Flower organ's cells make random decisions that determine size

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The sepals are the outer green leaf-like organs of the *Arabidopsis* flower. Credit: Caltech/Adrienne Roeder

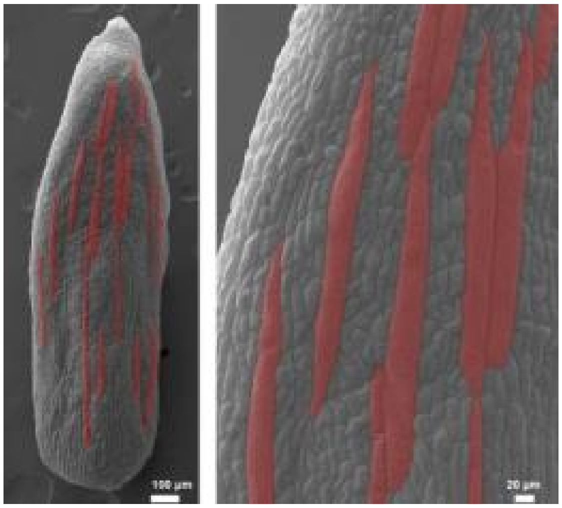
The sepals of the plant *Arabidopsis thaliana* -- commonly known as the mouse-eared cress—are characterized by an outer layer of cells that vary widely in their sizes, and are distributed in equally varied patterns and proportions.

Scientists have long wondered how the plant regulates cell division to create these patterns—in other words, how it decides which and how many cells will be large, which slightly smaller, and which very small.

Melding time-lapse imaging and computer modeling, a team of scientists led by biologists from the California Institute of Technology (Caltech) has provided a somewhat unexpected answer to this question.

"We conclude that probabilistic decisions of individual cells—rather than organ-wide mechanisms—can produce a characteristic and robust cell-size pattern in development," says Elliot Meyerowitz, the George W. Beadle Professor of Biology and chair of the Division of Biology at Caltech.

These findings were published on May 11 in the online journal PLoS Biology.



Scanning electron micrographs of an *Arabidopsis* sepal shows that the outer surface contains cells in a wide range of sizes from the highly elongated giant cells (falsely colored in red) to a variety of smaller cells. Credit: Caltech/Adrienne Roeder

A plant's sepals are the small green leaf-like organs that cup the petals of a flower, enclosing and protecting the flower before it blooms. The outer layer, or epidermis, of the *Arabidopsis* sepal consists of cells of widely varying sizes. These cells range in size from very small to very large; the largest cells are a type found only in the sepals and are dubbed, appropriately, "giant cells."

Each of the four sepals that cup an *Arabidopsis* flower has a unique pattern of cell sizes. What the Caltech-led team wanted to find out was what determines this pattern.

To gain insight into the process, Meyerowitz and Caltech postdoctoral scholar Adrienne Roeder imaged sepals during their early development. They tracked each round of cell divisions to determine how the different cell sizes were created, and what influences their distribution pattern. They then worked with senior postdoctoral scholar Vijay Chickarmane, who had designed a computer model to test the team's hypotheses about how the observed size-related patterning in the sepals comes to pass.

"We started using the live imaging of the sepals to gather data to make a hypothesis about the patterning," Roeder explains. "Then we ran that hypothesis as a model in the computer, to see whether it would give us the patterns we were seeing in the imaging."

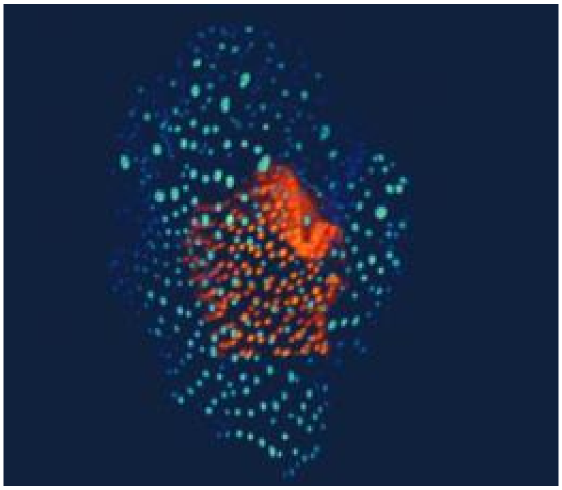
At first, the computer model was unable to produce the patterns found in the actual sepals. So the team tweaked the model until it independently produced the range of cell sizes the team had seen in the living organ.

They found the sepal generates its epidermal cell-size pattern based not on an organ-wide control mechanism, but on when or whether each individual cell decides to divide and on the length of its cell cycle. This sort of random, probabilistic development process results in sepal patterns that not only differ from flower to flower, but from sepal to sepal within an individual flower.

"This is so contrary to our normal way of thinking," says Roeder, "in which we assume that there's always something dictating exactly what each cell is going to do."

Cells in the sepal can undergo one of two growth cycles. The first is normal cell division, in which the cell duplicates its chromosomes and then splits into two smaller cells. The other is a specialized type of cell cycle called endoreduplication, in which the cell duplicates its chromosomes but does not split in two; instead, it simply continues to grow ever larger.

The team's original hypothesis was that "the earlier a cell decides to endoreduplicate, the longer it will have to grow," says Roeder. "And the more endocycles it goes through, the bigger it will get."



To determine how the cell division pattern contributes to cell size in the sepal, an individual sepal was imaged every six hours for 72 hours. The volume rendering of the first time point (0 hours) is shown in orange and of the last time point (72 hours) in green, revealing the growth of the sepal in that time period. Note that the initial sepal has all small nuclei -- indicating that all cells are still dividing -- while the mature sepal has some enlarged nuclei. In that latter group, the cells have stopped dividing and entered endoreduplication to become giant cells.

Credit: Caltech/Adrienne Roeder

For a cell to become a giant cell, she explains, it will generally need to endoreduplicate during its first cell cycle. If it waits a cycle or two to stop dividing, it will have less time to grow, and thus will be a slightly smaller cell. Cells that never endoreduplicate—i.e., cells that continue to divide with each cell cycle—will be among the smallest cells in the sepal.

"Each cell starts out with a chance to become a giant cell," Roeder says. "It's a probabilistic thing; each cell has a certain probability of making that decision. Once it makes the decision, however, its fate is determined."

But endoreduplication isn't the only thing that decides the ultimate size of a sepal cell, the research team found. A cell that endoreduplicates early can grow to be an even larger giant if its cell cycles are longer than average, giving it plenty of growing time.

To prove their point, the team performed a series of experiments in which they altered the levels of cell-cycle inhibitors in the sepal cells. When they decreased the inhibitor—increasing the frequency with which the cell divides, and thus reducing the length of the cell cycle—the sepal cells were unable to grow into giant cells.

"These findings back up our hypothesis," says Roeder. "And when you change the parameters in the computer model, as if you were reducing the level of a cell-cycle inhibitor, the model shows the same pattern."

Understanding exactly how sepal cells decide whether to grow big or small could some day lead to practical applications, Roeder notes. For instance, the utility of various crops as biofuels depends on how much cellulose they contain. A sepal with a large number of giant cells has much less cell-wall surface area than a sepal with lots of smaller cells; since the cell wall is where cellulose is found, giant-cell-laden sepals would be less useful as biofuel.

"This work gives us ideas about how growth happens in these plants," says Roeder. "And once we better understand plant growth and cell division, we can better manipulate them."

Provided by California Institute of Technology

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