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Plant Biology

Carnivorous plants help uncover universal rules of plant development

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ABSTRACT

From flowers to leaves and carnivorous plant traps, humble mounds of cells generate remarkably diverse plant organ shapes. How do plants coordinate growth to shape these blobs into fully-grown organs? By combining computational modelling with experiments in a carnivorous plant, we suggest a mechanism for how plants control growth patterns and how they can be modified to evolve new shapes.

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Look out your window, and you might see the broad leaves of a mulberry tree or thin needles of a pine. Perhaps you have an orchid on your windowsill and have noticed the extravagant curves of its petals. All these shapes emerge from the same beginnings—a microscopic mound of cells called a primordium. But how do plants make such varied final shapes from the same starting point?

To transform a dome-shaped primordium into organs of different shapes, plants need to control how much they grow in three dimensions. For example, to make a long and narrow pine needle growth happens more in one dimension, from the base to the tip, than the other two. To produce the wide leaves of the mulberry the primordium grows more in two dimensions: from the base to the tip and from left to right (laterally). This growth pattern makes the leaf both long and wide but still very thin. Patterning the leaf along this thin third dimension is crucial for lateral growth. To pattern their development plants can turn genes "on and off" at particular times and in specific places. For example, a gene that makes a red pigment may be "turned on" or expressed in flowers, but remain "turned off" in leaves. This means that although every plant cell contains the same genes (known as a genome) only a subset of them are expressed in a particular time and place, allowing a plant to differentiate. Different combinations of genes being express can lead to different developmental outcomes. In leaves, two different sets of genes are expressed from an early stage and mark the top and bottom sides of the leaf (also known as dorsal and ventral sides). In mutants lacking either top or bottom patterning, leaves fail to grow a blade and stay radial (very narrow and thin like a pine needle). In this study, we wanted to know how patterning the primordium into these two domains controls growth in three dimensions. We also wanted to understand how this process may evolve to produce other leaf shapes, like twisted and curved orchid flowers or the cup-shaped traps of carnivorous plants.

To address this, we studied the expression patterns of dorsal and ventral genes in the traps of the carnivorous plant *Utricularia gibba*. We looked at *PHAVOLUTA* (*PHV*) and *FILAMENTOUS* (*FIL*) genes which are expressed on the dorsal and ventral halves of flat leaves respectively. We found that in traps, *PHV* is expressed on the inside and *FIL* on the outside. This suggests that the inside of the trap corresponds to the dorsal surface of a flat leaf and the outside corresponds to the ventral surface. Next, we looked at this patterning in dome-shaped primordia, before shape differences between flat leaves and traps arise. In flat leaves dorsal and ventral genes are expressed equally in the primordium, dividing it in half. In the traps of *Utricularia,* the dorsal gene *PHV* is expressed in a much smaller domain than the ventral gene *FIL*. Could this explain the difference between making a flat leaf and a cup-shaped trap? To test if a smaller dorsal domain is important for trap formation, we created a *Utricularia* plant where we could induce expression of *PHV* everywhere. This stopped traps forming and replaced them with needle-shaped leaves. This suggests that, like in flat leaves, dorsal and ventral domains control trap growth in the lateral direction. But how do these different gene expression patterns cause different leaf shapes?

To answer this, we used computational models to simulate growing leaves. In our model, the growing leaf is like a continuous elastic volume (like growing playdough) where all points are connected. This simulates real plant cells stuck together in a leaf. Different regions express different genes and these genes control how fast it grows and how much it grows in each dimension. When two regions grow at different rates or in different orientations, the tissue deforms to balance out the differences and makes a new shape. The novel idea in our model is that the boundary between dorsal and ventral genes orients growth throughout the whole leaf. By changing its position and shape plants can dramatically influence the organ's final shape. In the flat-leaf model, dorsal and ventral domains are equally distributed in the primordium, and the boundary lies flat between the two. To generate the blade growth is higher in parallel to the dorso-ventral boundary. This makes the leaf long, wide and thin like a mulberry leaf. When the dorsal domain is reduced in comparison to the ventral, as in the *Utricularia* primordium, the boundary becomes curved. Keeping the same growth rules with this new boundary generates a cup like the *Utricularia gibba* trap.

This work proposes a new mechanism for how dorso-ventral patterning controls leaf shape development and illustrates that new leaf forms can evolve by changing the expression patterns of a common set of genes without affecting their function. We hope that in the future this will be a useful framework to understand the fundamental rules of plant development and evolution.