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Plant Biomechanics: No Pain, No Gain for Birch Tree Stems

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Allometric relationships between organism size and shape are often described in developmental or evolutionary terms. A new study characterizes a collapsing birch tree mutant and provides a genetic entry point into the biomechanical control of tree allometry.

If you were to revisit a tree from your childhood as an adult, you undoubtedly would be amazed at its upward growth. However, it didn't just get taller — it also gained weight from its larger trunk and additional branches. And trees can weigh a lot; South African savanna trees have above-ground biomasses ranging from 10 kg to nearly 10,000 kg [1], while a field in the United States contains pine trees as heavy as 3254 kg [2]. How do trees manage to stay upright under such staggering weight?

A closer inspection of your childhood tree might provide some answers to this question. As trees grow taller, they also become wider and stiffer, presumably in order to support the increasing weight of their trunks [3]. This positive relationship between maximum tree height and maximum basal stem diameter has been mathematically described [4] and experimentally confirmed in many studies for a wide range of tree species (summarized in [5]). Scaling of height and width in trees can be influenced by the hydraulic capacity and mechanical properties of tree stems, as well as by environmental factors like gravity and wind [4,6,7].

Scaling between the height and width of tree trunks is one example of a broad class of biological relationships referred to as allometry. In 1917, D'Arcy Thompson described the effect of size on shape in both plants and animals, and observed that longer (or taller) organisms were necessarily thicker [8] — the term allometry and additional theoretical and experimental details were added later by Huxley [9]. A classic example of evolutionary allometry is the 'mouse-to-elephant curve', which describes the

decrease in metabolic rate with increased body mass across species [10]. Not only do small organisms like mice have faster mass-specific metabolic rates than large organisms like elephants, but there is a precise mathematical relationship between the two parameters. While allometric scaling in trees has been well-documented, the precise mechanism by which it is accomplished is not known. An article in this issue of *Current Biology* provides a genetic entry point into this problem [11].

In this study, Alonso-Serra and colleagues perform the first genetic and cellular characterization of the naturally occurring *Betula pubescens* (downy birch) mutant, *Elimäki Original (eki)*. Clones from the original 70-year-old tree buckle and collapse after only three months of growth. Alonso-Serra *et al.* argue that this dramatic phenotype is due to defective allometry. *eki* stems increase in radius too slowly and unevenly, resulting in trees with weaker stems than wild type trees of the same height (Figure 1A,B). Thus, from a structural perspective, *eki* trees are more likely than the wild type to break when bent — a risk that increases as they grow taller and heavier.

What could explain these phenotypes at the cellular level? One likely culprit is a defect in the production of wood through a process called secondary growth. Just like animals, plants have a vascular system responsible for transporting water and solutes throughout the entire body. The vasculature is composed of channels that run the length of the tree and are made from two types of cells — xylem (which transports water and minerals) and phloem (which transports sugars). During

secondary, or radial, growth, a ring of tissue that runs along the length of the stem called the vascular cambium divides and differentiates to produce a layer of secondary xylem on the inner surface of the ring and a layer of secondary phloem on the outer surface of the ring. The maturation process of secondary xylem involves the production of rigid secondary cell walls, which are added alongside primary cell walls. These secondary cell walls give wood its strength, even after the tree has died, and the combination of secondary growth and wall development provide the size and strength required by trees to support their massive height.

Secondary xylem production is sensitive to increased weight or pressure [12,13] so it seemed possible that this process is disrupted in the *eki* mutants. Indeed, *eki* trees have fewer (and likely smaller) secondary xylem cells at their stem base than wild-type trees (Figure 1C). Furthermore, *eki* stems are weaker in bending tests, an effect the authors attribute to delayed deposition of key components of secondary cell walls. Thus, the collapsing phenotype of *eki* mutants may be due to an inability to properly control secondary growth in scale with increasing height, creating an allometry that is unable to sustain long-term upward growth.

To identify the genetic basis for these phenotypes, the authors grew wild-type and *eki* trees under specific greenhouse conditions that trigger early flowering, thereby reducing the time required for tree breeding. Genome resequencing and QTL mapping of backcrossed trees led to an exciting observation: the collapsing phenotype is linked to a single recessive genomic locus containing only 324 genes.



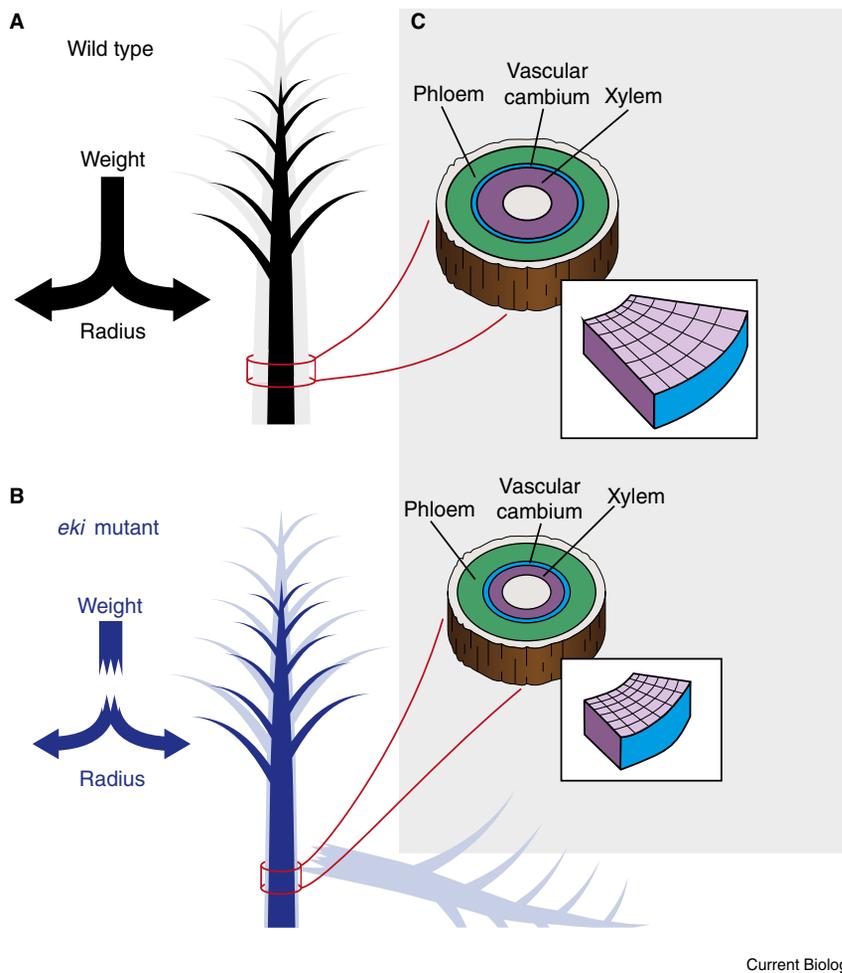


Figure 1. Mechanical allometry control in wild-type and *elimäki* downy birch trees. (A) Vertical growth in trees increases the trunk weight, which scales with increased radial growth of the tree base. (B) The coordination between vertical and radial growth in *eki* mutants is lost, as increases in height, and therefore weight, fail to elicit increases in radial growth. This eventually leads to sudden collapse of the tree. (C) Cross-section of basal stems from wild-type (top) and *eki* mutant (bottom) trees. In *eki* mutants, the region containing secondary xylem cells is reduced (inset), leading to thinner stems at the base.

The authors performed RNA-sequencing to identify genes that were differentially expressed between wild-type and *eki* trees. Some of these differentially expressed genes are also implicated in touch response in *Arabidopsis* [14,15], suggesting that the molecular pathways that mediate a tree's response to a transient mechanostimulus and to a steady increase in loading may have overlapping components. The *EKI* locus, whatever it encodes, must be an essential part of a mechanosensory mechanism that can somehow detect the gradual increase in weight of the trunk and then proportionally promote stem width.

Although Alonso-Serra *et al.* focused on birch trees, their results have interesting

parallels to the mammalian cardiovascular system, where allometric scaling laws for aortic diameter hold across species [16] and are altered by genetic mutations that affect their mechanical characteristics [17]. There are also interesting contrasts between plants and animals — unlike trees, bones require cyclical loading and unloading to build strength [18]. The molecular identity of the *EKI* gene and an understanding of how it controls secondary growth and development of the stem may help reveal the differences and the similarities between allometric scaling mechanisms in trees and in animals.

In summary, this new report identifies a genetic system in birch for the study of

cell and developmental processes that underlie tree allometry. The *eki* mutant exhibits altered allometric scaling of height and width, which can be attributed to a defect in the proper division, expansion and differentiation of xylem cells during wood development. This study thus exemplifies Thompson's original emphasis on the role of physical laws in determining predictable relationships between the size and shape of plants and animals. Your childhood tree has not just grown taller with age, but stronger and more resilient — something we can all strive for.

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Insect Vision: Novel Mechanism for Contrast Constancy in Dim Light

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A general problem of sensory systems is how to simultaneously encode prevailing input as well as deviations from this baseline. A new study shows how the fly visual system has solved this by using parallel processing.

Whether it be a human or an insect, the role of early visual processing is to capture light from the environment and to transform this into neural signals that the brain can interpret. Visual signals are, in their most basic form, light that has reflected off surrounding surfaces and entered the eye. The intensity of this light is called the luminance, and the (temporal or spatial) derivative of luminance is called contrast. We know from years of experimentation that visually guided behaviours often scale in strength as contrast is increased. This is not unique to vision, but is a general principle of sensory systems. The primary benefit of using contrast signals to control behaviour is that they allow sensory systems to encode the large range of stimulus intensities that occur in the real world, within the limited dynamic range of neural signaling [1]. A new study by Ketkar *et al.* [2], reported in this issue of *Current Biology*, elaborates on this view by showing that early visual processing retains luminance information from the environment alongside contrast information.

Contrast constancy ensures that the contrast of a feature remains constant amidst varying levels of illumination. For example, if you read this text printed on a white piece of paper, the contrast of the

text appears to be similar whether you read it outside on a bright, sunny day or inside a comparatively dim room, even if the light intensity reaching your eyes varies enormously between these two scenarios. Contrast constancy is achieved by comparing the current contrast with the mean intensity of the recent past [3]. Because of this comparison with the past, however, contrast constancy begins to fail when the visual system is presented with rapid changes in light intensity. We can experience this ourselves if we try to keep reading this text immediately on entering a dimly lit room after spending time outside in bright sunshine. Over time, however, our visual system adapts to the new lower luminance levels, allowing us to read the text, but until that occurs our contrast sensitivity is impaired [4]. The new work of Ketkar *et al.* [2] suggests that flies may not experience similar problems.

A less extreme example of rapid luminance changes occurs when a fly moves through a natural environment. During its flight, shadows caused, for example, by clouds and trees (Figure 1A) cause the luminance reaching the eyes to fluctuate (Figure 1B). These luminance changes can be described by a temporal contrast profile (Figure 1C). For example,

when the fly moves from a brighter to a darker space, it will experience a negative temporal contrast signal (arrow, Figure 1C). Contrast is important, because features that are important to the fly, including potential predators or food, are often identified by their contrast against the background [5]. There are many ways to quantify contrast, but a commonly used one is the Weber contrast, which subtracts the luminance of the background from the luminance of the object, and divides this difference by the average luminance of the background (Figure 1F). As the denominator reflects the mean intensity of the recent past, a problem arises when the viewer experiences rapid decreases in luminance levels. In this case the denominator is a much larger number than the background against which the object is compared, which if left unaddressed results in contrast underestimation (bottom left, Figure 1G), and therefore a failure to detect prominent visual features.

Flies have a pair of compound eyes, each formed by hundreds of repeating, hexagonal optical units called ommatidia. Light that enters an ommatidium is directed onto photoreceptor cells, which generate a strong contrast-sensitive

