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Morphological plant modeling: Unleashing geometric and topologic potential within the plant sciences

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Abstract

Plant morphology is inherently mathematical. The geometries of leaves and flowers and intricate topologies of the root have fascinated plant biologists and mathematicians alike. Beyond providing aesthetic inspiration, understanding plant morphology has become pressing in an era of climate change and a growing population. Gaining an understanding of how to modify plant architecture through molecular biology and breeding is critical to improving agriculture, and the monitoring of ecosystems and global vegetation is vital to modeling a future with fewer natural resources. In this white paper, we begin by summarizing the rich history and state of the art in quantifying the form of plants, mathematical models of patterning in plants, and how plant morphology manifests dynamically across disparate scales of biological organization. We then explore the fundamental challenges that remain unanswered concerning plant morphology, from the barriers preventing the prediction of phenotype from genotype to modeling the fluttering of leaves in a light breeze. We end with a discussion concerning the education of plant morphology synthesizing biological and mathematical approaches and ways to facilitate research advances through outreach, cross-disciplinary training, and open science. Never has the need to model plant morphology been more imperative. Unleashing the potential of geometric and topological approaches in the plant sciences promises to transform our understanding of both plants and mathematics.

I. Introduction

A. Plant morphology from the perspective of plant biology

The basic morphology of most land plants—sessile, tubular and photosynthetic, with a growing tip from which lateral organs originate and with finely-branched subterranean organs that both anchor the plant and allow uptake of nutrients—has also evolved in other multicellular eukaryotes. A broad definition of "plant" might include all eukaryotes capable of photosynthesis (Niklas, 1997), which within green and red algae traces directly to the

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single primary endosymbiosis event that resulted in the incorporation of a cyanobacterial ancestor of the chloroplast into an ancient eukaryotic cell some one billion years ago. Among the green plants (Viridiplantae), branching shoot-like architectures with leaf-like appendages that are centers of photosynthesis have evolved in both land plants (Embryophyta) and aquatic green algae (Charophyta and Chlorophyta) (Kaplan and Hagemann, 1991). Algal holdfasts and vascular plant roots both anchor plants, but the vascular plant root extends the plant body much deeper into the soil where it also functions in nutrient uptake.

The study of plant morphology interfaces with all levels of biological organization (**Figure 1A**). Plant morphology can be descriptive and typological, as in systematics, focusing on biological homologies to discern groups of organisms (Mayr, 1981; Wiens, 2000). These studies additionally have important applications in agriculture and horticulture, beginning with careful selection of ideal phenotypes. In plant ecology, the morphology of communities, comprised of numerous individuals, defines vegetation types and biomes, including their relationship to the environment. Plant morphology also informs plant physiology, the study of the functions of plants, whereas plant genetics describes the inheritance and, in modern times, the molecular basis of plant morphology (Kaplan, 2001).

Plant morphology is more, though, than an attribute affecting all levels of plant organization; it is also dynamic. Developmentally, morphology reveals itself over the lifetime of a plant through varying rates of cell division, cell expansion, and anisotropic growth (Esau, 1960; Steeves and Sussex, 1989; Niklas, 1994) (**Figure 1B**). Responses to changes in environmental conditions further modulate the abovementioned parameters. Development is genetically programmed and driven by biochemical processes that are responsible for physical forces that change the observed patterning and growth of organs (Green, 1999; Peaucelle et al., 2011; Braybrook and Jönsson, 2016). Physical forces continue to inform plant development, such as the growth of a root through heterogeneous soil densities or the bending of branches and leaves to flows of air or water, long after the initiation and patterning of young primordia (Niklas, 1992; Silk and Erickson, 1979; Vogel,

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1984). Plant morphology evolves through inherited modifications of structure or development, either incrementally or abruptly, over the generations (Niklas, 1997) (**Figure 1C**). A record of these changes over geologic time is preserved and correlates with the paleoclimate, illuminating our understanding of the form and function of extant plants today (Bailey and Sinnott, 1915). Development and evolution are the biological mechanisms through which plant morphology arises, regardless of whether in a systematic, ecological, physiological, or genetic context (**Figure 1**).

B. Plant morphology from the perspective of mathematics

In 1790, Johann Wolfgang von Goethe pioneered a perspective that transformed the way we think about plant morphology: the idea that the essence of plant morphology is an underlying process of deformation, and that seemingly differently shaped leaves and floral organs within a single plant are homologously related (Goethe, 1790; Friedman and Diggle, 2011). The modern challenge that Goethe's paradigm presents is to quantitatively describe deformations in phenotype by their underlying genetic, developmental, and environmental causes. Thus, the fundamental challenge from a mathematical standpoint is how to define shape descriptors to compare plant morphology in the context of a single deformation process; or, how to remove all deformations from the shape that are not relevant to the biological question of interest (Mio and Srivastava, 2004; Lie et al., 2010). A plethora of mathematical approaches, utilizing techniques ranging from geometry and topology to graph theory, exist to describe plant morphology and analyze it with statistical methods.

An important class of shape descriptors detail plant morphology from the perspective of topology (**Figure 2A**). Topological analyses can compare shape characteristics independently of events that deform and transform plant shape geometrically, providing a framework by which plant morphology can be modeled. Algorithms that reduce the branching architecture of plants to a set of intersecting lines or curve segments, constituting a mathematical graph, are an intuitive representation of the plant form. Each curve segment is denoted by an edge, and a vertex denotes a connection. Augmenting each

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vertex with a 3D coordinate results in a skeletal 3D representation of plant architecture derivable from imaging data (Bucksch et al., 2010; Bucksch, 2014a; Aiteanu and Klein, 2014). Such skeletal descriptions are used to derive quantitative measurements of lengths, diameters, and angles (Bucksch and Fleck, 2011; Raumonen et al., 2013; Seidel et al., 2015). Having an architectural description in place allows the definition of orders, either biologically or in a more abstract sense. The relationships between orders, such as degree of self-similarity (Prusinkiewicz, 2004) or nestedness (Godin and Ferraro, 2010) are used to quantitatively summarize patterns of plant morphology.

Computer simulations use principles from graph theory, such as graph rewriting, to define rules successively augmenting a graph with vertices and edges as plant development unfolds. These rules recapitulate the differences observed in plant architectures across plant species (Kurth, 1994; Prusinkiewicz et al., 2001). Morse theory (Milnor, 1963) provides a rich toolset with which to model the morphology of plants. Roughly speaking, a Morse function expands over the plant surface where the "intersection" or contour between the Morse function and plant surface is evaluated during the expansion process. Events such as merging, splitting, appearance, or disappearance of contours provide avenues to quantify relationships between orders. Persistent homology (**Figure 2B-C**) extends Morse theory with functions that deform a given plant shape gradually to define self-similarity (MacPherson and Schweinhardt, 2012) and morphological properties (Edelsbrunner and Harer, 2010) on the basis of event statistics.

In the 1980s, David Kendall defined an elegant alternative statistical framework to the previously introduced topological descriptors that are capable of comparing outlines of shapes independently of scale, rotation, and translation (Kendall, 1984). His idea to compare the outline of shapes in a transformation-invariant fashion infused rapidly into biology (Bookstein, 1997). Furthermore, Kendall's idea inspired the development of methods such as elliptical Fourier descriptors (Kuhl and Giardina, 1982) and new trends employing the Laplace Beltrami operator (Reuter et al., 2009), both relying on the spectral decompositions of shapes (Chitwood et al., 2012a; Chitwood et al., 2012b; Laga et al. 2014).

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From a mathematical point of view, developmental processes construct surfaces in a three-dimensional space. Yet, this space in which development is embedded imposes constraints on plant forms observed. Awareness of these constraints has led to new interpretations of plant morphology (Prusinkiewicz and DeReuille, 2010; Bucksch et al., 2014b) and might explain, at least in part, observations such as symmetry or asymmetry in leaf shape (Martinez et al., 2016).

Parallel to strictly mathematical descriptions of plant morphology, Ronald Fisher developed a statistical framework to partition variance into different sources of variability, whether genetic, developmental, or environmental (Fisher, 1925). Specifically, with respect to plant morphology, the iris flower dataset (Fisher, 1936) was used to develop novel methods to differentiate three *Iris* species based on the length and width of sepals and petals. The dataset is still used to this day as a benchmark to compare statistical methods[1].

In this white paper, we begin by summarizing the history and importance of the inextricable link between mathematical approaches with advances in our understanding of plant morphology. We proceed by outlining emerging questions at the interface of mathematics and plant morphology, focusing on the acquisition of data, modeling, and data-driven questions at all levels of plant organization. We conclude by describing milestones that will signal the further infusion of mathematics into the plant sciences, including integrated curriculums, outreach, and open science.

II. A primer of the history, importance, and potential of mathematics in plant biology

Perhaps because of their intricate topologies, geometries, and iterative growth, the morphology of plants has inspired mathematicians; conversely, the biologist's conception of the plant shape requires a mathematical basis. Below we briefly summarize the rich history and state of the art in quantifying the plant form, mathematical models of

[1] The Iris flower dataset, https://en.wikipedia.org/wiki/Iris_flower_data_set (retrieved September 24, 2016)

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patterning in plants, and how plant morphology manifests dynamically across disparate scales of biological organization and over time.

A. Quantifying plant morphology

1. Capturing the dynamics of plant morphology across time. Techniques to temporally monitor plant development in 3D have been developed that are minimally invasive, allowing the tracking of cell and whole organ morphology, and even plant behavior, over timescales from seconds to days. Confocal microscopy, which eliminates out-of-focus light using a pinhole, can be used to create optical sections of objects and reconstruct 3D models (**Figure 3A**). Variations on confocal technology, such as Spinning Disk Confocal Microscopy (SDCM; Oreopolous et al., 2013) and Light-Sheet Fluorescence Microscopy (LSFM; Maizel et al., 2011; Sena et al., 2011; von Wangenheim et al., 2016), that minimize photo damage of live samples, can be used to understand plant organogenesis using time-lapse imaging.

For example, by comparing cell proliferation rates of complex and simple leaf primordia over time, the patterning of complex leaves in *Cardamine hirsuta* was demonstrated to result from inhibition of growth at the boundary between leaflets (Vlad et al., 2014). Similarly, early morphogenesis of lateral root primordia in *Arabidopsis* (**Figure 3A**) can be temporally modeled by patterns of successive cell divisions (Maizel et al., 2011; von Wangenheim et al. 2016). Cell lineage tracing during leaf organogenesis in *Arabidopsis* allowed for the spatial mapping of variation in growth rate. The formulation of leaf growth as a mathematical model incorporates local variations as a function of ontogenetic time (Kuchen et al., 2012; Tauriello et al., 2015). Such studies demonstrate the power of temporally tracking the origins of plant morphology down to the cellular level, revealing the full, spatio-temporal morphology of plants. As we will discuss later, other technologies can measure the consequences of plant development at grander, emergent scales. Computerized tomography (CT) (**Figure 3B**) and Magnetic Resonance Imaging (MRI) can be used to monitor the growth and morphology of mature organs, while radar, LIDAR, and satellite imaging can monitor ecosystems and global vegetation (**Figures 3-4**).

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2. Morphometrics and allometry: the measurement of shape and size. Once morphological data has been collected, cells, young organ primordia, individual leaves, and roots—and by extension canopies, root systems, and populations—can be described using morphometric approaches. Shape features can be measured by hand, but increasingly machine vision (Wilf et al., 2016) and other automated approaches are used to place landmarks or derive elliptical Fourier descriptors from digital images of plant organs, allowing for statistical and spectral decompositions of shapes, respectively (Iwata et al., 1998; Langlade et al., 2005; Chitwood et al., 2012c; 2013; 2014a; 2014b; 2014c; Rellan-Alvarez et al., 2015). Underlying the shapes of plant organs are differential rates of cell expansion. Cellular expansion rates vary locally and can change rapidly deforming primordia into diverse mature organ morphologies (Rolland-Lagan et al., 2003; Remmler and Rolland-Lagan, 2012; Das Gupta and Nath, 2015). Allometry, or the relationship between shape and size, is a principal consideration when analyzing the factors linking the growth of an organ to its resultant morphology. Just as allometry scales from the cellular to tissue and organ levels, it scales from the individual to population levels, explaining intricate morphologies on a global scale (Duncanson et al., 2015; Huang et al., 2016; Paul et al., 2015).

B. Modeling pattern formation in plants

1. Turing, phyllotaxy, and reaction-diffusion modeling. The beautiful patterns apparent in the regular arrangement of leaves on stems and their connection to mathematics have inspired scientists to create models explaining these phenomena. Alan Turing, a pioneering figure in twentieth-century science, developed a longstanding interest in phyllotaxy, the arrangement of leaves on a plant. Turing's approach to the problem was twofold: first, a detailed geometrical analysis of the patterns (Turing, 1992); and second, an application of his theory of morphogenesis through local activation and long-range inhibition (Turing, 1952). Combining physical experiments with computer simulations, Douady and Couder (1996) subsequently modeled a diffusible chemical produced by developing primordia that would inhibit the initiation of nearby primordia, successfully recapitulating known

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phyllotactic patterns. Such reaction-diffusion systems, which model *de novo* pattern formation as a process resulting from the spatial diffusion and interaction of substances over space and time, can be applied to a wide variety of processes governing plant pattern formation, including stem cell homeostasis and patterning of the shoot apical meristem (Bernasconi, 1994; Meinhardt, 2004; Hohm et al., 2010; Fujita et al., 2011), floral organ number (Kitazawa and Fujimoto, 2015), the regular spacing of root hairs (Meinhardt and Gierer, 1974), and vascular patterning (Meinhardt, 1976). Studies on pattern formation in plants, which originally inspired Turing and other reaction-diffusion modelers, have contributed to universal theories of pattern formation throughout life (Gierer and Meinhardt, 1972; Pearson, 1993).

2. Auxin transport-feedback models of patterning. The plant hormone auxin has been determined (at least in part) to empirically contribute to many of the abovementioned patterning events. Auxin distribution in plants is achieved through complex, transport-feedback mechanisms. In order to understand how a single hormone could produce such diverse patterns in a self-organizing manner, these feedback mechanisms have been extensively modeled with dynamic system techniques (a complete review of auxin transport mechanisms and their role in plant pattern formation is outside the scope of this manuscript, but see Smith and Bayer, 2009). Auxin transport creates discrete patterning events that are inconsistent with the gradients through which morphogens in animals typically act, demonstrating that pattern formation in plants and animals is fundamentally different (Bhalerao and Bennett, 2003). Elegant work combining modeling with experimental verification has demonstrated the role of auxin in diverse plant patterning processes including embryonic patterning (Moller and Weijers, 2009), patterning of the female gametophyte (Pagnussat et al., 2009), vascular patterning (Scarpella et al., 2006; Donner et al., 2009), the patterning of serrations and leaflets in complex leaves (Koenig et al., 2009), lateral root formation (Casimiro et al., 2001), and phyllotaxy (Reinhardt et al., 2003; Smith et al., 2006), among other processes too numerous to list here.

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3. Geometric models of cell division orientation. Plant morphology is determined largely at the organismal level, rather than an emergent property resulting from the collective behavior of cells as in animals (Kaplan and Hagemann, 1991). Yet, as multicellular organisms, cell division and expansion are inextricably linked to plant development (Alim et al., 2012). Several attempts have been made to formulate universal rules predicting the position of cell divisions. In the nineteenth century, Sachs proposed that plant cells divide into two equally sized daughter cells with a division plane at right angles to the pre-existing walls (Sachs, 1878). Leo Errera drew analogies between plant cells and soap bubbles and posited that cells minimize their surface area. The predicted division plane among those cells that respect Sachs' rules is thus the shortest possible (Errera, 1886). Yet, this rule fails to fully account for observed patterns in cell division planes. Bessons and Dumais proposed that the probability for a given plane of division is inversely proportional to the exponential of its length (Besson and Dumais, 2011). Recently, for the *Arabidopsis* embryo, these observations were extended into 3D (Yoshida et al., 2014), in which symmetric divisions occur along a plane predicted by the Bessons-Dumais rule, but asymmetric divisions do not. Inhibition of auxin response causes all cells to divide according to the "shortest wall" rule, suggesting that auxin allows cells to deviate from the default rule.

4. Tensor-based modeling of growth. The pattern of cell walls in a root or shoot meristem follows observable regularities. Two families of orthogonal lines can describe the patterns observed in cell walls: periclines (divisions parallel to a local axis) and anticlines (divisions normal to a local axis) (Sachs, 1878). Attempts to understand the origin of this regularity led to the development of tensor-based models for growth and cell divisions. These models share the underlying assumption of three mutually orthogonal principal directions of growth (PDG) at each point of a growing meristem and the assumption that cells divide in relation to PDGs (Hejnowicz and Romberger, 1984). Several tensor-based growth models have been developed for the shoot apical meristem, the primary root meristem (Hejnowicz and Karczewski, 1993; Nakielski, 2008), and the lateral root (Szymanowska-Pułka and

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Nakielski, 2010; Szymanowska-Pulka et al., 2012). Such models provide a histogenetic link between theories explaining cell division patterns with the morphogenesis of plant organs.

5. Quantifying branching structures. Maybe because of their prominent appearance in everyday life, branching structures are one of the first geometrical forms recognized in plants. Their representation is intuitive because they can easily be reduced to intersecting line segments. A plethora of approaches to reduce imaged branching structures in 2D and 3D to lines or skeletons exist (see Bucksch 2011 and Bucksch, 2014a for an overview). In principle, skeletons let us navigate through a branching structure and take measurements of branch length and diameter. In tree crowns (Bucksch and Fleck 2011; Schilling et al.; 2012, Delagrange et al. 2014), skeletons are a fundamental descriptor towards understanding self-shadowing in tree crowns and measuring biomass allocation over time. Skeletonization methods are also a popular method to quantify the branching architecture of roots, both statically at a single time point (Lobet et al., 2011; Galkovskyi et al., 2012) and dynamically capturing root growth (Symonova et al., 2015).

The beauty and complexity of branch architectures has inspired a rich history of efforts to quantitatively summarize them. One of the earliest efforts by Leonardo da Vinci described allometric laws in the branching of tree crowns. Da Vinci quantified the hierarchical relationships between diameters and length of branches (Long, 1994; Eloy, 2011), a phenomenon later similarly observed in tree roots (Oppelt et al., 2001). Biologists visually observed these underlying laws and created classes of tree architecture, noting, "trees in the forest rarely exist in the ideal state …" (Halle et al., 1978). Quantitatively revealing the "ideal state" of tree architecture has consumed researchers for over four decades. Early fractal approaches to capture the repetitive and modular appearance of branching structures are described in Henry Horn's pioneering book *The Adaptive Geometry of Trees* (Horn, 1971), which inspired researchers for decades (Borchert and Slade, 1981; Zeide and Pfeifer, 1991, Valladares, 1999; Godin and Ferraro, 2010). In turn, this view of a genetic mechanism driving the developmental program of tree architecture has been realized computationally (Palubicki, 2013), simulating the development of tree architectures

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(Runions et al., 2007; Palubicki et al., 2009). Equivalently, functional-structural root models simulate the efficiency of nutrient and water uptake following the development of roots (Nielsen et al., 1994; Dunabin et al., 2013).

C. Dynamic interactions of morphology between biological scales, with the environment, and over time

1. Kinematics. Although we have already discussed time-dynamic models of plant morphogenesis and cellular division patterns above, the emergent morphologies that arise from cells, tissues, and organs interact with the surrounding environment in functional ways. For example, in roots there are three developmental zones starting at the tip that propel cells through the soil medium: 1) the meristematic zone, where cells are actively proliferating; 2) the elongation zone, where cells stop dividing and begin to expand; and 3) the differentiation zone, where cells acquire their terminal cell fate (Barnes, 1898). Root growth is controlled by both displacement via production of new cells (meristematic zone) and expansion of existing cells (elongation zone). Describing a growth system with both expanding and contracting components is a challenge. One approach to solve this problem, pioneered by Wendy Silk (Silk and Erickson, 1979; Silk, 1984), is to adopt the formalism of compressible fluid dynamics to describe plant growth in terms of kinematics. This approach treats the plant "fluid" as a continuous medium, neglecting molecular-scale heterogeneity. Considering the root as a homogenous fluid (which is theoretically supported, if land plants are considered to be giant, single-celled organisms; Kaplan and Hagemann, 1991; Coneva and Chitwood, 2015), this approach can be applied to questions such as the relationship between water potentials and roots growth (Sharp et al., 1988; 1990) and the allometric growth of leaves (Bernstein et al., 1993; 1995).

2. Plant-wind interactions. While conceptualizing the root as a homogenous fluid can be a useful simplification, the reality is that plants—the terrestrial Embryophyta and aquatic Charophyta and Chlorophyta—live within currents of air and water. Work from Steven Vogel and Laura Miller views the architecture of plants from the perspective of their fluid

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dynamic properties (Vogel, 1970; 1989; 1992; 2009; Miller et al., 2012). Plants that live in mechanically extreme environments, such as those with frequent hurricanes, strong winds, and tornados, appear to be better adapted to resist wind forces. Plant architecture is modified at all levels to reduce the drag that acts on a plant and avoid resonant forcing in addition to structural reinforcements of the trunk and roots. Even at low wind speeds, exchange through leaf and petiole designs that augment passive movements in the wind, such as leaf flutter, may be physiologically relevant (Schuepp, 1972; Grace, 1978; Roden and Pearcy, 1993; Roden, 2003). Regardless of whether a plant lives in environments with frequent winds, the morphology of plants must reckon with other fluid dynamic effects, such as the boundary layer (Schuepp, 1993). The effects of leaf size on the boundary layer are well-known, influencing transpiration losses, the diffusion of photosynthetic gases, and heat dissipation (Parkhurst and Loucks, 1972). In addition to shape and size, plant morphology at finer scales, including epidermal features such as trichomes and wax deposition, may influence the boundary layer and therefore plant fitness. Later, we detail models of plant-fluid interactions in depth.

3. Leaf shape and the paleorecord. Plant morphology responds dynamically to turbulent environments and can plastically respond, developmentally, to subtler changes. But what is the relationship between plant morphology and geologic time? Ultimately, the shape of leaves is subject to selection pressures from a variety of sources, whether the influence of high winds, herbivory, thermoregulation, or light interception. Plant morphology may be constrained by hydraulic, biomechanical, developmental, or phylogenetic effects (Nicotra et al., 2011). Any one of these factors—and other unknowns—can create patterns observed in both extant and fossil leaf assemblages (Chitwood and Sinha, 2016).

Larger leaves, with fewer and less pronounced serrations, predominate in warmer, wetter climates whereas smaller leaves, with larger and more numerous serrations, tend to be found in colder, drier temperate environments (Bailey and Sinnott, 1915). This fundamental relationship between leaf dissection with temperature and precipitation has been demonstrated across geographies and in different phylogenetic groups, although

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often the correlation differs or is more or less robust depending on context (Wolfe, 1979; 1993; Wing and Greenwood, 1993; Wilf, 1997; Wilf et al., 1998; Huff et al., 2003; Jacobs and Herendeen, 2004; Royer et al., 2005; Spicer et al., 2009; Peppe et al., 2011). Plasticity in leaf shape during the lifetime of an individual plant correlates with temperature and precipitation similarly to the fossil record, demonstrating parallels in the morphological response of plants to changes in environmental conditions over developmental and evolutionary timescales (Royer et al., 2009; Chitwood et al., 2016). Measuring plant morphology in evolving populations provides insights into adaptive versus neutral features (Moyle, 2008; Nordborg and Weigel, 2008; Brachi et al., 2011), revealing insights into the relationship between morphology and function (Wright et al., 2004).

III. Emerging questions and barriers in the mathematical analysis of plant morphology

A true synthesis of plant morphology, comprehensively modeling observed biological phenomena and incorporating a mathematical perspective, remains out of reach. In this section we highlight the challenges facing the study of plant morphology, including the limits of acquiring morphological data, phenotype prediction, responses of plants to the environment, integrating models across biological scales, and the modeling of complex phenomena that remain elusive, such as the reconfiguration of plant architecture to gale force winds.

A. Technological limits acquiring plant morphological data

Before the invention of digital photography in 1969 (Smith, 2010), the measurement of plant architecture was a manual process performed directly on the plant or using traditional photographs (Atkins, 1843; 1853). Describing morphology at smaller anatomical or cellular scales involved qualitative descriptions, sketches, and the use of camera lucida to faithfully record the perceptions of the researcher (von Nägeli, 1863). Digital imaging devices enabled the shape of plants to be captured on all biological scales in

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2D and 3D. The most accessible scale is plant architecture. In general, technology to record plant architecture produces two kinds of data: surface samples and volumetric data. Stereovision data are generated from different views of 2D digital images (Boyde, 1973; Dumais and Kwiatkowska, 2002). Through matching of identical features, a spatial alignment of the images is computed that allows the calculation of depth information.

Time of flight scanners, such as terrestrial laser scanning, overcome unit-less measurement by recording the round-trip time of hundreds of thousands of laser beams sent at different angles from the scanner to the first plant surface within the line of sight (Vosselman and Maas, 2010) (**Figure 4**). The constant speed of light allows the calculation of the distance between the point hit on the plant surface and the laser scanner. Both stereovision and laser scanning produce surface samples or point clouds as output. However, both face algorithmic challenges if plant parts occlude each other, as both rely on the reflection of waves from the plant surface (Bucksch, 2011).

Penetrating the plant surface to resolve occlusions is possible with X-ray and magnetic resonance imaging (MRI). While both technologies circumvent occlusions and can even penetrate soil, their limitation is the requirement of a closed imaging volume. X-ray systems rely on the principle that different tissues and materials absorb different amounts of X-ray radiation (Kumi et al., 2015.) (**Figure 3B**). A detector plate records the remaining X-ray radiation. If X-ray images are taken from various angles around the plant, then a 3D model can be reconstructed from the absorption levels. The field produced with two cylindrical magnets defines the imaging volume of an MRI (van Dusschoten et al., 2016). The hydrogen molecules of the plant align with the field of the first magnet. Creating a second magnetic field causes a detectable change in hydrogen alignment, from which the 3D structure of a plant can be reconstructed. The resulting data are voxels that encode the local hydrogen density as an intensity value. Both surface-penetrating imaging technologies intrinsically limit the imaging volume, either by the need of a detector plate or the closed cylinder needed to establish a magnetic field. Thus, MRI and X-ray are destructive if applied

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to mature plant organs such as roots in the field or tree crowns that are larger than the imaging volume (Fiorani et al., 2012).

Radar provides another non-invasive technique to study individual tree and forest structures over wide areas. Radar pulses can either penetrate or reflect from foliage, depending on the selected wavelength (Kaasalainen et al., 2015). Most radar applications occur in forestry and are being operated from satellites or airplanes, although more compact and agile systems are being developed for precision forestry above- and below-ground (Feng et al., 2016).

B. The genetic basis of plant morphology

One of the outstanding challenges in plant biology is to link the inheritance and activity of genes with observed phenotypes. This is particularly challenging for the study of plant morphology, as both the genetic landscape and morphospaces are complex: modeling each of these phenomena alone is difficult, let alone trying to model morphology as a result of genetic phenomena (Benfey and Mitchell-Olds, 2008; Lynch and Brown, 2012; Chitwood and Topp, 2015). Although classic examples exist in which plant morphology is radically altered by the effects of a few genes (Doebley, 2004; Clark et al., 2006; Kimura et al., 2008), many morphological traits have a polygenic basis (Langlade et al., 2005; Tian et al., 2011; Chitwood et al., 2013; 2014b). Two approaches to link genotype to phenotype for complex traits are quantitative trait loci (QTL) analysis and genome wide association studies (GWAS). Both approaches identify statistical associations between genetic variants and phenotype, the former usually through a controlled cross and the latter often relying on historical recombination and linkage disequilibrium (Flint-Garcia et al., 2003; Meyer and Purugganan, 2013).

QTL analyses for plant morphology span scales from the cellular to the whole organ level. At the cellular level, root cortex cell number (Ron et al., 2013), the cellular basis of carpel size (Frary et al., 2000), and epidermal cell area and number (Tisne et al., 2008) have been

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analyzed. The genetic basis of cellular architecture ultimately affects organ morphology, and quantitative genetic bases for fruit shape (Monforte, et al., 2014; Paran and van der Knaap, 2007), root architecture (Zhu et al., 2005; Clark et al., 2011; Topp et al., 2013; Zurek, et al., 2015) and leaf shape (Langlade et al., 2005; Ku et al., 2010; Tian et al., 2011; Chitwood et al., 2013; 2014a; 2014b; Zhang et al., 2014; Truong et al., 2015) have been described. Increasingly, studies are linking the effects of cell shape and organ morphology to pleiotropic effects on plant architecture. Thompson et al. (2015) link shoot apical meristem (SAM) shape to adult plant traits such as leaf shape, flowering time, and yield. Similarly, high-throughput image processing of the SAM in a diverse panel of maize inbreds has uncovered candidate genes involved in hormone transport, cell division, and cell size that correlate the morphology of the meristem with SNPs residing within candidate genes (Leiboff et al., 2015).

Natural variation in cell, tissue, or organ morphology ultimately impacts plant physiology. For example, root cortical aerenchyma formation reduces the metabolic costs of soil exploration, thereby improving plant growth under conditions of suboptimal availability of water and nutrients (Zhu et al. 2010; Postma and Lynch, 2011; York et al., 2013; Lynch et al., 2014; Lynch, 2013; 2015, Chimungu et al. 2015). Maize genotypes with greater root cortical cell size or reduced root cortical cell file number also have reduced metabolic costs, and therefore deeper rooting and increased water capture under drought (Chimungu et al., 2014a; 2014b). The radial distribution of auxin in the rice root leads to differential cell expansion and more vertical root angles, resulting in greater water capture in drying soils. The genetic basis of this effect was mapped to *DRO1* (Uga et al., 2013), and exemplifies how the control of cellular organization by a single gene can have profound effects at the organismal level and the interaction of plants with their environments.

High-throughput phenotyping techniques are increasingly used to reveal the genetic basis of natural variation. In doing so, phenotyping techniques complement classic approaches of reverse genetics and often lead to novel insights even in a well-studied species like *Arabidopsis*. Such techniques reveal a genetic basis for such dynamic traits as root growth

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(Slovack et al., 2014) and by studying the genetic basis of cellular traits can reveal the developmental genetic basis of root architecture (Meijón et al., 2014). Similarly, high-resolution sampling of root gravitropism has led to an unprecedented understanding of the dynamics of the genetic basis of plasticity (Miller et al., 2007; Brooks et al., 2010; Spalding and Miller, 2013). Molecular technologies, such as next-generation sequencing, also provide a mean for the high-throughput determination of the genetic basis of molecular traits. eQTL analysis (gene expression QTL) reveals the genetic basis of tens of thousands of transcript abundance levels (Jansen and Nap, 2001; Druka et al., 2010). Such an approach demonstrates that single loci with profound pleiotropic effects on plant architecture, such as *ERECTA* in *Arabidopsis*, can influence the expression of numerous genes in the genome (Keurentjes et al., 2007). The genetic basis of gene expression can be linked to QTL affecting plant morphology (Majewski and Pastinen, 2011; Chitwood et al., 2013; 2014b; Anderson et al., 2014; Ranjan et al., 2016), providing yet another genetic link between emergent levels of organization.

C. The environmental basis of plant morphology

Phenotypic plasticity is defined as the ability of one genotype to produce different phenotypes based on environment (Bradshaw 1965; DeWitt and Scheiner, 2004) and adds to the phenotypic complexity created by genetics and development. This produces both challenges and opportunities for mathematical modeling. Trait variation in response to the environment has been defined classically using reaction norms (originally "Reaktionsnorm") where the value of a certain trait is plotted against different environments (Woltereck, 1909). If the reaction norm line is flat, the trait is not plastic; if the reaction norm varies across the environment the trait is plastic and the slope of the reaction norm line will be a measure of the plasticity. Significant differences in slopes among genotypes indicate a GxE interaction (Via and Lande, 1985). If a certain trait in one genotype remains constant in contrasting environments, the trait is said to be canalized (Waddington, 1953).

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Seminal work by Clausen, Keck, and Hiesey (1941) demonstrated using several clonal species in a series of reciprocal transplants that although heredity exerts the most measureable effects on plant morphology, environment is also a major source of phenotypic variance. Research continues to explore the range of phenotypic variation expressed by a given genotype (phenotypic plasticity + developmental noise) in the context of different environments, as this has important implications for many fields, such as conservation, evolution, and agriculture (Nicotra et al., 2010; DeWitt, 2016). Many studies examine phenotypes across latitudinal or altitudinal gradients, or other environmental clines, to characterize the range of variation possible and its relationship to the environment (Cordell et al. 1998; Díaz et al., 2016). Community effects are also essential to understanding the origins of plant morphology, and there has been increased interest in the role of biotic effects such as hybridization, pathogens, shading, and crowding (Nicotra et al., 2010; Holeski et al., 2012; Atlan et al., 2015), as well as abiotic contributors such as nutrient availability (Dorken and Barrett, 2004), to plasticity.

Many plastic responses by plants to the environment are conserved and have been studied in detail from the molecular to ecological levels. One such example is phototropism: plants can sense the direction of illumination and grow towards it (Briggs, 2014). Another example of shoot environmental plasticity is neighbor detection and shade avoidance (Casal, 2013; Schmitt et al., 2003). Light transmitted through or reflected from leaves has a unique spectral signature that plants use as a cue for incipient or ongoing photosynthetic competition. In response to neighbor shade, some plants make striking morphological changes to compete for light. Elongation of stems and petioles can increase two-fold or more. This increase in stem elongation comes at the expense of allocation to laminar outgrowth of leaves and fruit and seed set. Additionally, plants undergoing shade avoidance show increased apical dominance (reduced branching) as growth upwards is favored over growth outwards to reach light before competitors. Understanding the molecular basis of the shade avoidance response has implications for agriculture. Improvements are anticipated through manipulation of resource allocation in competition

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scenarios of neighboring plants at high planting densities versus crop production standards (Carriedo et al., 2016).

Below ground, plants encounter diverse sources of environmental variability, including water availability, soil chemistry, and physical properties like soil hardness and movement. These factors vary not only between individual plants (Razak et al., 2013), but within an individual root system, to which plants respond in diverse ways (Drew, 1975; Robbins and Dinneny, 2015). Plasticity at a micro-environmental scale has been linked to developmental and molecular mechanisms (Bao et al., 2014). The scientific challenge is here to integrate these effects at a whole root system level to understand the optimal acquisition in resource limited conditions (Rellan-Alvarez, et al., 2016) (**Figure 5**).

D. Integrating models from different levels of organization

Most of the mathematical models highlighted in the previous sections have been designed independently to study plant development at specific spatial and temporal scales. Since it is extremely difficult to examine complex interdependent processes occurring at multiple spatio-temporal scales, mathematical modeling can be used as a complementary tool with which to disentangle component processes and investigate how their coupling may lead to emergent patterns at a systems level (Hamant, 2008; Band and King, 2012; Jenzen and Fozard 2015; Band et al. 2012).

A detailed multiscale model may involve hundreds of variables and parameters. It is likely that the exact values of most parameters will not be known, nor even identifiable. Thus, to be practical, a multiscale model should generate well-constrained predictions despite significant parameter uncertainty (Gutenkunst et al., 2007, Hofhuis et al., 2016). It is desirable that a multiscale model has certain modularity in its design such that individual modules are responsible for modeling specific spatial aspects of the system (Baldazzi et al., 2012). Global sensitivity analysis can be applied to reveal how individual modules function when other modules are perturbed (Sudret, 2008). Most importantly, a multiscale model

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must be tested against available data. An important future problem in plant mathematical biology is how to integrate existing mathematical models that describe plant morphogenesis at different spatial scales (Hill et al., 2013).

It is a useful exercise to illustrate the challenges of integrating models at the molecular and cellular levels with an example. At the molecular scale, mathematical models describe the spatiotemporal dynamics of key biomolecules and phytohormones controlling the function and fate of individual cells. Some of these biomolecules can be diffusive, but others, such as membrane-bound receptors, may be spatially localized (Battogtokh and Tyson, 2016). The distribution of molecules in the cell i (i=1..N) can be described by a system of partial differential equations, $\frac{dX_i}{dt} = f(X,\mu) + D_X \sum_{j=neighbors}(X_j - X_i)$, where the components of X are the levels of biomolecules in a given cell, the nonlinear functions f describe the kinetics of the reactions between the molecules, μ is the set of model parameters, DX is a diagonal matrix of diffusion coefficients, N is the number of the cells, and the sum in the last term is for the diffusion of the biomolecules between the cells (Fujita et al., 2011).

At the cellular scale, mathematical models describe dynamics of cell networks where the mechanical pressures exerted on the cell walls are important factors for cell growth and division (Jensen and Fozard, 2015) (**Figure 6A**). In models describing plant development in a two-dimensional cross-section geometry, cells are often modeled as polygons defined by walls between neighboring cells. The spatial position of a vertex, where the cell walls of three neighboring cells coalesce, is a convenient variable for mathematical modeling of the dynamics of cellular networks (Prusinkiewicz and Lindenmayer, 2012). A given vertex is driven by the sum of forces acting on it, the turgor pressures from the neighboring cells, and the elastic forces exerted on the cell walls. Thus, the time evolution of the vertex j located at the position x can be described by the dynamic equation: $\frac{d^2X_j}{dt^2} = F_j$, where Fj is the total force acting on the vertex j. By numerically integrating the dynamic equations for the positions of all the vertexes in the polygonal cells, the dynamics of the cell network can be simulated. Additionally, certain rules can be adopted for cell division (Besson and

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Dumais, 2011), which may depend on the size of a cell (Fujita et al., 2011), on its location in the network (Prusinkiewicz et al., 2001), and on the local levels of hormones and biomolecules (Dello Ioio et al., 2008).

A multiscale model can be assembled by combining the models at molecular and cellular levels. Such a model allows the computation of spatiotemporal dynamics of biomolecules X for realistic initial and boundary conditions on the dynamic cellular networks. Mutations and deletions of the genes encoding the biomolecules can be modeled by changing the parameters, or by modifying the reaction terms in the function f. By inspecting the effects of such modifications on the dynamics of cellular networks, the relationship between genotypes and phenotypes can be predicted. In the aforementioned model by Fujita et al. (2011), the biomolecules X describe the dynamics of the proteins involved in the stem cell regulation of the SAM in *Arabidopsis*. It can simulate SAM development in wild type and mutant plants, demonstrating how integrative models can be valuable tools in predictive modeling of plant development (**Figure 6B**).

E. Modeling the interaction between plant morphology and fluid dynamics

Modeling plant morphology is a complicated endeavor, but the forces that interact with plants, such as currents of wind and water, are sometimes even more complex and affect the development and evolution of plant architecture. Smaller scale airflows around plants can affect plant health as much as gale force winds, but are determined by plant morphology at an exquisite level of detail. For example, how does vegetation density affect average flow speeds within complex canopies and how do the dynamics of the airflow affect the movement of the trunks, stems, branches, and individual leaves? Simulating flow on scales that span the individual leaf to the entire canopy are not currently feasible but nonetheless critical for understanding plant morphology. Below, we highlight efforts to model the interaction of currents with plant morphology at two extreme scales—light breezes and gale force winds.

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1. The role of light breezes in cooling and gas exchange. Leaf shape and material properties that alter the boundary layer of the fluid over the surface of the leaf or enhance passive movement can potentially augment gas and heat exchange. For example, it has been proposed that the broad leaves of some trees flutter for the purpose of convective and evaporative heat transfer (Thom, 1968; Grant, 1983). Fluttering may also allow more light to penetrate the canopy (Roden and Pearcy, 1993).

One way to quantify the relative importance of advective and diffusive transport rates is by using the Peclet number. The Peclet number is given as Pe = UL/D, where U is a velocity, such as wind speed, L is a length, such as the length of the leaf, and D is the diffusivity of the quantity of interest (heat, O_2, CO_2, etc.). If Pe << 1, then the transport of the heat or chemical gradient is dominated by diffusion. If Pe>>1, then the movement of chemicals and the dissipation of heat is dominated by advection. Note that diffusive transport alone is a relatively slow process.

The morphology and movement of leaves change the boundary layer near the surface, and subsequently alter the relative importance of advective and diffusive transport represented by the Peclet number. Boundary layers describe the fluid layers close to surfaces in which the flow of air or water approaches zero. Note that for any viscous fluid, the velocity of air at a surface relative to the velocity of the surface itself is always zero. This is called the no-slip condition. Diffusive transport is typically dominant very close to surfaces, and advective transport dominates farther from surfaces.

The morphology and mechanical properties of leaves can alter the boundary layer. For example, trichomes, the hair-like protrusions on the surfaces of leaves, can effectively thicken the boundary layer around a leaf under some conditions (Benz and Martin, 2006). Denser or longer trichomes that increase the boundary layer may decrease rates of heat dissipation, evaporation, and gas exchange. Other configurations of trichomes may increase turbulence in the boundary layer and increase gas exchange and heat dissipation (Schreuder et al., 2001). Furthermore, any movement of the leaf relative to the movement

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of the air or water may, in some cases, act to decrease the boundary layer and increase gas exchange, evaporation, and heat dissipation (Roden and Pearcy, 1993). Each of these parameters may be altered by the plant to improve the overall function of the leaf (Vogel, 2012).

2. Effect of extreme winds and currents on broad leaves. Plants use flexibility as one strategy to reduce the drag acting upon them while simultaneously avoiding the violent oscillations observed in many bluff structures subjected to strong winds. Vogel (1989) was the first to provide quantitative data on drag reduction in plants. He found that single broad leaves reconfigure at high flow velocities into cone shapes that reduce flutter and drag when compared to paper cut-outs of similar shape and flexibility (**Figure 7A-B**). He later found that a similar phenomenon occurs in water for herbaceous plants and proposed that this mechanism increases survival rates in flash floods (Vogel, 2006). Subsequent experimental studies on broad leaves and flowers also support rapid repositioning in response to strong wind as a general mechanism to reduce drag (Niklas, 1992; Ennos, 1997; Etnier and Vogel, 2000), and simple mathematical models of a flexible beam immersed in a two-dimensional flow exhibit similar behavior (Alben et al., 2002). At the larger scale, Vogel (1989) noticed that leaf clusters and leaflets tend to reconfigure into larger drag reducing structures and speculated that a similar phenomenon is also true for groups of branches (**Figure 7C**).

Passive reconfiguration of flexible structures in strong flows are prevalent throughout the natural world (Vogel, 1994). One key feature that is important to drag and flutter reduction is the shape of the reconfiguration. A wide range of broad leaves reconfigure into cone shapes as both single leaves and clusters (Vogel, 1989; 2006). The branches and fronds of flexible trees such as palms and willows appear to reconfigure into grouped conical shapes in strong winds and hurricanes. The daffodil *Narcissus spp.* (Etnier, 2000) and sessile marine organisms such as sea anemones (Koehl; 1977a; 1977b) reconfigure into cone shapes through deformations of the petals or tentacles, respectively. Previous work has shown that the cone shape is significantly more stable than other reconfigurations such as

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U-shapes (Miller et al., 2012). The folding of the leaves and the interactions of surfaces are critical to determining the shape of the reconfiguration and its stability (**Figure 7**).

Of course there are likely other strategies that may be used in place of, or in addition to, conical reconfigurations. For example, Gosselin and de Langre (2011) showed how plants such as pines may act as a poroelastic structures to reduce drag. As mentioned in the previous section, there may also be situations in which flutter reduction is not desirable. In these cases, conical reconfiguration may not be present at wind speeds relevant to cooling and light transfer (0–4.5 m/s) when flutter could enhance these mechanisms.

Some plants also use active reconfiguration in flow. Plant responses to a mechanical stimulus, known as a thigmonastic movement, are thought to be regulated by electrical signal transduction. These electrical signals are action potentials that share many of the same properties as those that occur in animals (Bose, 1926; 1928; Volkov, 2000; 2006). In the case of the touch-me-not, *Mimosa pudica*, action potentials are generated as a result of various stimuli such as touch, heat, electrical voltage, or wind. The electrical signal is spread from the point of stimulus to the pinnae, petiole or stem (Bose, 1926; 1928) and will result in the folding of the pinnae and the collapse of the petiole or stem. The action potential generated from a weak stimulus will stop at the base of a single pinna so that the leaflets from neighboring pinna remain unfolded (Volkov et al., 2010). These movements are generated by motor organs called pulvini that consist of swollen joints.

Although it is now clear that flexible plants can reduce drag through reconfiguration, it is not at all obvious how leaves and leaf clusters minimize the effects of vortex induced oscillations. Previous work suggests that structural damping and stiffness nonlinearities (Niklas, 1992; Bruchert et al., 2003; Miller, 2005) may reduce these destructive oscillations, but this complex fluid-structure interaction problem remains relatively unexplored. The study of vortex induced oscillations is also a significant area of research in structural dynamics, and it seems likely that work in both fields may inform the other. In human-made structures, improvements have been made by modifying the cross sectional shapes

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and material properties of cables and other support structures to avoid self-excitation through vortex shedding (Wilson, 2003; Tomita et al., 1988; Luongo and Piccardo, 1998). Improving the stability of large flexible structures, such as banners and flags, in strong winds remains problematic.

IV. Milestones to accelerate the infusion of math into the plant sciences

Despite the rich history of integration between mathematics and plant biology, sadly many members of each discipline remain uninformed about the other. Mathematical modeling has provided foundational insights into plant biology, but until recently, only a minority of plant biologists have become versed in math, and even if quantitative, the expertise of plant biologists is often limited to programming, computation, and statistics. Reciprocally, mathematicians are often unaware of the tremendous empirical theory that plant biologists have developed and lack the perspective of their biological training, limiting their contributions to the plant sciences. Both mathematics and plant biology are timely disciplines, especially in a world ever increasingly geared towards a quantitative mindset and with dwindling natural resources. Both disciplines need to be emphasized more in early education and come together through opportunities to interact, including workshops, meetings, and funding opportunities. Both fields can immediately benefit from more open approaches to science.

A. Education

The accuracy of mathematics in helping to understand the "reality" of biological processes depends on how well the hypotheses supporting the definition of models fit with the real world (May, 2004). A modeling perspective is itself one of the principal advantages that integrating mathematics into plant science curriculums has to offer. Mathematics has been likened to "biology's next microscope", because of the insights into an otherwise invisible world it has to offer. Conversely, biology has been described as "mathematics' next physics", stimulating novel mathematical approaches because of the hitherto unrealized

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phenomena that it studies (Cohen, 2004). The scale of the needed interplay between mathematics and plant biology is enormous and may lead to new science disciplines at the interface of both: ranging from the cellular, tissue, organismal, and community levels to the global; touching upon genetic, transcriptional, proteomic, metabolite, and morphological data; studying the dynamic interactions of plants with the environment or the evolution of new forms over geologic time; and spanning quantification, statistics, and mechanistic mathematical models. It is important to remember that teaching this new synthesis is not as simple as educating students with "naïve" minds. Rather, curriculums must be tailored in such a way that students are competent to understand the skillsets they lack to tackle specific problems or attain more nuanced understanding of phenomena (Gross, 2004). Or to put this another way, students need to be taught how they can understand the limitations of their own knowledge.

The new age of research is becoming increasingly interdisciplinary and undergraduate, graduate, and post-graduate groups are actively trying to fix the archaic separation between mathematics and biology skillsets. While many graduate programs have specialization tracks under the umbrella of mathematics or biology-specific programs, more frequently departments are forming specially designed graduate groups for mathematical biology. Plant biology professors and researchers at the postdoctoral level need to reach out to these programs at their schools. We encourage researchers at the principal investigator and post-doctoral level to become more active in departments with their university that house young researchers being trained in these programs. Recruitment of students from these programs takes advantage of the inherent desire to pursue mathematics and biology-focused research. Since one of the main problems separating fields is each field learning the jargon of the other (Oleana, 2014), guest lectures in courses within these new graduate programs would introduce how each field approaches research. The most powerful way to connect mathematics and plant biology is to first acknowledge our presence to this emerging pool of young researchers.

B. Citizen science, the maker movement, and public outreach

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Citizen science, which is a method to make the general public aware of scientific problems and employ their help in solving them[2], is an ideal platform to initiate a synthesis between plant biology and mathematics because of the relatively low cost and accessibility of each field. A variety of research fields have successfully implemented citizen science and gamification approaches, including astronomy[3], animal biology[4], and cell biology[5].

Arguably, using citizen science to collect plant morphological diversity has already been achieved, but has yet to be analyzed fully. In total, it is estimated that the herbaria of the world possess greater than 207 million voucher specimens[6], representing the diverse lineages of land plants (and often algae as well) collected over their respective biogeographies over a timespan of centuries. Both herbaria and living collections of botanic gardens are dynamic. Although plant collecting is in decline, it is an active discipline and voucher submissions to herbaria should be encouraged (Prather et al., 2004). Botanic gardens not only possess living collections, but more than ever they spearhead bio-conservation efforts to ensure plant diversity exists in the future to be studied (Schatz, 2002). Digital documentation of the millions of vouchers held by the world's botanic gardens is actively underway, allowing for researchers and citizens alike to access and study for themselves the wealth of plant diversity across the globe and centuries (Smith et al., 2003; Corney et al., 2012; Ryan, 2013).

Beyond herbaria and botanic gardens, the developmental changes in plants responding to environmental variability and microclimatic changes over the course of a growing season can be analyzed by studying phenology. Citizen science projects such as the USA National Phenology Network[7] or Earthwatch[8] and associated programs such as My Tree Tracker[9]

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2 For example, see the White Paper on Citizen Science for Europe, http://www.socientize.eu/sites/default/files/white-paper_0.pdf (retrieved May 29, 2016)

3 Galaxy Zoo, http://www.galaxyzoo.org/ (retrieved May 29, 2016)

4 Wisconsin Wildlife Watch, https://www.zooniverse.org/projects/zooniverse/wisconsin-wildlife-watch (retrieved May 29, 2016)

5 Cell slider, http://www.cellslider.net/#/ (retrieved May 29, 2016)

6 List of herbaria, https://en.wikipedia.org/wiki/List_of_herbaria (retrieved May 29, 2016)

7 https://www.usanpn.org/# (retrieved May 29, 2016)

8 http://earthwatch.org/scientific-research/special-initiatives/urban-resiliency (retrieved May 29, 2016)

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document populations and individual plants over seasons and years, providing a distributed, decentralized network of scientific measurements. Integrating phenological data—essentially plant morphological measurements over time—with weather modeling and satellite data promises to provide meaningful predictions of the ecological consequences of climate change.

Citizen science is also enabled by low-cost, specialized equipment. Whether programing a camera to automatically take pictures at specific times or automating a watering schedule for a garden, the maker movement—a do-it-yourself cultural phenomenon that intersects with hacker culture—focuses on building custom, programmable hardware, whether via electronics, robotics, 3D-printing, or time-honored skills such as metal- and woodworking. The focus on programming is especially relevant for integrating mathematical approaches with plant science experiments. Originally built for education, single-board computers like Raspberry Pi, Hummingboard, or Cubieboard, are microcomputers that are widely adopted by educators, hobbyists and researchers that have enabled the maker culture. Single-board computers are used for diverse tasks, from logging and distributing data from environmental sensors to playing MineCraft. The low-cost of single-board computers computers ($5.00- $35.00, depending on model) makes tinkering more permissive for a greater population of citizen science than previously feasible. In classrooms, microcomputers can be used simply as a computer station, or incorporated into lesson plans using a variety of available teaching resources[10]. Single-board computers enable the early cultivation of interest in computational science through educational modules that can grow in complexity with student ability.

C. Workshops and funding opportunities

Simply bringing mathematicians and plant biologists together to interact, to learn about tools, approaches, and opportunities in each discipline that researchers may not be aware

[9] http://www.mytreetracker.org/cwis438/websites/MyTreeTracker/About.php?WebSiteID=23 (retrieved May 29, 2016)

[10] https://www.raspberrypi.org/resources/ (retrieved May 29, 2016)

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of, is a major barrier preventing the full integration of these two disciplines. This white paper itself is a testament to the power of bringing mathematicians and biologists together, resulting from a National Institute for Mathematical and Biological Synthesis (NIMBioS) workshop titled "Morphological Plant Modeling: Unleashing Geometric and Topologic Potential within the Plant Sciences", held at the University of Tennessee, Knoxville September 2-4, 2015[11] (**Figure 8**). Other mathematical institutes such as the Mathematical Biology Institute (MBI) at Ohio State University[12], the Statistical and Applied Mathematical Sciences Institute (SAMSI) in Research Triangle Park[13], the Institute for Mathematics and Its Applications at University of Minnesota[14], and the Centre for Plant Integrative Biology at the University of Nottingham[15] have also hosted workshops for mathematical and quantitative biologists from the undergraduate student to the faculty level.

There are efforts to unite biologists and mathematics through initiatives brought forth from The National Science Foundation, including Mathematical Biology Programs[16] and the Joint DMS/NIGMS Initiative to Support Research at the Interface of the Biological and Mathematical Sciences[17] (DMS/NIGMS). Outside of the Mathematics and Life Sciences Divisions, the Division of Physics houses a program on the Physics of Living Systems. Societies such as The Society for Mathematical Biology and the Society for Industrial and Applied Mathematics (SIAM) Life Science Activity Group[18] are focused on the dissemination of research at the intersection of math and biology, creating many opportunities to present research and provide funding. One of the problems in the creation of an active intersection of mathematicians and plant biologists is that scientists often describe themselves as one or the other. Ways to actively unite these fields would be to incorporate cross topic sessions, inviting scientists from mathematics and plant biology to speak in an effort to inform each discipline and initiatives for cross-trained scientists that bridge both

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11 http://www.nimbios.org/workshops/WS_plantmorph (retrieved May 29, 2016)

12 https://mbi.osu.edu/ (retrieved May 29, 2016)

13 http://www.samsi.info/ (retrieved May 29, 2016)

14 https://www.ima.umn.edu/ (retrieved May 29, 2016)

15 https://www.cpib.ac.uk/outreach/cpib-summer-school/ (retrieved May 29, 2016)

16 https://www.nsf.gov/funding/pgm_summ.jsp?pims_id=5690 (retrieved May 29, 2016)

17 http://www.nsf.gov/funding/pgm_summ.jsp?pims_id=5300&org=DMS (retrieved May 29, 2016)

18 https://www.siam.org/activity/life-sciences/ (retrieved May 29, 2016)

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disciplines. Funding initiatives to help promote these sessions and provide travel stipends to attend conferences for this specific purpose could greatly enhance collaboration of the plant sciences and mathematics. Another possibility is funding for a joint meeting where mathematicians and plant biologists are paired together to work on a dataset together. This has worked well in computer science contexts and reaches a broad audience[19].

D. Open Science

Ultimately, mathematicians and plant biology must unite at the level of jointly collecting data, analyzing it, and doing science together. Sharing data and code is perhaps the easiest way to unite these two disciplines, reducing redundancy and providing benchmarked datasets from which radically different interpretation of plant morphology can be compared. Great strides have already been made in creating an open science environment, but much work remains to increase the number of accessible datasets and code and to use such open access to facilitate communication between plant biologists and mathematicians that might not otherwise interact.

A number of platforms provide open, public access to datasets, figures, and code that can be shared, including Dryad[20], Dataverse[21], and Figshare[22]. These services are integrated to journals and the publication of articles to varying degrees, and have different limitations on the amount of data that can be stored and contrasting financial models. Beyond the ability to share data is the question of open data formats and accessibility. For example, in remote sensing research it is unfortunately common that proprietary data formats are shared, which prevents their use without specific software. ASCII format is universal, but it has issues with performance and storage size that can become an obstacle with large datasets. Open binary data formats are needed to ensure data availability and accessibility in interdisciplinary research. Hierarchical Data Formats (HDF) 4 and 5 are a good example of

[19] Hack the Dinos, American Museum of Natural History, http://www.amnh.org/calendar/hack-the-dinos (retrieved May 29, 2016)

[20] http://datadryad.org/ (retrieved May 29, 2016)

[21] http://dataverse.org/ (retrieved May 29, 2016)

[22] https://figshare.com/ (retrieved May 29, 2016)

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this[23]. For point cloud data describing 3D structures, ASPRS .las[24] and .e57 (Huber, 2011) formats have been designed with distributability in mind. Phenopackets is a new format that aims to handle a wide range of phenotypic and environmental data in big datasets[25].

Beyond datasets, making code openly available, citable and user friendly is a means to share methods to analyze data. Places to easily share code include web-based version controlled platforms like Bitbucket[26] or Github[27] and software repositories like Sourceforge[28]. Most of these platforms allow the easy generation of DOI associated with the dataset or code. For example, with Github you can automatically obtain a DOI for your repository through Zenodo[29]. Initiatives like Depsy[30] are trying to put into value the work of research software developers that most of the times goes unnoticed. Also, these repositories allow for distributed version control, which makes it easier for multiple developers to work and collaborate on the same code.

The most powerful open science tools bring datasets, code, and analysis together in unique, accessible ways. Meta-analysis datasets provide curated resources where numerous published and unpublished datasets related to a specific problem (or many problems) can be accessed by researchers[31]. The portability and interoperability of disparate datasets between software tools can be overcome with standardized formats. The crucial element is that such formats are somehow reflective of universal plant morphological features, bridging the gap between programming languages and biology, as seen in the Root System Mark-up Language (Lobet et al., 2015) and OpenAlea (Pradal et al., 2008). Bisque is a versatile platform to store, organize, and analyze image data, providing simultaneously open access to data and analyses as well as the requisite computation (Kvilekval et al.,

23 http://www.hdfgroup.org/ (retrieved May 29, 2016)

24 http://www.asprs.org/a/society/committees/standards/LAS_1_4_r13.pdf (retrieved May 29, 2016)

25 https://github.com/phenopackets (retrieved September 24, 2016)

26 https://bitbucket.org/ (retrieved May 29, 2016)

27 https://github.com/ (retrieved May 29, 2016)

28 https://sourceforge.net/ (retrieved May 29, 2016)

29 http://zenodo.org/ (retrieved May 29, 2016)

30 http://depsy.org/ (retrieved May 29, 2016)

31 BAAD: a Biomass And Allometry Database for woody plants, https://github.com/dfalster/baad (retrieved May 29, 2016)

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2010). CyVerse[32] (formerly iPlant) is a similar platform, on which academic users get 100 GB storage for free and can create analysis pipelines that can be shared and reused (Goff et al., 2011). For example, DIRT[33] is an automatic, high throughput computing platform (Bucksch et al., 2014c; Das et al., 2015) that the public can use hosted on CyVerse using the Texas Advanced Computing Center[34] (TACC) resources at UT Austin that robustly extracts root traits from digital images.

Regardless of the specific purpose of an open science dataset, analysis, or platform, the key point is that the data be accessible and generalizable to the widest audience as possible. For both plant biologists and mathematicians, formatting open data can take inordinate amounts of time. Effective data sharing can be accomplished by making raw data available as well as processed data, and documenting the steps that were used to arrived at the processed data[35]. Data should always be accompanied by a codebook, metadata describing each variable used, and when at all possible, be "tidy data" (that is, a data frame with columns for each variable and rows for each observation that is immediately accessible for data analysis and visualization, Wickham, 2014). Beyond datasets, there are recommendations for organizing file structures and documenting progress (Noble, 2009) as well as programming itself (Wilson et al., 2014). Further, the discoverability of biological data to mathematicians is key: ideally public data would be accompanied by information including outstanding questions that mathematics may be able to solve or reasons why the dataset should be explored in alternative ways to how it has already been analyzed. Well-formatted data can be made public easily enough, but experimental metadata alone may not be sufficient to generate further interest. While the above are attempts to make biological data more accessible to mathematicians, the reciprocal direction of sharing is less well represented. In fact, evidence suggests that using equations (one of the primary means by which mathematicians share their work) impedes communication with biologists

32 http://www.cyverse.org/ (retrieved August 20, 2016)

33 http://dirt.iplantcollaborative.org/ (retrieved August 20, 2016)

34 https://www.tacc.utexas.edu/ (retrieved August 20, 2016)

35 How to share data with a statistician, https://github.com/jtleek/datasharing (retrieved May 29, 2016)

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(Fawcett and Higginson, 2012). Providing context and narrative, in addition to the interactions between plant biology and mathematics outlined in this paper, should help the accessibility of math and its contingent equations to biologists.

V. Conclusion: Unleashing geometric and topologic potential within the plant sciences

The plant form is inherently architectural, from the shapes of leaves to the hierarchies in the branching patterns of shoots and roots. Plant morphology has served as an inspiration to mathematicians, who innovated new methods to quantify and model the plant form as a result of evolutionary, developmental and environmental responses (**Figures 1-2**). Plant morphology is an unresolved mystery to plant biologists, who seek to understand the molecular mechanisms by which such predetermined, yet seemingly endless variations of organizational patterns emerge.

Never have the resources to study plant morphology been more plentiful. Burgeoning imaging technologies—innovative confocal microscopy, X-ray imaging, MRI, radar, terrestrial laser scanning, among many others—have made detailed 3D models of plants feasible (**Figures 3-4**). Imaging across time and scales looks behind the curtains from the sub-cellular scale to the entirety of the earth surface. The mathematical methods to model plant morphology, from Turing's reaction-diffusion processes to innovative shape descriptors, quantify the plant form to be used in a wide-variety of biological applications (**Figure 6**).

Yet, all models are idealizations of reality and seemingly simple problems remain unresolved in the study of plant morphology. Integrating observations at different scales is a persistent challenge. We discussed for example that the ability to model the fluttering of leaves within a tree canopy remains out of reach (**Figure 7**). Interest in the hidden half of plant morphology—the root system—has only recently seen a renaissance with technologies capable of penetrating soil and visualizing roots *in situ* (**Figure 5**). Not only is

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describing phenotype problematic, but linking it to a genetic and (especially in plants) environmental basis, within the context of plant evolution, is still an unattained goal. Never have the answers to these questions been more vital and timely. Modifying plant architecture through molecular biology and breeding is key to develop agricultural outputs and sustainability. Monitoring the morphology of plants in response to a shifting environment is necessary to model global responses to climate change. Cross-disciplinary training of scientists, citizen science, and open science are all necessary components to address these needs (**Figure 8**). Unleashing the potential of geometric and topological approaches in the plant sciences promises to transform our understanding of both plants and mathematics, and to meet the challenges posed by a future with dwindling and uncertain natural resources.

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Figure Legends

Figure 1: Plant morphology from the perspective of biology. A) Adapted from Kaplan (2001). Plant morphology interfaces with all disciplines of plant biology—plant physiology, plant genetics, plant systematics, and plant ecology—influenced by both developmental and evolutionary forces. **B)** Artistic rendering of Goethe's *Urpflanze* concept (Goethe, 1837; Friedman and Diggle, 2011), demonstrating the importance of development in modulating the plant form. Goethe viewed the iterative development of plants as a transformation of lateral organ identities, from juvenile to adult leaves to reproductive structures. **C)** Evolutionary and ecological effects also shape plant morphology. Alexander von Humboldt's distribution of plants across the elevations of Chimborazo (Ecuador)

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demonstrates the effects of evolution and environment on plant morphology (Black and Black, 1839).

Figure 2: Plant morphology from the perspective of mathematics. A) The topological complexity of plants requires a mathematical framework to describe plant morphology. Shown is the top of a maize crown root 42 days after planting. Color represents root diameter. Image provided by Jonathan Lynch and Johannes Postma (Pennsylvania State University). **B)** Persistent homology deforms a given plant morphology using functions to define self-similarity in a structure. In this example, a color map of geodesic distance functions to the ground level of a tree (blue indicates smaller values near the proximal base and red larger values at the distal tips) is recorded as **C)** an H_0 barcode, in which "births" and "deaths" of connected components as a function of the distance function are recorded. Images provided by Mao Li (Danforth Plant Science Center).

Figure 3: Imaging techniques to capture plant morphology. A) Confocal sections of an Arabidopsis root. The upper panel shows a new lateral root primordium at an early stage of development (highlighted in yellow). At regular intervals new roots branch from the primary root. The lower panel shows the primary root meristem and the stem cell niche (highlighted in yellow) from which all cells derive. Scale bars: 100µm. Images provided by Alexis Maizel (Heidelberg University). **B)** Computational tomographic (CT) x-ray sections through a reconstructed maize ear (left and middle) and kernel (right). Images provided by Chris Topp (Donald Danforth Plant Science Center). **C)** Laser ablation tomography (LAT) image of a nodal root from a mature, field-grown maize plant, with color segmentation showing definition of cortical cells, aeraenchyma lacunae, and metaxylem vessels. Image provided by Jennifer Yang (Penn State).

Figure 4: Terrestrial laser scanning creates a point cloud reconstruction of a Finnish forest. A) Structure of a boreal forest site in Finland as seen with airborne (ALS) and terrestrial (TLS) laser scanning point clouds. The red (ground) and green (above ground) points are obtained from National Land Survey of Finland national ALS point clouds that

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cover hundreds of thousands of square kilometers with about 1 point per square meter resolution. The blue and magenta point clouds are results of two individual TLS measurements and have over 20 million points each within an area of about 500 square meters. TLS point density varies with range but can be thousands of points per square meter up to tens of meters away from the scanner position. **B)** An excerpt from a single TLS point cloud (blue). The TLS point cloud is so dense that individual tree point clouds (orange) and parts from them (yellow) can be selected for detailed analysis. **C)** A detail from a single TLS point cloud. Individual branches (yellow) 20 meters above ground can be inspected from the point cloud with centimeter level resolution to estimate their length and thickness. Images provided by Eetu Puttonen (Finnish Geospatial Research Institute in the National Land Survey of Finland). ALS data was obtained from the National Land Survey of Finland Topographic Database, 08/2012 (National Land Survey of Finland open data licence, version 1.0).

Figure 5: The environmental basis of plant morphology. Root system architecture of Arabidopsis Col-0 plants expressing ProUBQ10:LUC2o growing in **A)** control and **B)** water-deficient conditions using the GLO-Roots system (Rellán-Álvarez et al., 2015). Images provided by Ruben Rellán-Álvarez (Laboratorio Nacional de Genómica para la Biodiversidad, CINVESTAV).

Figure 6: Integration of tissue growth and reaction-diffusion models. A) Vertex model of cellular layers (Prusinjiewicz and Lindenmayer, 2012). K, l_a, and l_0 are the spring constant, current length, and rest length for wall a. K_P is a constant and S_A is the size of cell A. Δt is time step. Shown is a simulation of cell network growth. **B)** Reaction diffusion model of the shoot apical meristem for WUSCHEL and CLAVATA interactions (Fujita et al., 2011). u=WUS, v=CLV, i=cell index, Φ is a sigmoid function. $E, B, A_S, A_d, C, D, u_m, D_u, D_v$ are positive constants. Shown are the distributions of WUS and CLV levels within a dynamic cell network. Images provided by Dorjsuren Battogtokh (Virginia Tech).

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Figure 7: Modeling the interaction between plant morphology and fluid dynamics. A) 3D immersed boundary simulations of flow past a flexible rectangular sheet (left) and disk with a cut from the center to edge (right). Both structures are attached to a flexible petiole, and the flow is from left to right. The contours show the magnitude of vorticity (the rotation in the air). The circular disk reconfigures into a cone shape, similar to many broad leaves. **B)** Reconfiguration of tulip poplar leaves in 3 m/s (left) and 15 m/s flow (right). The leaves typically flutter at lower wind speeds and reconfigure into stable cones at high wind speeds. **C)** A cluster of redbud leaves in wind moving from right to left. The wind speed is increased from 3 m/s (left) to 6 m/s (middle) and 12 m/s (right). Note that the entire cluster reconfigures into a cone shape. This is different from the case of tulip poplars and maples where each leaf individually reconfigures into a conic shape. Images provided by Laura Miller (University of North Carolina, Chapel Hill).

Figure 8: Milestones to accelerate the infusion of math into the plant sciences. Group photo of the authors from the National Institute for Mathematical and Biological Synthesis (NIMBioS) meeting on plant morphological models (University of Tennessee, Knoxville, September 2-4, 2015) that inspired this manuscript. Workshops such as these, bringing mathematicians and plant biologists together, will be necessary to create a new synthesis of plant morphology.

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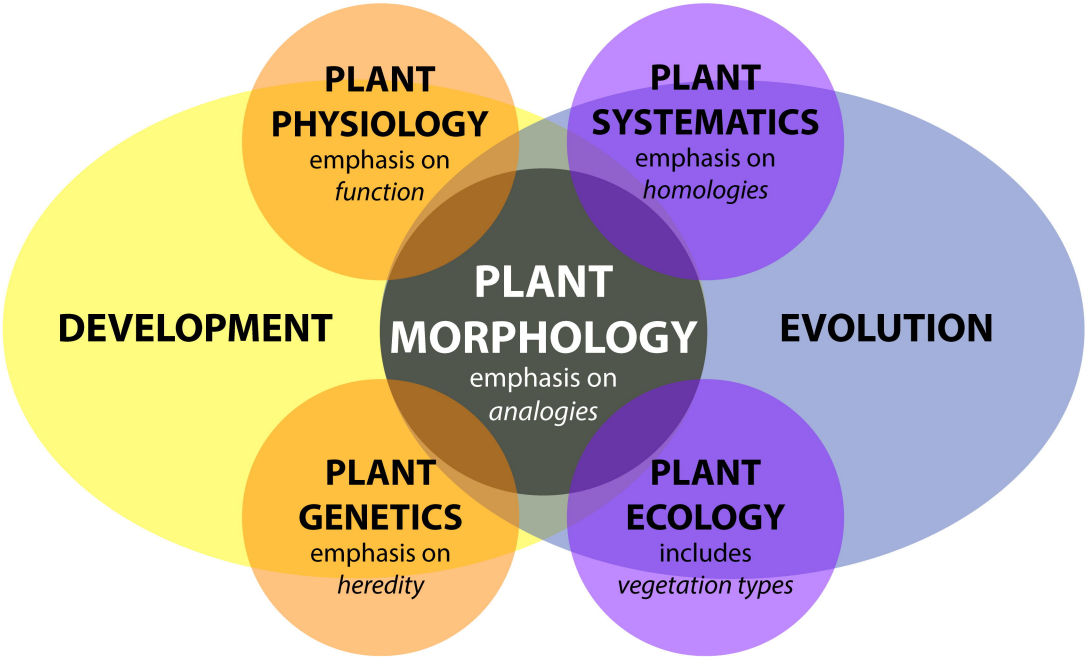
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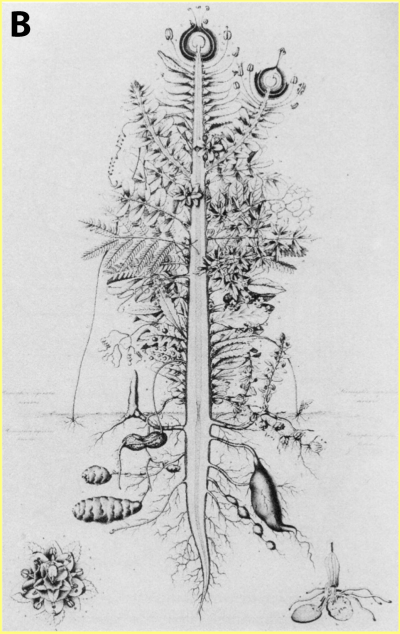

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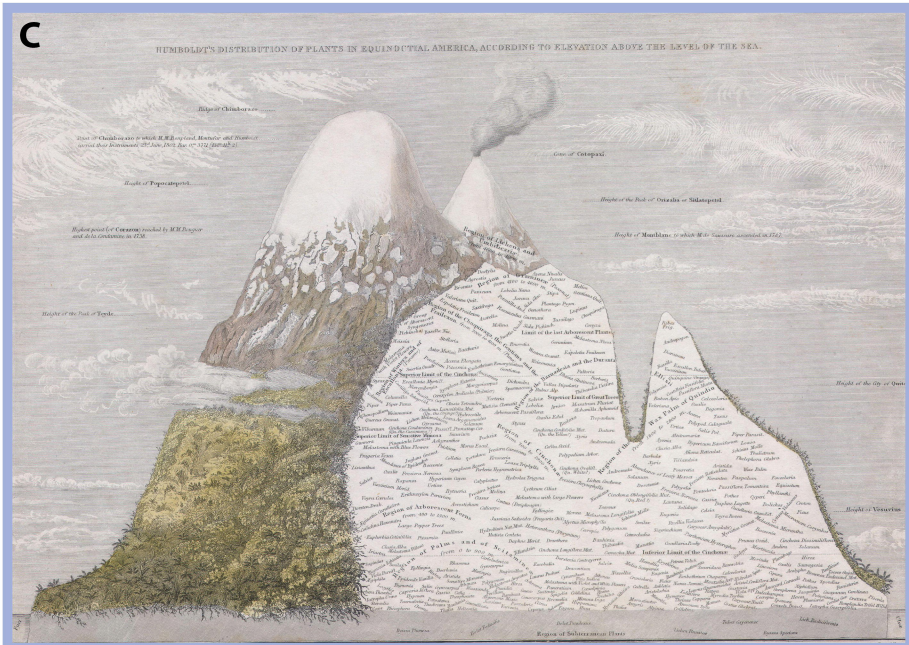
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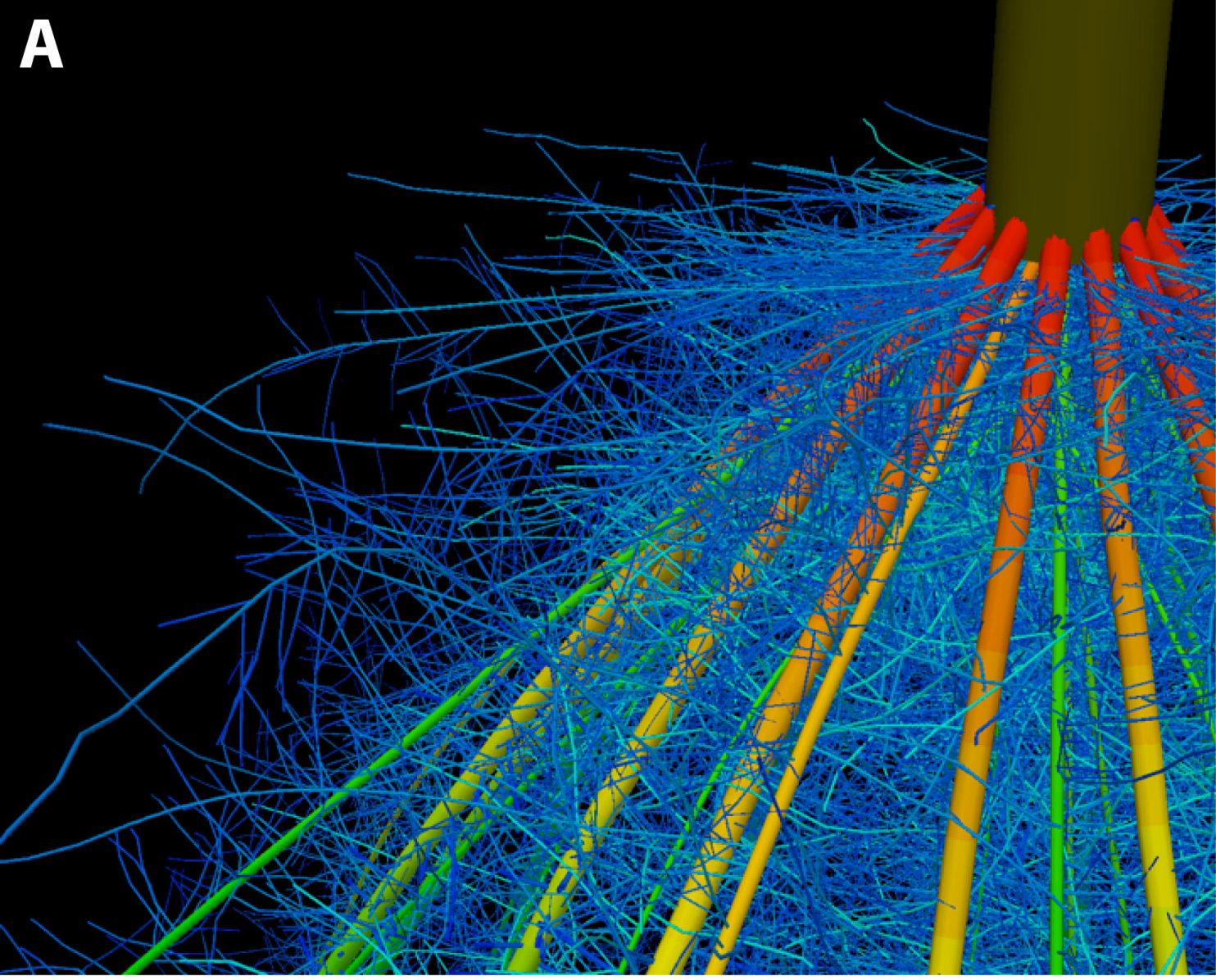
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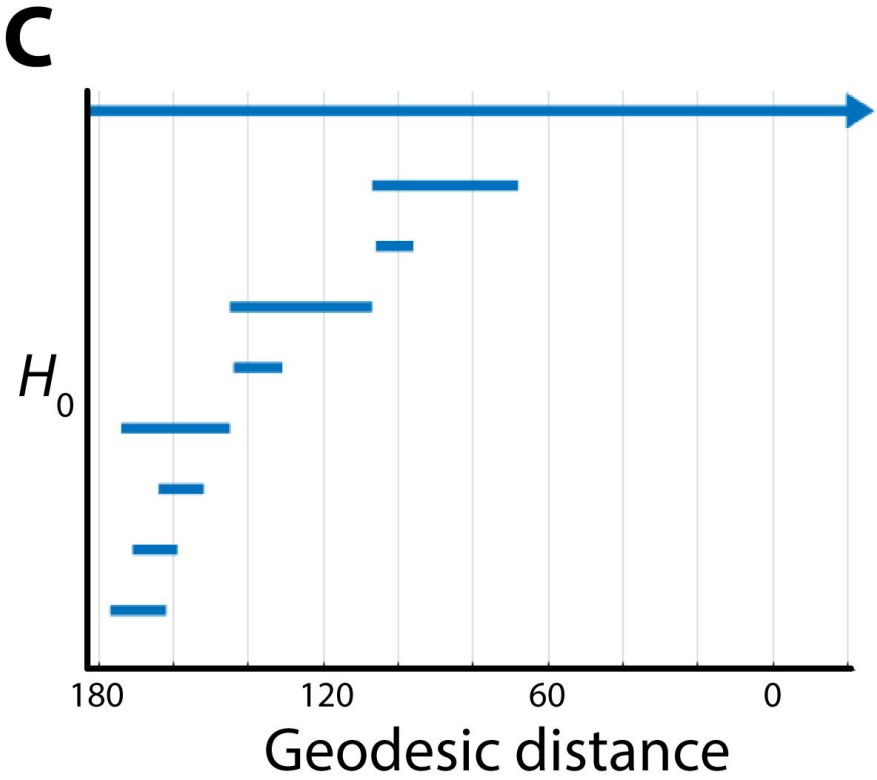
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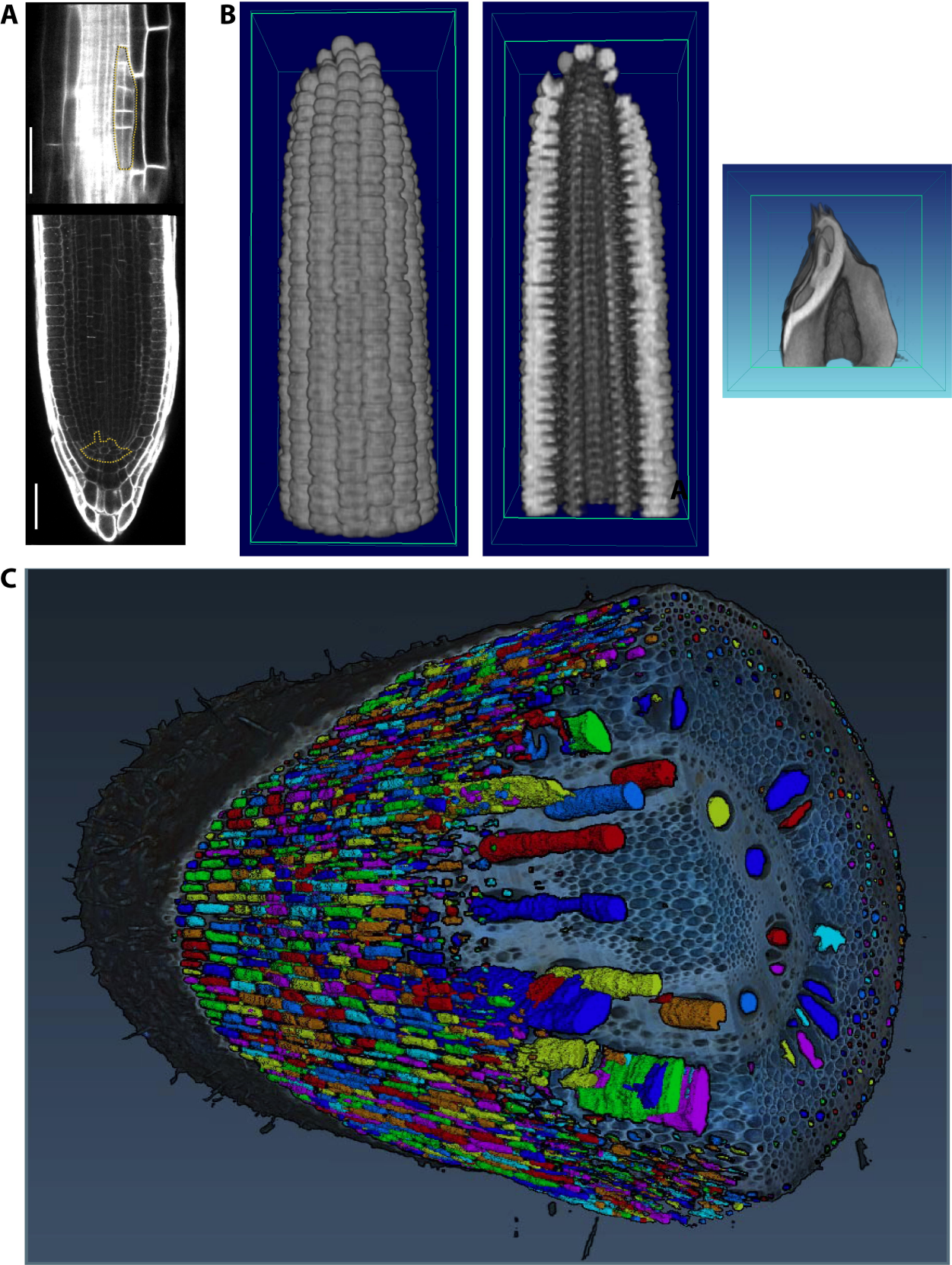
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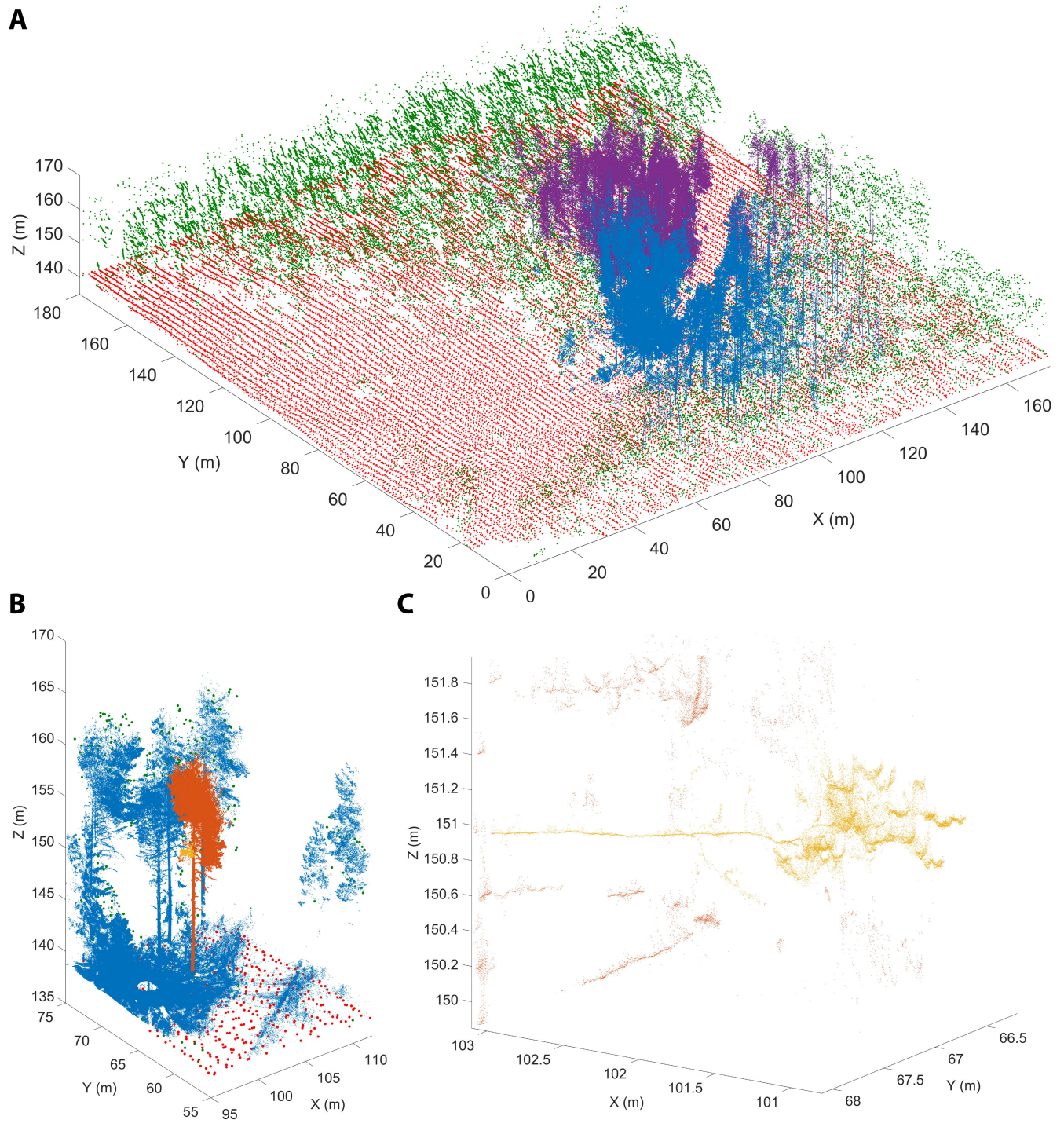
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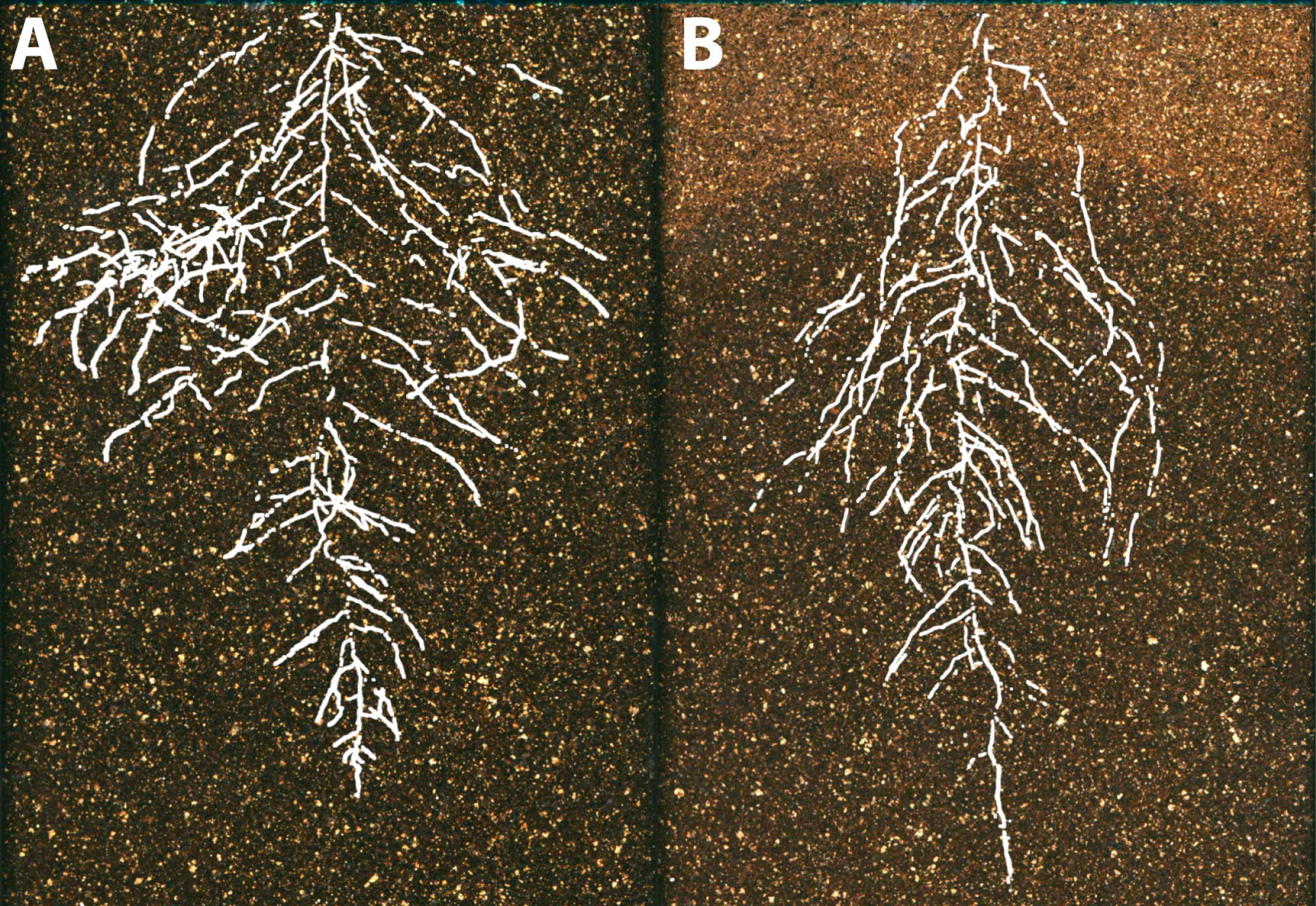
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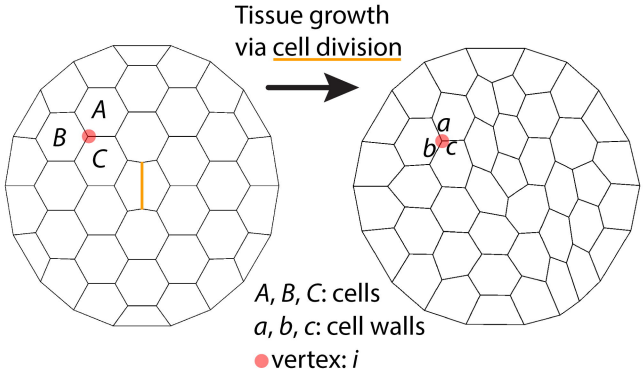
A

Total force on a vertex *i* $\vec{F}_i^T = \sum_{n \in a,b,c} \vec{F}_s^n + \frac{1}{2} \sum_{w \in a,b,c;} \sum_{m \in A,B,C} \vec{P}_w^m$

Spring force on a wall *a* $\vec{F}_s^a = -K(l_a - l_0)$

Turgor pressur on *a* from *A* $\vec{P}_A^a = \frac{K_P}{S_A}; \vec{l}_a \perp \vec{P}_A^a; \vec{l}_a \perp \vec{P}_B^a$

Dynamics of vertex *i* $\vec{x}_i(t+\Delta t) = \vec{x}_i(t) + \vec{F}_i^T \Delta t$

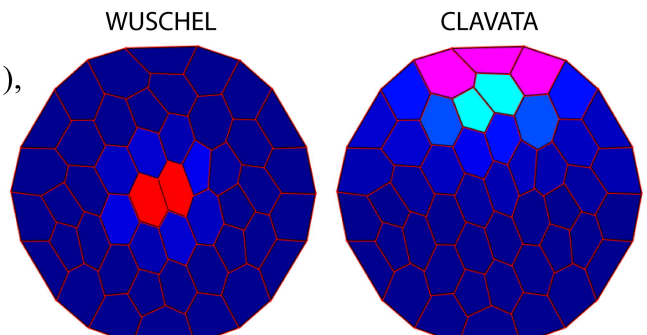


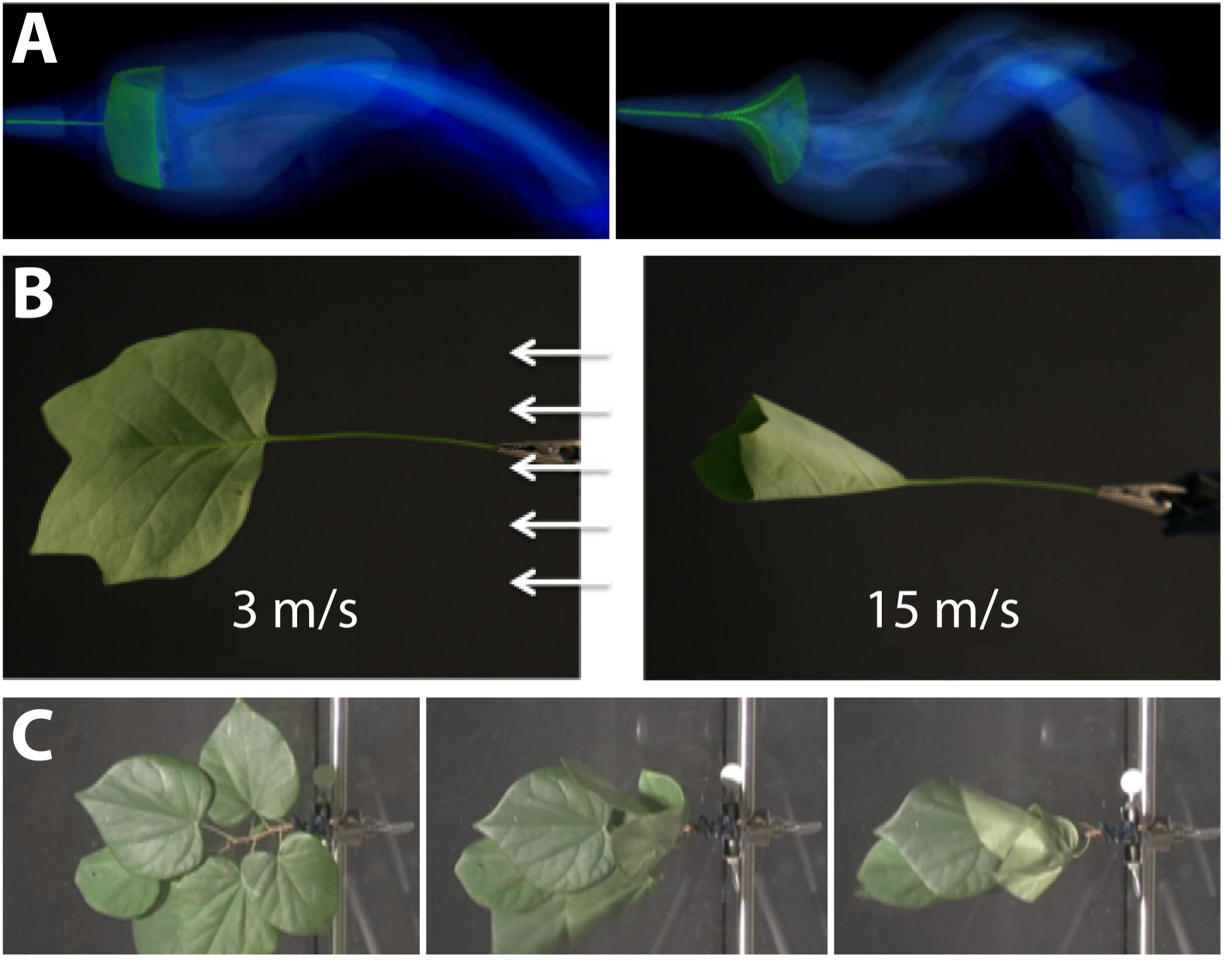
B

$$\frac{\partial u_i}{\partial t} = \Phi(E - B \cdot v_i + A_S \cdot u_i) - A_d \cdot u_i + D_u \sum_{j=neighbors} (u_j - u_i),$$

$$\frac{\partial v_i}{\partial t} = C \cdot u_i - D \cdot v_i + D_v \sum_{j=neighbors} (v_j - v_i),$$

$$\Phi(x) = \frac{A_d u_m}{2} \left(1 + \frac{2x/(A_d u_m) - 1}{\sqrt[n]{1 + |2x/(A_d u_m) - 1|^n}}\right).$$

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