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Woody Plant Evolution: Exceptional Lianas Reveal Rules of Woody Growth

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Sometimes the exceptions prove the rule, and lianas show some of the most exceptional stem anatomical variation in plants. New research describes the evolution and development of liana stem anatomical variants, and reveals new rules of woody growth.

Secondary growth is the process of radial, woody growth of plant stems from a cambial meristem. The evolution of secondary growth enabled a range of plant body plan innovations, ranging from massive forest trees that underpin major ecosystems to flexible lianas. But much of what we know about secondary growth and wood formation comes from a handful of model plants that do not encompass the enormous range of developmental and anatomical variation observed among species. Thus, significant questions remain about the development and evolution of secondary growth, including how ancestral mechanisms have been modified to produce the range of extant diversity [1,2]. Lianas are woody vines that display striking diversity in wood anatomy, which enable their flexibility and unique life histories. A new study by Chery and colleagues, published in this issue of *Current Biology*, takes advantage of liana anatomical diversity to examine the evolutionary and developmental origins of diversity of woody growth forms, and to identify basic principles of secondary growth [3].

Secondary growth involves several stereotypical developmental processes that are only partially described at the molecular genetic level [1]. As a stem transitions from elongative, primary growth, regions of meristematic cell division emerge first within the vascular bundles (fascicular cambium) and later in the regions between vascular bundles (interfascicular cambium). These regions of cell division ultimately join to make a unified cylinder of dividing cells that produce wood to the inside of the stem, and secondary phloem (inner bark) towards the outside. Fundamental points of developmental regulation include meristem initiation and maintenance, coordination of fascicular and interfascicular cambia, polarity and patterning of tissues, relative production of xylem vs. phloem, cell type specification, and relative growth rate around the circumference of the stem.

Lianas have developed unusual life histories that exploit the trees within tropical forests to provide mechanical support [4,5]. After an initial phase of self-supporting growth, lianas modify their growth to climbing vine forms after contacting a host tree. This strategy uses the host tree for mechanical support, allowing the lianas to reach high into the canopy to compete for light without growing large bodies themselves. Instead, lianas can make larger investments in reproduction and expansion of their photosynthetic canopies at the expense of the trees they exploit [4]. Key needs for this strategy include the ability to flex and twist without damaging internal tissues, and the ability to transport water and nutrients large distances within a relatively smaller diameter stem [6]. These need are met in part by unique anatomical variants observed among stems of different liana species.

In their new study, Chery and colleagues [3] carefully documented anatomical ontological features of species with *Paullinia*, a large group that includes lianas with different cambial anatomical variants, as well as non-liana species. Cambial variants include a variety of unusual stem anatomies [7] that impart specialized mechanical and

physiological properties to woody stems. Within *Paullinia*, some of the unusual cambial anatomical variants include species that show striking differences in the relative amount of secondary xylem vs. phloem that are produced by fascicular vs. interfascicular cambia, resulting in stems with adjoining sectors of 'phloem wedges' or 'furrowed xylem'. These cambial variants illustrate the semi-independent coordinated development from adjoining meristem types. A more extreme 'compound' stem anatomy presents as a central stem with satellite vascular structures. Compound cambial variants illustrate the ability of cells to acquire meristematic potential and produce a new meristem, as well as how polarity is established within the new structures. An example of a compound cambial variant liana (*P. alata)* is contrasted to a more stereotypical angiosperm anatomy of a forest tree from the genus *Populus* in Figure 1.

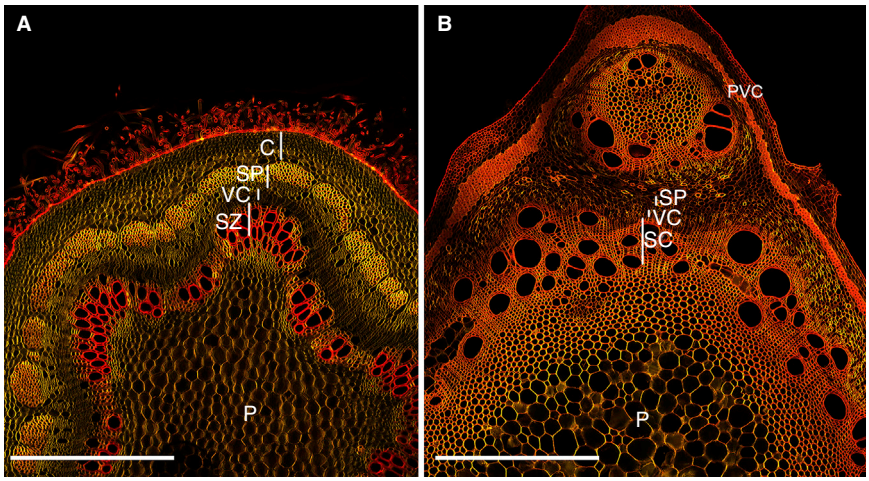

Figure 1. Contrasting stereotypical secondary growth in poplar stems with a liana.
(A) Cross-section of a poplar stem showing a single cambium-producing secondary xylem and secondary phloem. (B) Cross-section of stem from a liana (*Paullinia alata*) that displays a compound stem, which includes the production of peripheral vascular cylinder. C = cortex, P = pith, PVC = peripheral vascular cylinder, SP = secondary phloem, SZ = secondary xylem, VC = vascular cambium. Scale bars = 500μm. Images courtesy of Pakeeza Azizpor.

The strategy of Chery and colleagues [3] was to integrate information from developmental anatomy with comparative phylogenetics to understand the evolutionary origins and developmental trajectories of secondary growth variation within *Paullinia*. One fundamental question the authors addressed was the relationship between apical meristematic growth responsible for elongation of the stem, and the later-occurring secondary growth that increases the stem's girth. They found that an initial angular form of the stem during primary growth potentiates the generation of anatomical variation in later secondary growth. However, not all species with angular primary stems develop a liana habit. This suggests that the anatomical features of the primary stem may be associated with genes or mechanisms that are co-opted in lineages with cambial variants to modify secondary growth. The observation that distinct cambial variants arose multiple times within *Paullinia* strengthens the idea that co-option might underlie such facile evolutionary changes. This is consistent with prior observations that many regulators of primary meristems have been co-opted and are also expressed during secondary growth where they regulate specific developmental functions [8].

In addition to co-option, evidence was also put forward for the addition of developmental processes to extend an ancestral developmental plan to create novelty. This evolutionary process was suggested in the case of *Paullinia* lianas that produce *de novo* cambia outside of the normal vascular cambia, to generate cambial variants known as successive cambia [9]. This addition of development stages is poorly understood in plants, and *Paullinia* could be a system to investigate the underlying molecular genetic mechanisms.

At a more detailed level, it is typically assumed that fascicular and interfascicular cambia in stereotypical secondary growth join and act as a continuous and unified meristematic cylinder. In the lianas, the ability of these cambia to act quasi-independently was revealed. Specifically, in some *Paullinia* species the interfascicular cambium produces elevated amounts of secondary phloem vs. secondary xylem, while the adjacent fascicular cambium produces 'normal' ratios of the two tissues. The resulting anatomy has phloem 'wedges' interspersed around the stem, enhancing flexibility and likely phloem transport and function. This anatomical variant shows that the relative output of the single cell layer ultimately responsible for dividing to produce xylem vs. phloem daughter cells is tightly regulated, and that this process can be precisely varied within an individual plant.

What is next for lianas? In a practical sense, learning more about lianas is of increasing importance, as they are increasing in abundance in tropical forests in response to climate change [10,11]. This is contributing to structural changes that influence carbon cycles of tropical forests, and ultimately the ability of these forests to act as carbon sinks. But as illustrated here, lianas also provide an excellent model system to study the core mechanisms of secondary growth, by understanding the facile evolution and unusual anatomies of these plants. The notion that modular developmental mechanisms have shaped the evolution of anatomical diversity of woody growth has been suggested [12], and the carefully documented anatomical diversity placed within a phylogenetic framework by Chery and colleagues [3] provides the starting work for molecular and comparative evolutionary genomic investigations. Challenges include developing experimental tools and strategies for these unusual plants. But as more is learned about the evolution and development of the exceptional anatomical diversity of these plants, so we will learn about the developmental processes underlying the more stereotypical anatomy of forest trees and other woody plants that underpin major ecosystems and provide us with myriad products and benefits.

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Colour Vision: Self-Centered Fly Photoreceptors Communicate over Distances

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A new study shows that the synaptically interconnected axon terminals of colour-sensitive fly photoreceptors that sample the same point in visual space receive additional inhibition from surrounding units; the resulting additional chromatic comparisons result in an optimal decorrelation of photoreceptor inputs. There are striking parallels between newly identified horizontal interactions and those mediated by mammalian horizontal cells.

The ability to tell apart differently coloured objects solely based on their spectral content and irrespective of their relative intensity is implemented by many visual systems across animal species, be it nectar-collecting honeybees visiting colourful flowers or human art lovers strolling through galleries and museums [1]. In these phylogenetically diverse systems, colour vision emerges via the comparison of outputs from different photoreceptor classes, each containing one specific opsin molecule of defined spectral sensitivity, for instance, short (S), mid (M), and long (L) wavelength cones in humans. Psychophysical and physiological studies in trichromatic primates revealed how these signals are further processed via separated, color-opponent retinal circuits [2].

For instance, a 'yellow-blue' opponency mechanism compares signals of S cones with signals of both L and M cones [1]. The synaptic mechanisms for creating either ON- or OFF-pathways, mediating responses to light increments and decrements, respectively, with receptive fields of a center-surround organization (S-center with L+M surround in the case of 'yellow-blue' opponency) are being characterized in great detail [2]. Importantly, the L+M surround information is provided by GABAergic horizontal cells, thereby shaping the responses of bipolar cells (and ultimately retinal ganglion cells), equipping them with receptive fields where the S center and the L+M surround have opposite signs. It should be noted that horizontal cells even provide direct synaptic feedback inhibition onto cone photoreceptors, thereby directly shaping the response properties of mammalian cone cells [3]. Dissecting the circuitry underlying mammalian colour vision is challenging given the high diversity in cellular subtypes [4], the complex synaptic connectivity at an ultrastructural level [5], and the technical and ethical challenges of working with transgenic primate models [6].

In this issue of *Current Biology*, Heath *et al.* [7] report evidence that axon terminals of stochastically distributed, colour-sensitive photoreceptors of the so-called 'pale' and 'yellow' subtypes in the fruit fly *Drosophila melanogaster* are also inhibited by surrounding units. At first glance, this finding is exciting given the lack of evolutionary conservation between fly and mammalian visual