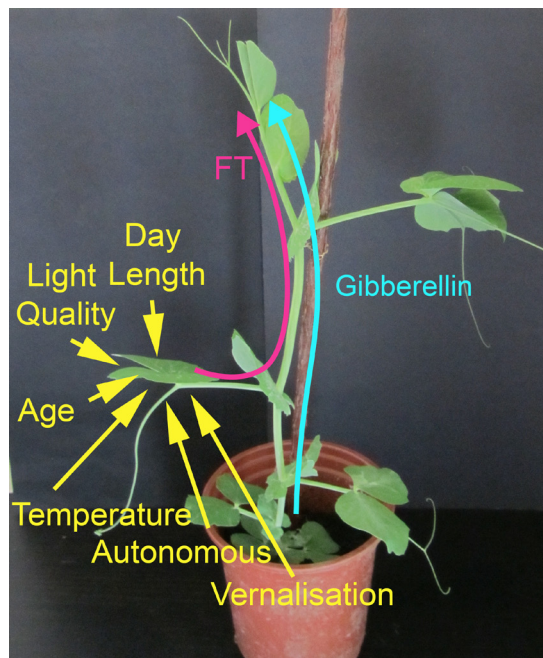


Figure 3. Flowering control in plants. Leaves act as the point of signal integration for multiple stimuli, resulting in the expression of the FT gene. FT protein then moves in the phloem to the shoot apex to promote flowering. The hormone gibberellin also promotes flowering, but not through FT.

seasons when their pollinators are available. This resulted in the ‘floral transition’ between vegetative and reproductive development being one of the most carefully controlled events in the life of a plant. Environmental and internal information is integrated through seven different pathways (Figure 3) to determine the correct flowering time, and most of these converge on a remarkable hormonal signal by the delightfully uninformative name of FLOWERING LOCUS

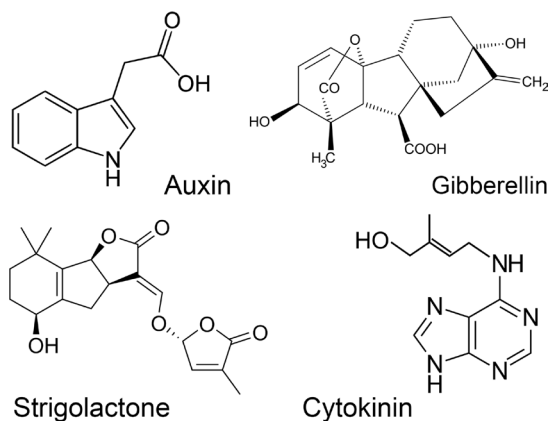


Figure 4. A rogue’s gallery of the simple hormonal signals that allow plants to coordinate their development over long distances

T (or FT for short). Unusually for a plant signalling molecule, FT is a relatively large (19 kDa) phosphatidylethanolamine-binding protein, which is nevertheless highly mobile within the plant body. FT acts as a sort of plant equivalent of luteinising hormone (LH) in pubescent humans, the long-distance signal that kick-starts development of the sexual organs. As demonstrated in a series of seminal grafting experiments in the 1930s, plants perceive flowering-inducing stimuli such as day length and temperature in their leaves, but respond by the production of flowers in the ‘shoot meristems’ (specialized regions of undifferentiated tissue; Figure 3). FT therefore acts as a ‘florigen’ signal that transmits information from the leaves to the meristems, just as LH transmits information from the pituitary gland to the gonads. By restricting the production of FT until environmental conditions are optimal – in the UK, typically the warmer temperatures and longer day lengths of spring – plants can synchronize their reproductive maturity to coincide with the availability of pollinators, and crucially, with the availability of potential mates.

Bloom and bust

Because plants are typically limited in their ability to defend their offspring, their reproductive success is usually a direct function of the number of seeds they deposit into the environment.^v Thus, once flowering has been initiated, plants must ‘decide’ how many offspring they can afford to raise and then produce the requisite flowers to achieve this seed-set. In essence, this ‘decision’ reflects the quantity of resources – light, stored energy, water and mineral nutrients – the plant has available when flowering. However, making this decision is rather complicated by the lack of any ‘central processor’ in plants; they must make these decisions without a brain, as it were. Each shoot meristem therefore acts independently, integrating environmental and internal information to produce the optimal number of flowers. Hormones are again key to this process, since they allow the plant to cheaply distribute information to each meristem from all across the plant body. For instance, information on the quantity of mineral nutrients – particularly nitrate and phosphate – in the soil must be communicated from the roots to the shoot meristems; in the tallest trees, this means transmitting signals over 100 m in distance. The molecules plants use to do this are surprisingly simple in nature; cytokinins are little more than adenine with a side-chain at position 6, while strigolactones have a slightly more exotic structure of a tricyclic lactone enol-ether bonded to a 2-methylbut-2,3-enolide ring (Figure 4). Despite their simplicity, cytokinins and strigolactones have profound

^vDifferent species might tend to make smaller numbers of high-quality seed, or larger numbers of tiny seed; but regardless, the more seed they make, the higher the probability of successfully establishing the next generation.

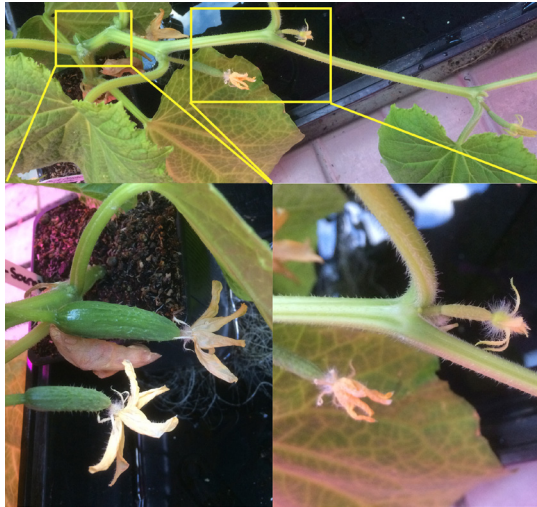


Figure 5. Siblingicide in action. The older two fruits on this cucumber plant (slightly out of view in the top photo, inset left from a different angle) have successfully inhibited the growth of the third fruit, and have caused the active senescence of the fourth fruit (inset right).

effects on plant growth, forming a ‘to-me-to-you’ double act to rival insulin and glucagon. Cytokinin – up-regulated by the *availability* of nitrate – strongly promotes the growth of inflorescences and flowers and lengthens flowering, while strigolactones – up-regulated by phosphate deficiency – strongly inhibit the growth of inflorescences and flowers. Thus, by measuring the balance of these hormones, shoot meristems can correctly gauge the optimal number of flowers to produce relative to the nutrients underground.

Forbidden fruit

For any seed plant, reproduction is an inherently probabilistic event; reproduction is never guaranteed. However, by increasing the amount of pollen they release, wind-pollinated plants can improve their odds of success in a relatively linear way. However, for animal-pollinated plants, the probability of successful mating becomes much more non-linear due to the involvement of a second species in their reproduction. Simply investing in more gametes does not necessarily improve the odds, which are more dependent on the behaviour of the pollinator. There might not be enough pollinators; the pollinators might stay home in the rain, the pollinator might turn up, but not visit another plant of the same species afterwards. Since not every flower will be pollinated, it is therefore generally necessary for animal-pollinated plants to produce excess flowers (‘over-flowering’) in order to guarantee the ‘target’ seed set. But what happens if there are still not enough pollinated flowers? Or, perhaps even worse, too many pollinated flowers? This is where the

hormonal control of plant reproduction really comes into its own.

Nature, as has been observed, is red in tooth and claw. Perhaps nowhere is this more starkly illustrated than by the siblicide that occurs in broods of many birds and mammals: the stronger offspring eliminating their weaker siblings to gain more parental investment. Remarkably (but much more quietly), this same process occurs throughout flowering plants,^{vi} for the same reasons. Completely dependent on their mothers^{vii} for resources, the fertile seeds produced by a plant will vigorously compete for maternal investment at the expense of their siblings, both actual and potential. This competition is driven by the most ubiquitous and simplest of all plant signalling molecules, indole-3-acetic acid, or ‘auxin’ (Figure 4). This molecule – a sawn-off tryptophan – is so important that plants cannot live without it, and it is involved in almost every aspect of plant growth and development. Exactly *how* such a simple molecule can *do so much* has vexed generations of plant scientists; perhaps the most likely answer is that auxin doesn’t *do anything*, but is rather a sort of ‘universal stimulus’, or a ‘cellular currency’. In the context of sibling rivalry, the export of auxin by seeds seems to act by strengthening their vascular connection to the mother, promoting the import of resources to the seed, and simultaneously diminishing the connectivity of its siblings to the mother. This competition acts at two levels: seed in the same fruit can inhibit each other’s development, but more commonly, the seed in the older, larger fruits collectively act to inhibit the development of other nearby fruit (Figure 5). The end result of this is inhibited growth or outright abortion of weaker fruit. Watch an apple tree throughout June; suddenly, perhaps after one windy night, a large proportion of fruit will be on the floor. This ‘June drop’ is the auxin-mediated eviction of sibling rivals from the maternal nest.

Shockingly, the mother is completely complicit in this siblicide; from the mother’s perspective, this auxin-driven system acts as a superb system for correcting the course of reproductive development. This is because, as well as affecting their siblings, the auxin exported from fruit also inhibits the on-going reproduction of the mother. Thus, if not enough fruit have been set, the mother will continue flowering until it has. Conversely, if too many flowers have been pollinated, new flowers can be inhibited, and excess

^{vi}The process is less marked in wind-pollinated plants, where over-flowering does not occur; but offspring still affect each other’s growth even in these species.

^{vii}Of course, most plants are hermaphrodite, and therefore equally male and female. However, mother/maternal tends to be used of the plant in the context of bearing offspring, because that is deemed an inherently female characteristic. It must be confessed that since many plants are highly self-fertile, the embryos born by a plant may be genetically equally derived from the female and male gametes, but the seed and fruit are entirely derived from female tissues.

fruit can be shed. In some fruit trees, a particularly heavy fruit-set can even inhibit flowering the following year, to prevent conflict between generations of offspring from the same mother. In these ways, auxin acts as a potent universal contraceptive that allows precise family-planning; parental resources are optimally invested, and parent-offspring and sibling-sibling conflict is minimized by producing the 'correct' number of seed relative to the environmental conditions. As most parents would testify, it does tend to be the case that having *some* kids is what prevents you having more.

Doing more with less

Of course, flowering plant reproduction isn't all sordid tales of fratricide and inbreeding. The very serious point

is that the vast majority of calories consumed on the planet are derived directly or indirectly from the seeds and fruits of flowering plants – 80% of them from just rice, wheat and maize. We need to dramatically increase crop yields in the next 30 years, without increasing land or fertilizer use, with decreasing pollinator availability and increasing temperatures that affect the optimal flowering period. It is thus a very, very appropriate time to try and better understand the hormonal signals that control flowering plant reproduction and how we might persuade crops to *do more with less*. The scope is there: because of bet-hedging and avoidance of intergenerational conflicts, plants tend to produce far fewer offspring than their physiological capacity allows. To improve yields, to feed the world, we need to unleash their full reproductive potential: once again, sexual revolution is in the air. ■

Further reading

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