Plant cell connections

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Plasmodesmata are nanoscopic channels that connect plant cells to each other. Plasmodesmata open and close in response to environmental factors, controlling what moves through them. Plant researcher Matthew Johnston explains how this plays an important part in plant defence against pathogens

Exam links

AQA Structure of eukaryotic cells; Mass transport in plants
Edexcel A Ultrastructure of plant cells; Translocation of organic solutes
Edexcel B Ultrastructure of eukaryotic cells; Movement of sugars through phloem
OCR A Ultrastructure of eukaryotic cells; The mechanism of translocation; Plant chemical defences
OCR B Ultrastructure of plant cells; The mechanism of translocation
WJEC Eduqas Detailed structure of phloem; Translocation of organic materials

Resources and signalling molecules have to be transported around multicellular organisms to allow them to function. Plant cells are surrounded by cellulose walls, which would limit this transport were it not for membrane-lined tunnels that traverse them. These connections of the cytoplasm of adjacent cells are called plasmodesmata (from the Greek words for something moulded or fitted, and bond or bridge), singular plasmodesma (see Figure 1).

Each plasmodesma has a strand of endoplasmic reticulum through the middle, termed the desmotubule. Plasmodesmata are only about 100 nm long (750 times narrower than a hair's breadth), and often cluster into groups in the cell surface membrane termed pit fields (see Figure 2). The small gap between the desmotubule and the cell surface membrane allows the movement of cytoplasm between cells, and so short-distance transport of signalling molecules. This is essential for plant development, such as the patterning of cell types in the root and the formation of flowers. Plasmodesmata also facilitate long-distance transport of molecules in the phloem (see Box 1).

What fits through?

Transport through plasmodesmata has been demonstrated. Fluorescent dyes of around the same molecular mass as glucose can be microinjected into a single cell. These dyes can be tracked under a fluorescence microscope and are seen to spread from cell to cell. Plasmodesmata display directionality of movement, so some molecules will only flow in one direction between cells.

This can be seen in snapdragon plants (*Antirrhinum majus* — see Figure 3) where the flowers of a plant without the protein DEFICIENS do not form petals or stamens. When DEFICIENS is expressed in vegetative tissue, the plants have flowers with petals but no stamens. Conversely, when expressed in reproductive tissue, plants have stamens and petals. This demonstrates that

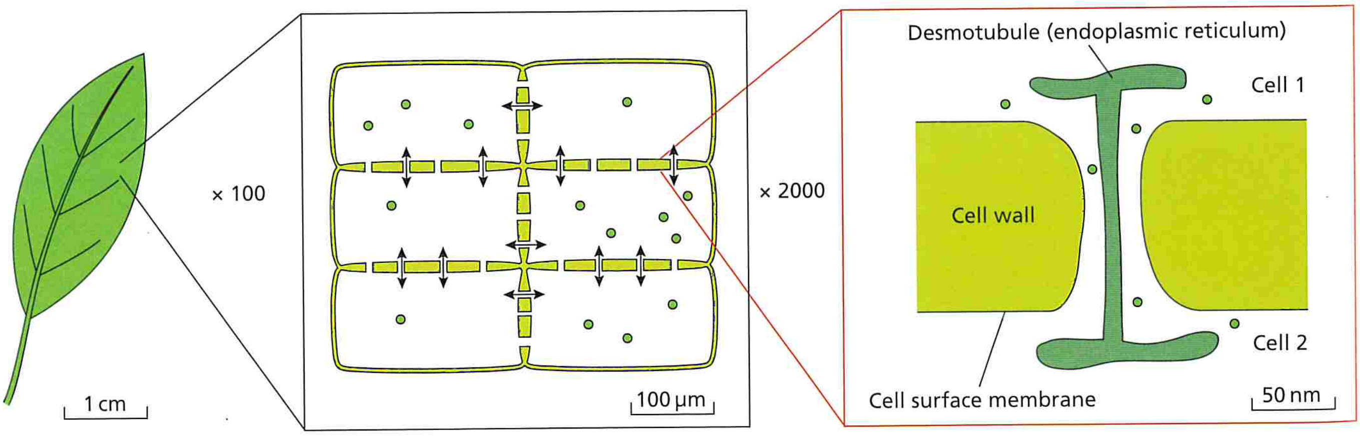

Figure 1 The structure of a plasmodesma. Plasmodesmata are nanoscopic tunnels, about 100 nm long, that connect adjacent plant cells. This allows the flow of molecules between plant cells

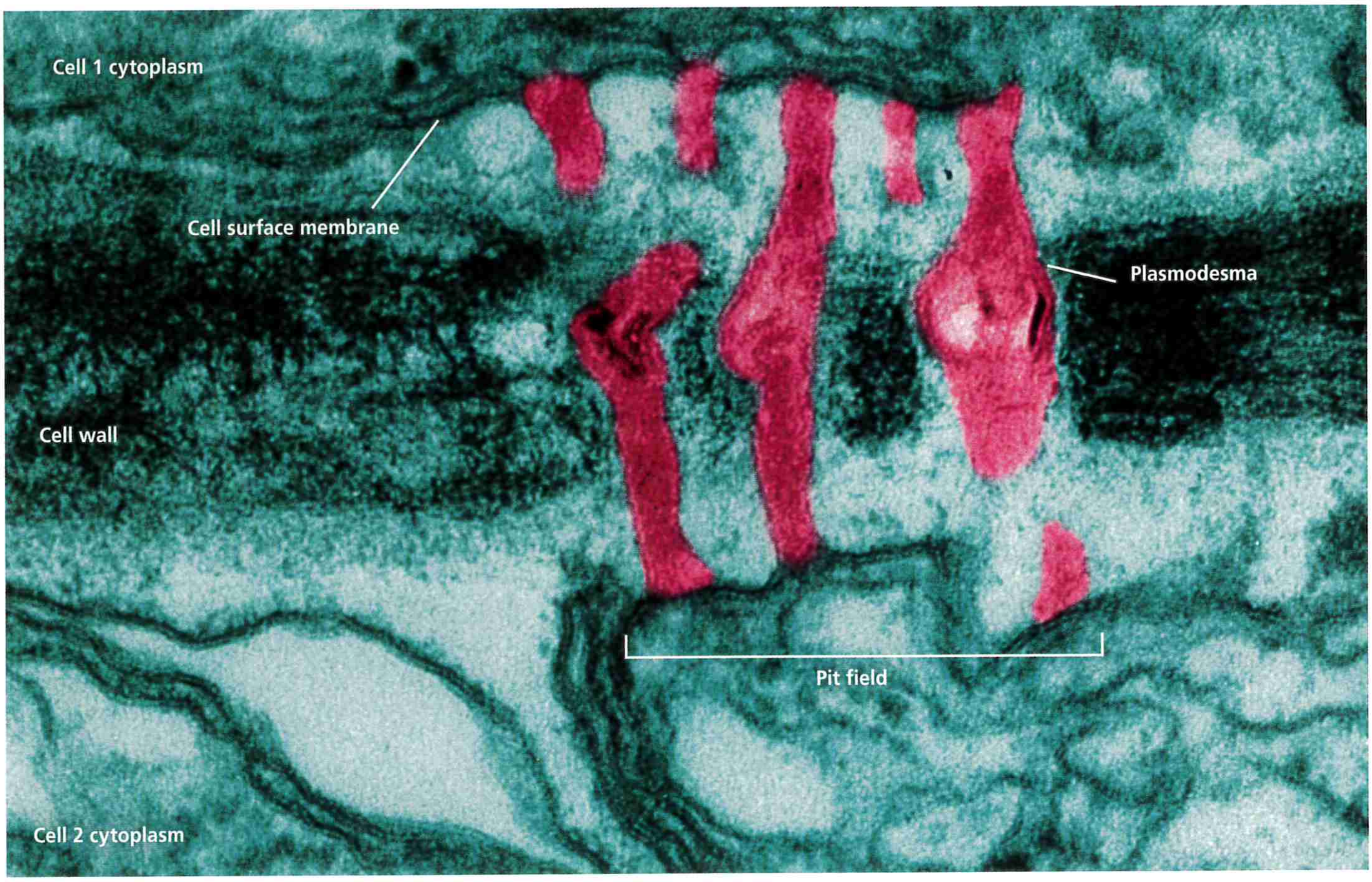

Figure 2 Coloured transmission electron micrograph of a pit field — a cluster of plasmodesmata (coloured pink) between two plant cells ×400 000

Box 1 Plasmodesmata and phloem

Phloem is a conduit for the movement of sucrose from photosynthetic parts to the rest of the plant. Unlike, xylem, which is dead tissue at maturity, phloem is alive and maintains cellular integrity.

The phloem is made up of two cell types: sieve elements and companion cells (see Figure 1.1). Sieve elements are highly modified with no nucleus or ribosomes, and so require companion cells to survive as they produce all the proteins the sieve elements require.

Perforations at the ends of sieve elements — the sieve plates — allow sucrose to flow through the plant. These holes are derived from plasmodesmata but have been modified to be at least ten times wider. The original plasmodesmata accumulate callose, much like in defence, which maintains the cell wall integrity as the size of the pore expands.

In addition to allowing transport of sucrose through the phloem, sieve element to sieve element, plasmodesmata are also the route through which the sieve elements are loaded with sucrose from companion cells. Companion cells are actively loaded with sucrose, meaning that energy (ATP) is used to concentrate sucrose against a concentration gradient. Sucrose then moves from the relatively high concentration in the companion cells into the sieve elements by simple diffusion through the connecting plasmodesmata.

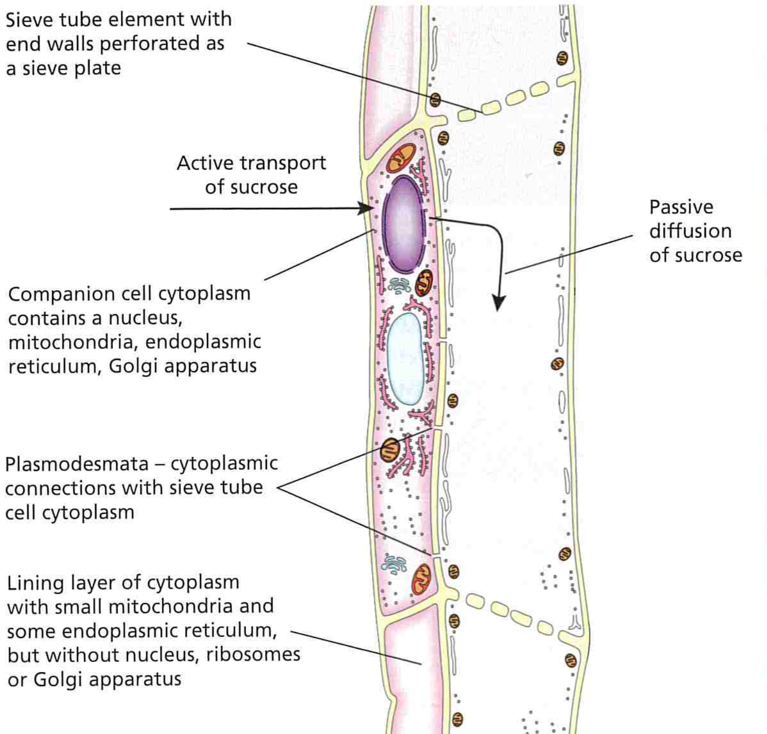

Figure 1.1 Phloem tissue ×400 000

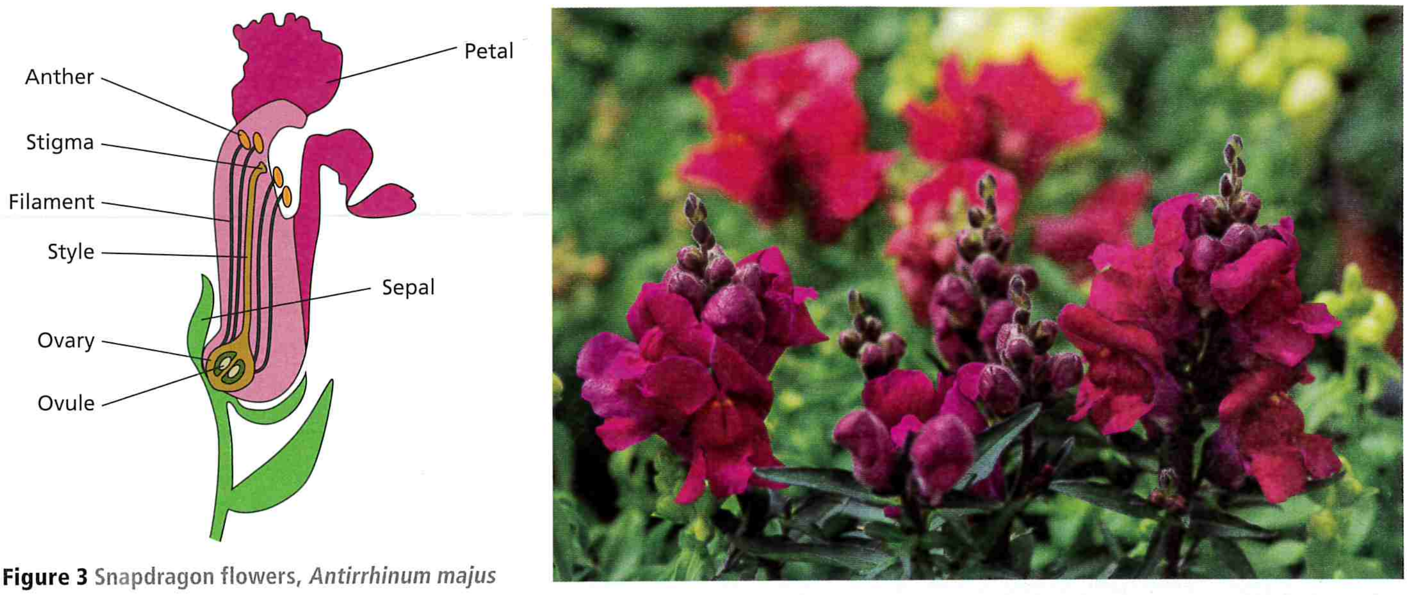

Figure 3 Snapdragon flowers, *Antirrhinum majus*

Box 2 Visualising transport through plasmodesmata

The fluorescent microscope images in Figure 2.1 show leaf cells of *Arabidopsis thaliana*. The plants have been bombarded with gold particles coated with DNA coding for a fluorescent protein. In each case, a single cell has been transformed and is expressing GFP. GFP detected in cells outside the central, brightest cell must be from cell-to-cell movement. The plasmodesmata are more blocked in the cells of leaf B than those in leaf A because leaf B has launched a defence response. Transport of GFP through leaf B is thus reduced.

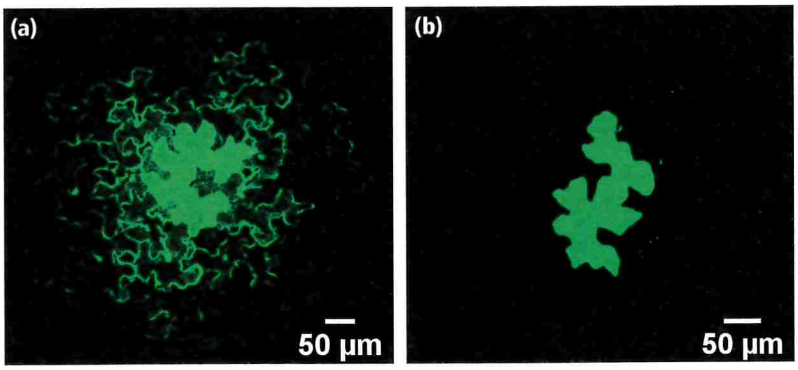

Figure 2.1 **(a)** Leaf A, plasmodesmata open; **(b)** leaf B, plasmodesmata closed

DEFICIENS moves from the centre of a flower outward, from reproductive tissue to the petals, but not vice versa.

A significant amount of research has been put into determining the maximum size of molecule that can fit though a plasmodesma, called the **size exclusion limit**. Because injected dyes linked to large molecules did not move from cell to cell, it had been thought that proteins were also too large to pass through plasmodesmata. It is now thought that microinjecting dyes damages plant cells, causing a reduction in the size exclusion limit, as proteins have been shown to move (see Box 2). This opened up a remarkable possibility: do plant cells respond to stimuli to alter movement of molecules through plasmodesmata?

Plasmodesmata in defence

Scientists have conducted experiments to test whether plant cells can alter their size exclusion limit dynamically in response to environmental changes. They have used molecules that are associated with defence responses (pathogen-associated molecular patterns — PAMPs, see Box 3). In one such

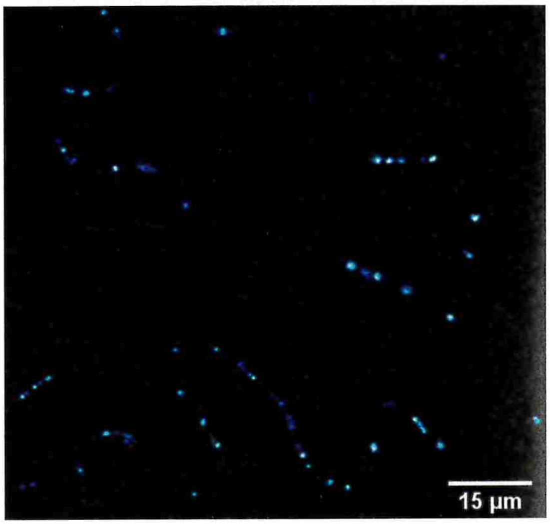

Figure 4 Fluorescent micrograph of a plant cell stained with aniline blue and illuminated by ultraviolet light. This shows pit fields (clusters of plasmodesmata – see Figure 2) where there is a high accumulation of callose

Terms explained

GFP Green fluorescent protein. A protein derived from jellyfish widely used in cell biology. When blue light is shone on this protein, it emits green light, allowing specific proteins to be tracked in a cell.

Overexpression Where an organism is genetically manipulated to produce more protein than it normally would.

Pathogen A broad term for any agent that can cause disease.

Size exclusion limit The maximum size of molecule that can move through a plasmodesma.

Box 3 Plant defence

Plants come under attack from pathogens every day, leading to 10–40% yield losses in staple crops. Unlike animals, plants do not have a circulating immune system with white blood cells. Instead, defence responses occur at the point of invasion. The most widely accepted model was coined the 'zigzag model', which is a two-tier defence mechanism. The plant cell first identifies pathogens by conserved molecules, PAMPs, which activate the first tier of defence — PAMP-triggered immunity. Some pathogens are specialised and secrete proteins (termed effectors) into the plant cell, overcoming and suppressing the first level of defence and starting a successful infection. Some plants, in turn, have specialised receptors that detect the secreted effectors, triggering the second tier of defence — effector-triggered immunity, protecting the plant again. This back-and-forth can continue multiple times, leading to more effectors preventing effector-triggered immunity, and more receptors detecting these effectors.

A plant cell detects PAMPs, conserved molecules from a pathogen, and activates the defence response, PAMP-triggered immunity (PTI, see (1) in Figure 3.1). Some pathogens have proteins (effectors), which they secrete to stop PTI (2). These make the plant susceptible again. However, the plant can respond in kind and detect the effectors, triggering plant defence again, effector-triggered immunity (ETI (3)).

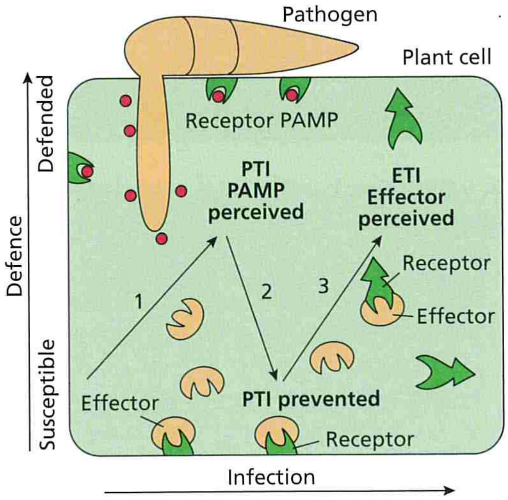

Figure 3.1 Plant defence

Further reading

Plant transformation using particle bombardment: **https://tinyurl.com/yemokee9**

Faulkner, C. (2018), 'Plasmodesmata and the symplast', *Current Biology*, Vol. 28, No. 24, R1374–R1378.

'Faces of plant cell biology: Dr Christine Faulkner': **www.plantcellbiology.com/2014/03/dr-christine-faulkner**

experiment, chitin — a major component of fungal cell walls (a fungal PAMP) — was injected into leaves, where single cells produced the fluorescent marker **GFP**. Reduced spread of GFP from cell to cell showed that the leaf had closed its plasmodesmata in response to the PAMP.

The plasmodesmal receptor for chitin has been discovered and plants that have had this receptor genetically removed (knock-out mutants) are available. A normal, wild-type plant was compared with the receptor knock-out to see whether a fungal **pathogen** was better able to infect the wild-type or the knock-out mutant. The fungus grew more successfully on the mutant plant, allowing the conclusion that the receptor is involved in plant defence against pathogens. More generally this demonstrates that plasmodesmal closure is an important part of the first tier of the plant defence response — PAMP-triggered immunity, PTI — as outlined in Box 3).

What blocks plasmodesmata?

Callose is a polymer of β-glucose (as is cellulose). This impermeable polysaccharide is rapidly deposited at plasmodesmata in response to infection or damage to plants. Callose can be visualised at pit fields using a dye called aniline blue (see Figure 4).

This raises the question, could plasmodesmata be blocked to a greater extent than would naturally occur, and so make plants more resistant to pathogens. There are several ways of doing this, but one method is to **overexpress** proteins that trigger callose deposition. These proteins are called plasmodesmata-localised proteins (PDLPs) and transgenic plants have been created with novel DNA that causes them to make more PDLPs than wild-type plants.

Using aniline blue, it can be seen that callose concentrations are higher in the transgenic plants. These plants are more resistant than wild-type plants to both viruses and bacteria. However, the transgenic plants also had developmental defects and were dwarfed. (This underlines the importance of cell-to-cell communication in normal growth processes.) Consequently, if this technique were to be used in crops, the crops may be more resistant to pathogens, but they would probably have a reduced yield.

This highlights the necessity for a more detailed understanding of plasmodesmata to allow more sophisticated engineering of plasmodesmal blockage in defence. One possibility for the future would be to overexpress the PDLP protein only transiently, when the first line of plant defence is triggered, so as to defend the plant only when required and avoid any developmental side effects.

Things to discuss

- How else could resistance–yield trade-off be overcome?
- What benefits could the plant gain by the blocking of plasmodesmata?

Matthew Johnston is a PhD student in Dr Christine Faulkner's laboratory at the John Innes Centre, Norwich. He specialises in signalling events at plasmodesmata, especially in a defence context.

Key points

- Plasmodesmata are connections between plant cells which allow the movement of molecules between adjacent cells.
- Plasmodesmata are dynamic and can be blocked in response to pathogen attack by the deposition of callose.
- Blockage of plasmodesmata is an important part of plant defence, increasing resistance to pathogens.