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1 **Morphological plant modeling:**
2 **Unleashing geometric and topologic potential**
3 **within the plant sciences**
4

5 Alexander Bucksch^{1,2,3,§}, Acheampong Atta-Boateng⁴, Akomian Fortuné Azihou⁵, Mathilde
6 Balduzzi⁶, Dorjsuren Battogtokh⁷, Aly Baumgartner⁸, Brad M. Binder⁹, Siobhan A.
7 Braybrook¹⁰, Cynthia Chang¹¹, Viktoirya Coneva¹², Thomas J. DeWitt¹³, Alexander G.
8 Fletcher¹⁴, Malia A. Gehan¹², Diego Hernan Diaz-Martinez¹⁵, Lilan Hong¹⁶, Anjali S. Iyer-
9 Pascuzzi¹⁷, Laura L. Klein¹⁸, Samuel Leiboff¹⁹, Mao Li¹⁵, Jonathan P. Lynch²⁰, Alexis Maizel²¹,
10 Julin N. Maloof²², R.J. Cody Markelz²², Ciera C. Martinez²³, Laura A. Miller²⁴, Washington
11 Mio¹⁵, Wojtek Palubicki¹⁰, Hendrik Poorter²⁵, Christophe Pradal²⁶, Charles A. Price²⁷, Eetu
12 Puttonen²⁸, John Reese²⁹, Rubén Rellán-Álvarez³⁰, Edgar P. Spalding³¹, Erin E. Sparks³²,
13 Christopher N. Topp¹², Joseph Williams²⁹, Daniel H. Chitwood^{12,§}
14

15 ¹Department of Plant Biology, University of Georgia, Athens, GA USA

16 ²Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA USA

17 ³Institute of Bioinformatics, University of Georgia, Athens, GA USA

18 ⁴School of Forestry and Environmental Studies, Yale University, New Haven, CT USA

19 ⁵Laboratory of Applied Ecology, Faculty of Agronomic Sciences, University of Abomey-
20 Calavi, 01 BP 526 Cotonou, Benin

21 ⁶VirtualPlants, Inria, Montpellier, France

22 ⁷Department of Biological Sciences, Virginia Polytechnic Institute and State University,
23 Blacksburg, VA USA

24 ⁸Department of Geosciences, Baylor University, Waco, TX USA

25 ⁹Department of Biochemistry & Cellular and Molecular Biology, University of Tennessee,
26 Knoxville, TN USA

27 ¹⁰The Sainsbury Laboratory, University of Cambridge, Cambridge, UK

28 ¹¹Division of Biology, University of Washington, Bothell, WA USA

29 ¹²Donald Danforth Plant Science Center, St. Louis, MO USA

30 ¹³Department of Wildlife & Fisheries Sciences and Department of Plant Pathology &
31 Microbiology, Texas A&M University, College Station, TX USA

32 ¹⁴School of Mathematics & Statistics and Bateson Centre, University of Sheffield, Sheffield,
33 UK

34 ¹⁵Department of Mathematics, Florida State University, Tallahassee, FL USA

35 ¹⁶Weill Institute for Cell and Molecular Biology and Section of Plant Biology, School of
36 Integrative Plant Sciences, Cornell University, Ithaca, NY USA

37 ¹⁷Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN USA

- 38 ¹⁸Department of Biology, Saint Louis University, St. Louis, MO USA
39 ¹⁹School of Integrative Plant Science, Cornell University, Ithaca, NY USA
40 ²⁰Department of Plant Science, The Pennsylvania State University, University Park, PA USA
41 ²¹Center for Organismal Studies, Heidelberg University, Heidelberg, Germany
42 ²²Department of Plant Biology, University of California, Davis, CA USA
43 ²³Department of Molecular and Cell Biology, University of California, Berkeley, CA USA
44 ²⁴Program in Bioinformatics and Computational Biology, The University of North Carolina,
45 Chapel Hill, NC USA
46 ²⁵Forschungszentrum Jülich, Jülich, Germany
47 ²⁶CIRAD, UMR AGAP and Inria, VirtualPlants, Montpellier, France
48 ²⁷National Institute for Mathematical and Biological Synthesis, University of Tennessee,
49 Knoxville, TN USA
50 ²⁸Finnish Geospatial Research Institute and Centre of Excellence in Laser Scanning
51 Research, National Land Survey of Finland, Masala, Finland
52 ²⁹Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN
53 USA
54 ³⁰Unidad de Genómica Avanzada, Laboratorio Nacional de Genómica para la Biodiversidad,
55 CINVESTAV, Irapuato, México
56 ³¹Department of Botany, University of Wisconsin, Madison, WI USA
57 ³²Department of Biology, Duke University, Durham, NC USA

58
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61

62 [§]To whom correspondence should be addressed:

63

64 Daniel H. Chitwood

65 Donald Danforth Plant Science Center

66 dchitwood@danforthcenter.org

67

68 Alexander Bucksch

69 University of Georgia

70 bucksch@uga.edu

71 **Abstract**

72

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

91

92 **I. Introduction**

93

94 *A. Plant morphology from the perspective of plant biology*

95

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

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

109

110 The study of plant morphology interfaces with all levels of biological organization (**Figure**
111 **1A**). Plant morphology can be descriptive and typological, as in systematics, focusing on
112 biological homologies to discern groups of organisms (Mayr, 1981; Wiens, 2000). These
113 studies additionally have important applications in agriculture and horticulture, beginning
114 with careful selection of ideal phenotypes. In plant ecology, the morphology of
115 communities, comprised of numerous individuals, defines vegetation types and biomes,
116 including their relationship to the environment. Plant morphology also informs plant
117 physiology, the study of the functions of plants, whereas plant genetics describes the
118 inheritance and, in modern times, the molecular basis of plant morphology (Kaplan, 2001).

119

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

131 1984). Plant morphology evolves through inherited modifications of structure or
132 development, either incrementally or abruptly, over the generations (Niklas, 1997) (**Figure**
133 **1C**). A record of these changes over geologic time is preserved and correlates with the
134 paleoclimate, illuminating our understanding of the form and function of extant plants
135 today (Bailey and Sinnott, 1915). Development and evolution are the biological
136 mechanisms through which plant morphology arises, regardless of whether in a systematic,
137 ecological, physiological, or genetic context (**Figure 1**).

138

139 *B. Plant morphology from the perspective of mathematics*

140

141 In 1790, Johann Wolfgang von Goethe pioneered a perspective that transformed the way
142 we think about plant morphology: the idea that the essence of plant morphology is an
143 underlying process of deformation, and that seemingly differently shaped leaves and floral
144 organs within a single plant are homologously related (Goethe, 1790; Friedman and Diggle,
145 2011). The modern challenge that Goethe's paradigm presents is to quantitatively describe
146 deformations in phenotype by their underlying genetic, developmental, and environmental
147 causes. Thus, the fundamental challenge from a mathematical standpoint is how to define
148 shape descriptors to compare plant morphology in the context of a single deformation
149 process; or, how to remove all deformations from the shape that are not relevant to the
150 biological question of interest (Mio and Srivastava, 2004; Lie et al., 2010). A plethora of
151 mathematical approaches, utilizing techniques ranging from geometry and topology to
152 graph theory, exist to describe plant morphology and analyze it with statistical methods.

153

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

161 vertex with a 3D coordinate results in a skeletal 3D representation of plant architecture
162 derivable from imaging data (Bucksch et al., 2010; Bucksch, 2014a; Aiteanu and Klein,
163 2014). Such skeletal descriptions are used to derive quantitative measurements of lengths,
164 diameters, and angles (Bucksch and Fleck, 2011; Raunonen et al., 2013; Seidel et al., 2015).
165 Having an architectural description in place allows the definition of orders, either
166 biologically or in a more abstract sense. The relationships between orders, such as degree
167 of self-similarity (Prusinkiewicz, 2004) or nestedness (Godin and Ferraro, 2010) are used
168 to quantitatively summarize patterns of plant morphology.

169

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

182

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

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

197
198 Parallel to strictly mathematical descriptions of plant morphology, Ronald Fisher
199 developed a statistical framework to partition variance into different sources of variability,
200 whether genetic, developmental, or environmental (Fisher, 1925). Specifically, with respect
201 to plant morphology, the iris flower dataset (Fisher, 1936) was used to develop novel
202 methods to differentiate three *Iris* species based on the length and width of sepals and
203 petals. The dataset is still used to this day as a benchmark to compare statistical methods¹.

204
205 In this white paper, we begin by summarizing the history and importance of the
206 inextricable link between mathematical approaches with advances in our understanding of
207 plant morphology. We proceed by outlining emerging questions at the interface of
208 mathematics and plant morphology, focusing on the acquisition of data, modeling, and
209 data-driven questions at all levels of plant organization. We conclude by describing
210 milestones that will signal the further infusion of mathematics into the plant sciences,
211 including integrated curriculums, outreach, and open science.

212 213 **II. A primer of the history, importance, and potential of mathematics in plant biology**

214
215 Perhaps because of their intricate topologies, geometries, and iterative growth, the
216 morphology of plants has inspired mathematicians; conversely, the biologist's conception
217 of the plant shape requires a mathematical basis. Below we briefly summarize the rich
218 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)

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

221

222 *A. Quantifying plant morphology*

223

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

233

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

249

250 *2. Morphometrics and allometry: the measurement of shape and size.* Once morphological
251 data has been collected, cells, young organ primordia, individual leaves, and roots—and by
252 extension canopies, root systems, and populations—can be described using morphometric
253 approaches. Shape features can be measured by hand, but increasingly machine vision
254 (Wilf et al., 2016) and other automated approaches are used to place landmarks or derive
255 elliptical Fourier descriptors from digital images of plant organs, allowing for statistical
256 and spectral decompositions of shapes, respectively (Iwata et al., 1998; Langlade et al.,
257 2005; Chitwood et al., 2012c; 2013; 2014a; 2014b; 2014c; Rellán-Alvarez et al., 2015).
258 Underlying the shapes of plant organs are differential rates of cell expansion. Cellular
259 expansion rates vary locally and can change rapidly deforming primordia into diverse
260 mature organ morphologies (Rolland-Lagan et al., 2003; Remmler and Rolland-Lagan,
261 2012; Das Gupta and Nath, 2015). Allometry, or the relationship between shape and size, is
262 a principal consideration when analyzing the factors linking the growth of an organ to its
263 resultant morphology. Just as allometry scales from the cellular to tissue and organ levels,
264 it scales from the individual to population levels, explaining intricate morphologies on a
265 global scale (Duncanson et al., 2015; Huang et al., 2016; Paul et al., 2015).

266

267 *B. Modeling pattern formation in plants*

268

269 *1. Turing, phyllotaxy, and reaction-diffusion modeling.* The beautiful patterns apparent in the
270 regular arrangement of leaves on stems and their connection to mathematics have inspired
271 scientists to create models explaining these phenomena. Alan Turing, a pioneering figure in
272 twentieth-century science, developed a longstanding interest in phyllotaxy, the
273 arrangement of leaves on a plant. Turing's approach to the problem was twofold: first, a
274 detailed geometrical analysis of the patterns (Turing, 1992); and second, an application of
275 his theory of morphogenesis through local activation and long-range inhibition (Turing,
276 1952). Combining physical experiments with computer simulations, Douady and Couder
277 (1996) subsequently modeled a diffusible chemical produced by developing primordia that
278 would inhibit the initiation of nearby primordia, successfully recapitulating known

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

289

290 *2. Auxin transport-feedback models of patterning.* The plant hormone auxin has been
291 determined (at least in part) to empirically contribute to many of the abovementioned
292 patterning events. Auxin distribution in plants is achieved through complex, transport-
293 feedback mechanisms. In order to understand how a single hormone could produce such
294 diverse patterns in a self-organizing manner, these feedback mechanisms have been
295 extensively modeled with dynamic system techniques (a complete review of auxin
296 transport mechanisms and their role in plant pattern formation is outside the scope of this
297 manuscript, but see Smith and Bayer, 2009). Auxin transport creates discrete patterning
298 events that are inconsistent with the gradients through which morphogens in animals
299 typically act, demonstrating that pattern formation in plants and animals is fundamentally
300 different (Bhalerao and Bennett, 2003). Elegant work combining modeling with
301 experimental verification has demonstrated the role of auxin in diverse plant patterning
302 processes including embryonic patterning (Moller and Weijers, 2009), patterning of the
303 female gametophyte (Pagnussat et al., 2009), vascular patterning (Scarpella et al., 2006;
304 Donner et al., 2009), the patterning of serrations and leaflets in complex leaves (Koenig et
305 al., 2009), lateral root formation (Casimiro et al., 2001), and phyllotaxy (Reinhardt et al.,
306 2003; Smith et al., 2006), among other processes too numerous to list here.

307

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

325
326 *4. Tensor-based modeling of growth.* The pattern of cell walls in a root or shoot meristem
327 follows observable regularities. Two families of orthogonal lines can describe the patterns
328 observed in cell walls: periclinal (divisions parallel to a local axis) and anticlinal (divisions
329 normal to a local axis) (Sachs, 1878). Attempts to understand the origin of this regularity
330 led to the development of tensor-based models for growth and cell divisions. These models
331 share the underlying assumption of three mutually orthogonal principal directions of
332 growth (PDG) at each point of a growing meristem and the assumption that cells divide in
333 relation to PDGs (Hejnowicz and Romberger, 1984). Several tensor-based growth models
334 have been developed for the shoot apical meristem, the primary root meristem (Hejnowicz
335 and Karczewski, 1993; Nakielski, 2008), and the lateral root (Szymanowska-Pułka and

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

338

339 *5. Quantifying branching structures.* Maybe because of their prominent appearance in
340 everyday life, branching structures are one of the first geometrical forms recognized in
341 plants. Their representation is intuitive because they can easily be reduced to intersecting
342 line segments. A plethora of approaches to reduce imaged branching structures in 2D and
343 3D to lines or skeletons exist (see Bucksch 2011 and Bucksch, 2014a for an overview). In
344 principle, skeletons let us navigate through a branching structure and take measurements
345 of branch length and diameter. In tree crowns (Bucksch and Fleck 2011; Schilling et al.;
346 2012, Delagrangé et al. 2014), skeletons are a fundamental descriptor towards
347 understanding self-shadowing in tree crowns and measuring biomass allocation over time.
348 Skeletonization methods are also a popular method to quantify the branching architecture
349 of roots, both statically at a single time point (Lobet et al., 2011; Galkovskyi et al., 2012)
350 and dynamically capturing root growth (Symonova et al., 2015).

351

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

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

369

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

372

373 *1. Kinematics.* Although we have already discussed time-dynamic models of plant
374 morphogenesis and cellular division patterns above, the emergent morphologies that arise
375 from cells, tissues, and organs interact with the surrounding environment in functional
376 ways. For example, in roots there are three developmental zones starting at the tip that
377 propel cells through the soil medium: 1) the meristematic zone, where cells are actively
378 proliferating; 2) the elongation zone, where cells stop dividing and begin to expand; and 3)
379 the differentiation zone, where cells acquire their terminal cell fate (Barnes, 1898). Root
380 growth is controlled by both displacement via production of new cells (meristematic zone)
381 and expansion of existing cells (elongation zone). Describing a growth system with both
382 expanding and contracting components is a challenge. One approach to solve this problem,
383 pioneered by Wendy Silk (Silk and Erickson, 1979; Silk, 1984), is to adopt the formalism of
384 compressible fluid dynamics to describe plant growth in terms of kinematics. This
385 approach treats the plant “fluid” as a continuous medium, neglecting molecular-scale
386 heterogeneity. Considering the root as a homogenous fluid (which is theoretically
387 supported, if land plants are considered to be giant, single-celled organisms; Kaplan and
388 Hagemann, 1991; Coneva and Chitwood, 2015), this approach can be applied to questions
389 such as the relationship between water potentials and roots growth (Sharp et al., 1988;
390 1990) and the allometric growth of leaves (Bernstein et al., 1993; 1995).

391

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

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

411
412 *3. Leafshape and the paleorecord.* Plant morphology responds dynamically to turbulent
413 environments and can plastically respond, developmentally, to subtler changes. But what is
414 the relationship between plant morphology and geologic time? Ultimately, the shape of
415 leaves is subject to selection pressures from a variety of sources, whether the influence of
416 high winds, herbivory, thermoregulation, or light interception. Plant morphology may be
417 constrained by hydraulic, biomechanical, developmental, or phylogenetic effects (Nicotra et
418 al., 2011). Any one of these factors—and other unknowns—can create patterns observed in
419 both extant and fossil leaf assemblages (Chitwood and Sinha, 2016).

420
421 Larger leaves, with fewer and less pronounced serrations, predominate in warmer, wetter
422 climates whereas smaller leaves, with larger and more numerous serrations, tend to be
423 found in colder, drier temperate environments (Bailey and Sinnott, 1915). This
424 fundamental relationship between leaf dissection with temperature and precipitation has
425 been demonstrated across geographies and in different phylogenetic groups, although

426 often the correlation differs or is more or less robust depending on context (Wolfe, 1979;
427 1993; Wing and Greenwood, 1993; Wilf, 1997; Wilf et al., 1998; Huff et al., 2003; Jacobs and
428 Herendeen, 2004; Royer et al., 2005; Spicer et al., 2009; Peppe et al., 2011). Plasticity in leaf
429 shape during the lifetime of an individual plant correlates with temperature and
430 precipitation similarly to the fossil record, demonstrating parallels in the morphological
431 response of plants to changes in environmental conditions over developmental and
432 evolutionary timescales (Royer et al., 2009; Chitwood et al., 2016). Measuring plant
433 morphology in evolving populations provides insights into adaptive versus neutral features
434 (Moyle, 2008; Nordborg and Weigel, 2008; Brachi et al., 2011), revealing insights into the
435 relationship between morphology and function (Wright et al., 2004).

436

437 **III. Emerging questions and barriers in the mathematical analysis of plant** 438 **morphology**

439

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

447

448 *A. Technological limits acquiring plant morphological data*

449

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

456 2D and 3D. The most accessible scale is plant architecture. In general, technology to record
457 plant architecture produces two kinds of data: surface samples and volumetric data.
458 Stereovision data are generated from different views of 2D digital images (Boyde, 1973;
459 Dumais and Kwiatkowska, 2002). Through matching of identical features, a spatial
460 alignment of the images is computed that allows the calculation of depth information.
461
462 Time of flight scanners, such as terrestrial laser scanning, overcome unit-less measurement
463 by recording the round-trip time of hundreds of thousands of laser beams sent at different
464 angles from the scanner to the first plant surface within the line of sight (Vosselman and
465 Maas, 2010) (**Figure 4**). The constant speed of light allows the calculation of the distance
466 between the point hit on the plant surface and the laser scanner. Both stereovision and
467 laser scanning produce surface samples or point clouds as output. However, both face
468 algorithmic challenges if plant parts occlude each other, as both rely on the reflection of
469 waves from the plant surface (Bucksch, 2011).
470
471 Penetrating the plant surface to resolve occlusions is possible with X-ray and magnetic
472 resonance imaging (MRI). While both technologies circumvent occlusions and can even
473 penetrate soil, their limitation is the requirement of a closed imaging volume. X-ray
474 systems rely on the principle that different tissues and materials absorb different amounts
475 of X-ray radiation (Kumi et al., 2015.) (**Figure 3B**). A detector plate records the remaining
476 X-ray radiation. If X-ray images are taken from various angles around the plant, then a 3D
477 model can be reconstructed from the absorption levels. The field produced with two
478 cylindrical magnets defines the imaging volume of an MRI (van Dusschoten et al., 2016).
479 The hydrogen molecules of the plant align with the field of the first magnet. Creating a
480 second magnetic field causes a detectable change in hydrogen alignment, from which the
481 3D structure of a plant can be reconstructed. The resulting data are voxels that encode the
482 local hydrogen density as an intensity value. Both surface-penetrating imaging technologies
483 intrinsically limit the imaging volume, either by the need of a detector plate or the closed
484 cylinder needed to establish a magnetic field. Thus, MRI and X-ray are destructive if applied

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

487

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

494

495 *B. The genetic basis of plant morphology*

496

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

511

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

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

527
528 Natural variation in cell, tissue, or organ morphology ultimately impacts plant physiology.
529 For example, root cortical aerenchyma formation reduces the metabolic costs of soil
530 exploration, thereby improving plant growth under conditions of suboptimal availability of
531 water and nutrients (Zhu et al. 2010; Postma and Lynch, 2011; York et al., 2013; Lynch et
532 al., 2014; Lynch, 2013; 2015, Chimungu et al. 2015). Maize genotypes with greater root
533 cortical cell size or reduced root cortical cell file number also have reduced metabolic costs,
534 and therefore deeper rooting and increased water capture under drought (Chimungu et al.,
535 2014a; 2014b). The radial distribution of auxin in the rice root leads to differential cell
536 expansion and more vertical root angles, resulting in greater water capture in drying soils.
537 The genetic basis of this effect was mapped to *DRO1* (Uga et al., 2013), and exemplifies how
538 the control of cellular organization by a single gene can have profound effects at the
539 organismal level and the interaction of plants with their environments.

540
541 High-throughput phenotyping techniques are increasingly used to reveal the genetic basis
542 of natural variation. In doing so, phenotyping techniques complement classic approaches of
543 reverse genetics and often lead to novel insights even in a well-studied species like
544 *Arabidopsis*. Such techniques reveal a genetic basis for such dynamic traits as root growth

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

559

560 *C. The environmental basis of plant morphology*

561

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

574

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

589

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

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

606
607 Below ground, plants encounter diverse sources of environmental variability, including
608 water availability, soil chemistry, and physical properties like soil hardness and movement.
609 These factors vary not only between individual plants (Razak et al., 2013), but within an
610 individual root system, to which plants respond in diverse ways (Drew, 1975; Robbins and
611 Dinneny, 2015). Plasticity at a micro-environmental scale has been linked to developmental
612 and molecular mechanisms (Bao et al., 2014). The scientific challenge is here to integrate
613 these effects at a whole root system level to understand the optimal acquisition in resource
614 limited conditions (Rellan-Alvarez, et al., 2016) (**Figure 5**).

615
616 *D. Integrating models from different levels of organization*

617
618 Most of the mathematical models highlighted in the previous sections have been designed
619 independently to study plant development at specific spatial and temporal scales. Since it is
620 extremely difficult to examine complex interdependent processes occurring at multiple
621 spatio-temporal scales, mathematical modeling can be used as a complementary tool with
622 which to disentangle component processes and investigate how their coupling may lead to
623 emergent patterns at a systems level (Hamant, 2008; Band and King, 2012; Jenzen and
624 Fozard 2015; Band et al. 2012).

625
626 A detailed multiscale model may involve hundreds of variables and parameters. It is likely
627 that the exact values of most parameters will not be known, nor even identifiable. Thus, to
628 be practical, a multiscale model should generate well-constrained predictions despite
629 significant parameter uncertainty (Gutenkunst et al., 2007, Hofhuis et al., 2016). It is
630 desirable that a multiscale model has certain modularity in its design such that individual
631 modules are responsible for modeling specific spatial aspects of the system (Baldazzi et al.,
632 2012). Global sensitivity analysis can be applied to reveal how individual modules function
633 when other modules are perturbed (Sudret, 2008). Most importantly, a multiscale model

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

637
638 It is a useful exercise to illustrate the challenges of integrating models at the molecular and
639 cellular levels with an example. At the molecular scale, mathematical models describe the
640 spatiotemporal dynamics of key biomolecules and phytohormones controlling the function
641 and fate of individual cells. Some of these biomolecules can be diffusive, but others, such as
642 membrane-bound receptors, may be spatially localized (Battogtokh and Tyson, 2016). The
643 distribution of molecules in the cell i ($i=1..N$) can be described by a system of partial
644 differential equations, $\frac{dX_i}{dt} = f(X, \mu) + D_X \sum_{j=neighbors} (X_j - X_i)$, where the components of
645 X are the levels of biomolecules in a given cell, the nonlinear functions f describe the
646 kinetics of the reactions between the molecules, μ is the set of model parameters, D_X is a
647 diagonal matrix of diffusion coefficients, N is the number of the cells, and the sum in the last
648 term is for the diffusion of the biomolecules between the cells (Fujita et al., 2011).

649
650 At the cellular scale, mathematical models describe dynamics of cell networks where the
651 mechanical pressures exerted on the cell walls are important factors for cell growth and
652 division (Jensen and Fozard, 2015) (**Figure 6A**). In models describing plant development in
653 a two-dimensional cross-section geometry, cells are often modeled as polygons defined by
654 walls between neighboring cells. The spatial position of a vertex, where the cell walls of
655 three neighboring cells coalesce, is a convenient variable for mathematical modeling of the
656 dynamics of cellular networks (Prusinkiewicz and Lindenmayer, 2012). A given vertex is
657 driven by the sum of forces acting on it, the turgor pressures from the neighboring cells,
658 and the elastic forces exerted on the cell walls. Thus, the time evolution of the vertex j
659 located at the position x can be described by the dynamic equation: $\frac{d^2x_j}{dt^2} = F_j$, where F_j is
660 the total force acting on the vertex j . By numerically integrating the dynamic equations for
661 the positions of all the vertexes in the polygonal cells, the dynamics of the cell network can
662 be simulated. Additionally, certain rules can be adopted for cell division (Besson and

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

666
667 A multiscale model can be assembled by combining the models at molecular and cellular
668 levels. Such a model allows the computation of spatiotemporal dynamics of biomolecules X
669 for realistic initial and boundary conditions on the dynamic cellular networks. Mutations
670 and deletions of the genes encoding the biomolecules can be modeled by changing the
671 parameters, or by modifying the reaction terms in the function f . By inspecting the effects
672 of such modifications on the dynamics of cellular networks, the relationship between
673 genotypes and phenotypes can be predicted. In the aforementioned model by Fujita et al.
674 (2011), the biomolecules X describe the dynamics of the proteins involved in the stem cell
675 regulation of the SAM in *Arabidopsis*. It can simulate SAM development in wild type and
676 mutant plants, demonstrating how integrative models can be valuable tools in predictive
677 modeling of plant development (**Figure 6B**).

678
679 *E. Modeling the interaction between plant morphology and fluid dynamics*

680
681 Modeling plant morphology is a complicated endeavor, but the forces that interact with
682 plants, such as currents of wind and water, are sometimes even more complex and affect
683 the development and evolution of plant architecture. Smaller scale airflows around plants
684 can affect plant health as much as gale force winds, but are determined by plant
685 morphology at an exquisite level of detail. For example, how does vegetation density affect
686 average flow speeds within complex canopies and how do the dynamics of the airflow
687 affect the movement of the trunks, stems, branches, and individual leaves? Simulating flow
688 on scales that span the individual leaf to the entire canopy are not currently feasible but
689 nonetheless critical for understanding plant morphology. Below, we highlight efforts to
690 model the interaction of currents with plant morphology at two extreme scales—light
691 breezes and gale force winds.

692

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

699

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

707

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

715

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

723 of the air or water may, in some cases, act to decrease the boundary layer and increase gas
724 exchange, evaporation, and heat dissipation (Roden and Pearcy, 1993). Each of these
725 parameters may be altered by the plant to improve the overall function of the leaf (Vogel,
726 2012).

727

728 *2. Effect of extreme winds and currents on broad leaves.* Plants use flexibility as one strategy
729 to reduce the drag acting upon them while simultaneously avoiding the violent oscillations
730 observed in many bluff structures subjected to strong winds. Vogel (1989) was the first to
731 provide quantitative data on drag reduction in plants. He found that single broad leaves
732 reconfigure at high flow velocities into cone shapes that reduce flutter and drag when
733 compared to paper cut-outs of similar shape and flexibility (**Figure 7A-B**). He later found
734 that a similar phenomenon occurs in water for herbaceous plants and proposed that this
735 mechanism increases survival rates in flash floods (Vogel, 2006). Subsequent experimental
736 studies on broad leaves and flowers also support rapid repositioning in response to strong
737 wind as a general mechanism to reduce drag (Niklas, 1992; Ennos, 1997; Etnier and Vogel,
738 2000), and simple mathematical models of a flexible beam immersed in a two-dimensional
739 flow exhibit similar behavior (Alben et al., 2002). At the larger scale, Vogel (1989) noticed
740 that leaf clusters and leaflets tend to reconfigure into larger drag reducing structures and
741 speculated that a similar phenomenon is also true for groups of branches (**Figure 7C**).

742

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

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

754

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

761

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

773

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

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

786

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

788

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

802

803 *A. Education*

804

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

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

824

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

840

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

842

843 Citizen science, which is a method to make the general public aware of scientific problems
844 and employ their help in solving them², is an ideal platform to initiate a synthesis between
845 plant biology and mathematics because of the relatively low cost and accessibility of each
846 field. A variety of research fields have successfully implemented citizen science and
847 gamification approaches, including astronomy³, animal biology⁴, and cell biology⁵.

848

849 Arguably, using citizen science to collect plant morphological diversity has already been
850 achieved, but has yet to be analyzed fully. In total, it is estimated that the herbaria of the
851 world possess greater than 207 million voucher specimens⁶, representing the diverse
852 lineages of land plants (and often algae as well) collected over their respective
853 biogeographies over a timespan of centuries. Both herbaria and living collections of botanic
854 gardens are dynamic. Although plant collecting is in decline, it is an active discipline and
855 voucher submissions to herbaria should be encouraged (Prather et al., 2004). Botanic
856 gardens not only possess living collections, but more than ever they spearhead bio-
857 conservation efforts to ensure plant diversity exists in the future to be studied (Schatz,
858 2002). Digital documentation of the millions of vouchers held by the world's botanic
859 gardens is actively underway, allowing for researchers and citizens alike to access and
860 study for themselves the wealth of plant diversity across the globe and centuries (Smith et
861 al., 2003; Corney et al., 2012; Ryan, 2013).

862

863 Beyond herbaria and botanic gardens, the developmental changes in plants responding to
864 environmental variability and microclimatic changes over the course of a growing season
865 can be analyzed by studying phenology. Citizen science projects such as the USA National
866 Phenology Network⁷ or Earthwatch⁸ and associated programs such as My Tree Tracker⁹

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.galaxy.zoo.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)

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

872

873 Citizen science is also enabled by low-cost, specialized equipment. Whether programming a
874 camera to automatically take pictures at specific times or automating a watering schedule
875 for a garden, the maker movement—a do-it-yourself cultural phenomenon that intersects
876 with hacker culture—focuses on building custom, programmable hardware, whether via
877 electronics, robotics, 3D-printing, or time-honored skills such as metal- and woodworking.
878 The focus on programming is especially relevant for integrating mathematical approaches
879 with plant science experiments. Originally built for education, single-board computers like
880 Raspberry Pi, Hummingboard, or Cubieboard, are microcomputers that are widely adopted
881 by educators, hobbyists and researchers that have enabled the maker culture. Single-board
882 computers are used for diverse tasks, from logging and distributing data from
883 environmental sensors to playing MineCraft. The low-cost of single-board computers
884 computers (\$5.00- \$35.00, depending on model) makes tinkering more permissive for a
885 greater population of citizen science than previously feasible. In classrooms,
886 microcomputers can be used simply as a computer station, or incorporated into lesson
887 plans using a variety of available teaching resources¹⁰. Single-board computers enable the
888 early cultivation of interest in computational science through educational modules that can
889 grow in complexity with student ability.

890

891 *C. Workshops and funding opportunities*

892

893 Simply bringing mathematicians and plant biologists together to interact, to learn about
894 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)

895 of, is a major barrier preventing the full integration of these two disciplines. This white
896 paper itself is a testament to the power of bringing mathematicians and biologists together,
897 resulting from a National Institute for Mathematical and Biological Synthesis (NIMBioS)
898 workshop titled “Morphological Plant Modeling: Unleashing Geometric and Topologic
899 Potential within the Plant Sciences”, held at the University of Tennessee, Knoxville
900 September 2-4, 2015¹¹ (**Figure 8**). Other mathematical institutes such as the Mathematical
901 Biology Institute (MBI) at Ohio State University¹², the Statistical and Applied Mathematical
902 Sciences Institute (SAMSI) in Research Triangle Park¹³, the Institute for Mathematics and
903 Its Applications at University of Minnesota¹⁴, and the Centre for Plant Integrative Biology at
904 the University of Nottingham¹⁵ have also hosted workshops for mathematical and
905 quantitative biologists from the undergraduate student to the faculty level.
906 There are efforts to unite biologists and mathematics through initiatives brought forth
907 from The National Science Foundation, including Mathematical Biology Programs¹⁶ and the
908 Joint DMS/NIGMS Initiative to Support Research at the Interface of the Biological and
909 Mathematical Sciences¹⁷ (DMS/NIGMS). Outside of the Mathematics and Life Sciences
910 Divisions, the Division of Physics houses a program on the Physics of Living Systems.
911 Societies such as The Society for Mathematical Biology and the Society for Industrial and
912 Applied Mathematics (SIAM) Life Science Activity Group¹⁸ are focused on the dissemination
913 of research at the intersection of math and biology, creating many opportunities to present
914 research and provide funding. One of the problems in the creation of an active intersection
915 of mathematicians and plant biologists is that scientists often describe themselves as one
916 or the other. Ways to actively unite these fields would be to incorporate cross topic
917 sessions, inviting scientists from mathematics and plant biology to speak in an effort to
918 inform each discipline and initiatives for cross-trained scientists that bridge both

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.qplib.ac.uk/outreach/qplib-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)

919 disciplines. Funding initiatives to help promote these sessions and provide travel stipends
920 to attend conferences for this specific purpose could greatly enhance collaboration of the
921 plant sciences and mathematics. Another possibility is funding for a joint meeting where
922 mathematicians and plant biologists are paired together to work on a dataset together. This
923 has worked well in computer science contexts and reaches a broad audience¹⁹.

924

925 *D. Open Science*

926

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

935

936 A number of platforms provide open, public access to datasets, figures, and code that can be
937 shared, including Dryad²⁰, Dataverse²¹, and Figshare²². These services are integrated to
938 journals and the publication of articles to varying degrees, and have different limitations on
939 the amount of data that can be stored and contrasting financial models. Beyond the ability
940 to share data is the question of open data formats and accessibility. For example, in remote
941 sensing research it is unfortunately common that proprietary data formats are shared,
942 which prevents their use without specific software. ASCII format is universal, but it has
943 issues with performance and storage size that can become an obstacle with large datasets.
944 Open binary data formats are needed to ensure data availability and accessibility in
945 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)

946 this²³. For point cloud data describing 3D structures, ASPRS .las²⁴ and .e57 (Huber, 2011)
947 formats have been designed with distributability in mind. Phenopackets is a new format
948 that aims to handle a wide range of phenotypic and environmental data in big datasets²⁵.

949
950 Beyond datasets, making code openly available, citable and user friendly is a means to
951 share methods to analyze data. Places to easily share code include web-based version
952 controlled platforms like Bitbucket²⁶ or Github²⁷ and software repositories like
953 Sourceforge²⁸. Most of these platforms allow the easy generation of DOI associated with the
954 dataset or code. For example, with Github you can automatically obtain a DOI for your
955 repository through Zenodo²⁹. Initiatives like Depsy³⁰ are trying to put into value the work
956 of research software developers that most of the times goes unnoticed. Also, these
957 repositories allow for distributed version control, which makes it easier for multiple
958 developers to work and collaborate on the same code.

959
960 The most powerful open science tools bring datasets, code, and analysis together in unique,
961 accessible ways. Meta-analysis datasets provide curated resources where numerous
962 published and unpublished datasets related to a specific problem (or many problems) can
963 be accessed by researchers³¹. The portability and interoperability of disparate datasets
964 between software tools can be overcome with standardized formats. The crucial element is
965 that such formats are somehow reflective of universal plant morphological features,
966 bridging the gap between programming languages and biology, as seen in the Root System
967 Mark-up Language (Lobet et al., 2015) and OpenAlea (Pradal et al., 2008). Bisque is a
968 versatile platform to store, organize, and analyze image data, providing simultaneously
969 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)

970 2010). CyVerse³² (formerly iPlant) is a similar platform, on which academic users get 100
971 GB storage for free and can create analysis pipelines that can be shared and reused (Goff et
972 al., 2011). For example, DIRT³³ is an automatic, high throughput computing platform
973 (Bucksch et al., 2014c; Das et al., 2015) that the public can use hosted on CyVerse using the
974 Texas Advanced Computing Center³⁴ (TACC) resources at UT Austin that robustly extracts
975 root traits from digital images.

976

977 Regardless of the specific purpose of an open science dataset, analysis, or platform, the key
978 point is that the data be accessible and generalizable to the widest audience as possible. For
979 both plant biologists and mathematicians, formatting open data can take inordinate
980 amounts of time. Effective data sharing can be accomplished by making raw data available
981 as well as processed data, and documenting the steps that were used to arrived at the
982 processed data³⁵. Data should always be accompanied by a codebook, metadata describing
983 each variable used, and when at all possible, be “tidy data” (that is, a data frame with
984 columns for each variable and rows for each observation that is immediately accessible for
985 data analysis and visualization, Wickham, 2014). Beyond datasets, there are
986 recommendations for organizing file structures and documenting progress (Noble, 2009)
987 as well as programming itself (Wilson et al., 2014). Further, the discoverability of biological
988 data to mathematicians is key: ideally public data would be accompanied by information
989 including outstanding questions that mathematics may be able to solve or reasons why the
990 dataset should be explored in alternative ways to how it has already been analyzed. Well-
991 formatted data can be made public easily enough, but experimental metadata alone may
992 not be sufficient to generate further interest. While the above are attempts to make
993 biological data more accessible to mathematicians, the reciprocal direction of sharing is
994 less well represented. In fact, evidence suggests that using equations (one of the primary
995 means by which mathematicians share their work) impedes communication with biologists

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

33 <http://dir.t.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)

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

999

1000 **V. Conclusion: Unleashing geometric and topologic potential within the plant** 1001 **sciences**

1002

1003 The plant form is inherently architectural, from the shapes of leaves to the hierarchies in
1004 the branching patterns of shoots and roots. Plant morphology has served as an inspiration
1005 to mathematicians, who innovated new methods to quantify and model the plant form as a
1006 result of evolutionary, developmental and environmental responses (**Figures 1-2**). Plant
1007 morphology is an unresolved mystery to plant biologists, who seek to understand the
1008 molecular mechanisms by which such predetermined, yet seemingly endless variations of
1009 organizational patterns emerge.

1010

1011 Never have the resources to study plant morphology been more plentiful. Burgeoning
1012 imaging technologies—innovative confocal microscopy, X-ray imaging, MRI, radar,
1013 terrestrial laser scanning, among many others—have made detailed 3D models of plants
1014 feasible (**Figures 3-4**). Imaging across time and scales looks behind the curtains from the
1015 sub-cellular scale to the entirety of the earth surface. The mathematical methods to model
1016 plant morphology, from Turing’s reaction-diffusion processes to innovative shape
1017 descriptors, quantify the plant form to be used in a wide-variety of biological applications
1018 (**Figure 6**).

1019

1020 Yet, all models are idealizations of reality and seemingly simple problems remain
1021 unresolved in the study of plant morphology. Integrating observations at different scales is
1022 a persistent challenge. We discussed for example that the ability to model the fluttering of
1023 leaves within a tree canopy remains out of reach (**Figure 7**). Interest in the hidden half of
1024 plant morphology—the root system—has only recently seen a renaissance with
1025 technologies capable of penetrating soil and visualizing roots *in situ* (**Figure 5**). Not only is

1026 describing phenotype problematic, but linking it to a genetic and (especially in plants)
1027 environmental basis, within the context of plant evolution, is still an unattained goal. Never
1028 have the answers to these questions been more vital and timely. Modifying plant
1029 architecture through molecular biology and breeding is key to develop agricultural outputs
1030 and sustainability. Monitoring the morphology of plants in response to a shifting
1031 environment is necessary to model global responses to climate change. Cross-disciplinary
1032 training of scientists, citizen science, and open science are all necessary components to
1033 address these needs (**Figure 8**). Unleashing the potential of geometric and topological
1034 approaches in the plant sciences promises to transform our understanding of both plants
1035 and mathematics, and to meet the challenges posed by a future with dwindling and
1036 uncertain natural resources.

1037

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1039

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1044

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1046

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1051

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2110 **Figure Legends**

2111

2112 **Figure 1: Plant morphology from the perspective of biology. A)** Adapted from Kaplan
2113 (2001). Plant morphology interfaces with all disciplines of plant biology—plant physiology,
2114 plant genetics, plant systematics, and plant ecology—influenced by both developmental
2115 and evolutionary forces. **B)** Artistic rendering of Goethe’s *Urpflanze* concept (Goethe, 1837;
2116 Friedman and Diggle, 2011), demonstrating the importance of development in modulating
2117 the plant form. Goethe viewed the iterative development of plants as a transformation of
2118 lateral organ identities, from juvenile to adult leaves to reproductive structures. **C)**
2119 Evolutionary and ecological effects also shape plant morphology. Alexander von
2120 Humboldt’s distribution of plants across the elevations of Chimborazo (Ecuador)

2121 demonstrates the effects of evolution and environment on plant morphology (Black and
2122 Black, 1839).

2123

2124 **Figure 2: Plant morphology from the perspective of mathematics. A)** The topological
2125 complexity of plants requires a mathematical framework to describe plant morphology.
2126 Shown is the top of a maize crown root 42 days after planting. Color represents root
2127 diameter. Image provided by Jonathan Lynch and Johannes Postma (Pennsylvania State
2128 University). **B)** Persistent homology deforms a given plant morphology using functions to
2129 define self-similarity in a structure. In this example, a color map of geodesic distance
2130 functions to the ground level of a tree (blue indicates smaller values near the proximal base
2131 and red larger values at the distal tips) is recorded as **C)** an H_0 barcode, in which “births”
2132 and “deaths” of connected components as a function of the distance function are recorded.
2133 Images provided by Mao Li (Danforth Plant Science Center).

2134

2135 **Figure 3: Imaging techniques to capture plant morphology. A)** Confocal sections of an
2136 Arabidopsis root. The upper panel shows a new lateral root primordium at an early stage of
2137 development (highlighted in yellow). At regular intervals new roots branch from the
2138 primary root. The lower panel shows the primary root meristem and the stem cell niche
2139 (highlighted in yellow) from which all cells derive. Scale bars: 100 μ m. Images provided by
2140 Alexis Maizel (Heidelberg University). **B)** Computational tomographic (CT) x-ray sections
2141 through a reconstructed maize ear (left and middle) and kernel (right). Images provided by
2142 Chris Topp (Donald Danforth Plant Science Center). **C)** Laser ablation tomography (LAT)
2143 image of a nodal root from a mature, field-grown maize plant, with color segmentation
2144 showing definition of cortical cells, aerenchyma lacunae, and metaxylem vessels. Image
2145 provided by Jennifer Yang (Penn State).

2146

2147 **Figure 4: Terrestrial laser scanning creates a point cloud reconstruction of a Finnish**
2148 **forest. A)** Structure of a boreal forest site in Finland as seen with airborne (ALS) and
2149 terrestrial (TLS) laser scanning point clouds. The red (ground) and green (above ground)
2150 points are obtained from National Land Survey of Finland national ALS point clouds that

2151 cover hundreds of thousands of square kilometers with about 1 point per square meter
2152 resolution. The blue and magenta point clouds are results of two individual TLS
2153 measurements and have over 20 million points each within an area of about 500 square
2154 meters. TLS point density varies with range but can be thousands of points per square
2155 meter up to tens of meters away from the scanner position. **B)** An excerpt from a single TLS
2156 point cloud (blue). The TLS point cloud is so dense that individual tree point clouds
2157 (orange) and parts from them (yellow) can be selected for detailed analysis. **C)** A detail
2158 from a single TLS point cloud. Individual branches (yellow) 20 meters above ground can be
2159 inspected from the point cloud with centimeter level resolution to estimate their length
2160 and thickness. Images provided by Eetu Puttonen (Finnish Geospatial Research Institute in
2161 the National Land Survey of Finland). ALS data was obtained from the National Land
2162 Survey of Finland Topographic Database, 08/2012 (National Land Survey of Finland open
2163 data licence, version 1.0).

2164

2165 **Figure 5: The environmental basis of plant morphology.** Root system architecture of
2166 *Arabidopsis Col-0* plants expressing ProUBQ10:LUC2o growing in **A)** control and **B)** water-
2167 deficient conditions using the GLO-Roots system (Rellán-Álvarez et al., 2015). Images
2168 provided by Ruben Rellán-Álvarez (Laboratorio Nacional de Genómica para la
2169 Biodiversidad, CINVESTAV).

2170

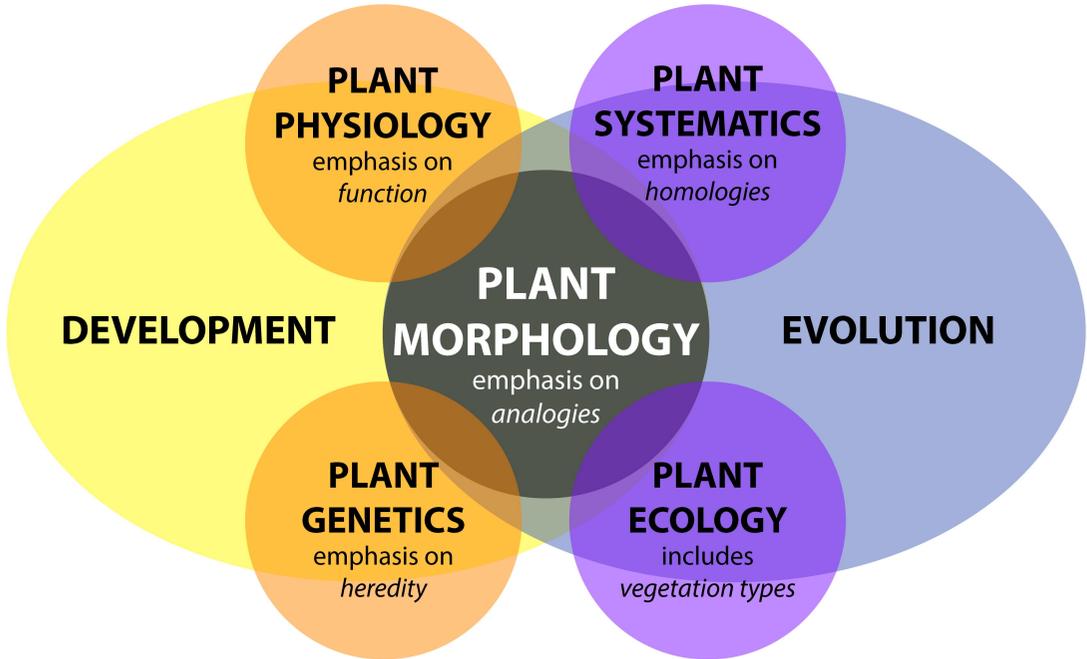
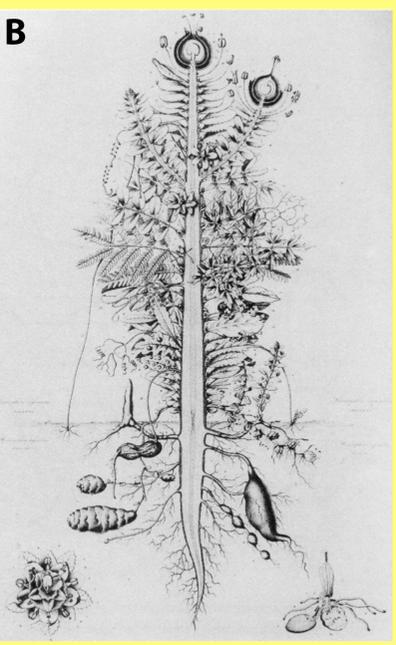
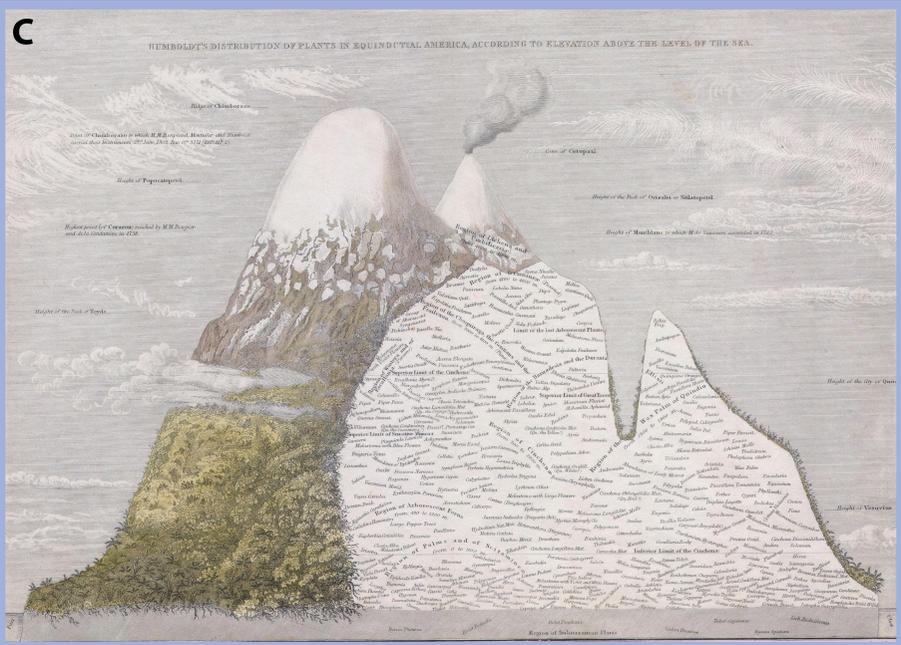
2171 **Figure 6: Integration of tissue growth and reaction-diffusion models.** **A)** Vertex model
2172 of cellular layers (Prusiniewicz and Lindenmayer, 2012). K , l_w and l_0 are the spring
2173 constant, current length, and rest length for wall a . K_p is a constant and S_A is the size of cell
2174 A . Δt is time step. Shown is a simulation of cell network growth. **B)** Reaction diffusion
2175 model of the shoot apical meristem for WUSCHEL and CLAVATA interactions (Fujita et al.,
2176 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
2177 positive constants. Shown are the distributions of WUS and CLV levels within a dynamic
2178 cell network. Images provided by Dorjsuren Battogtokh (Virginia Tech).

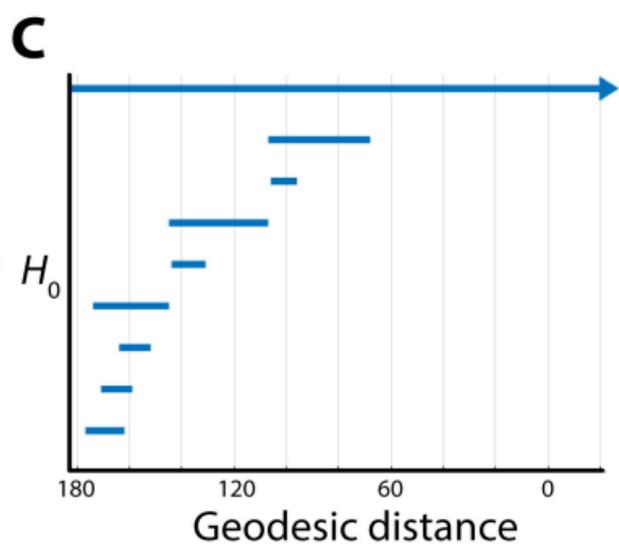
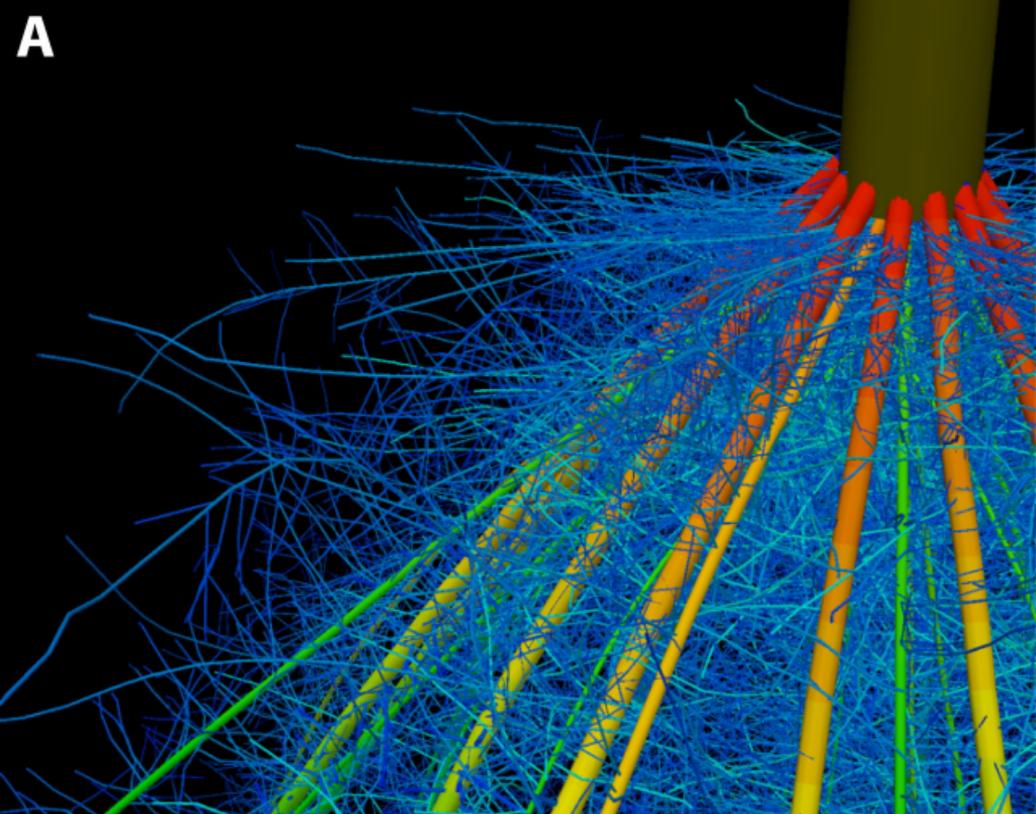
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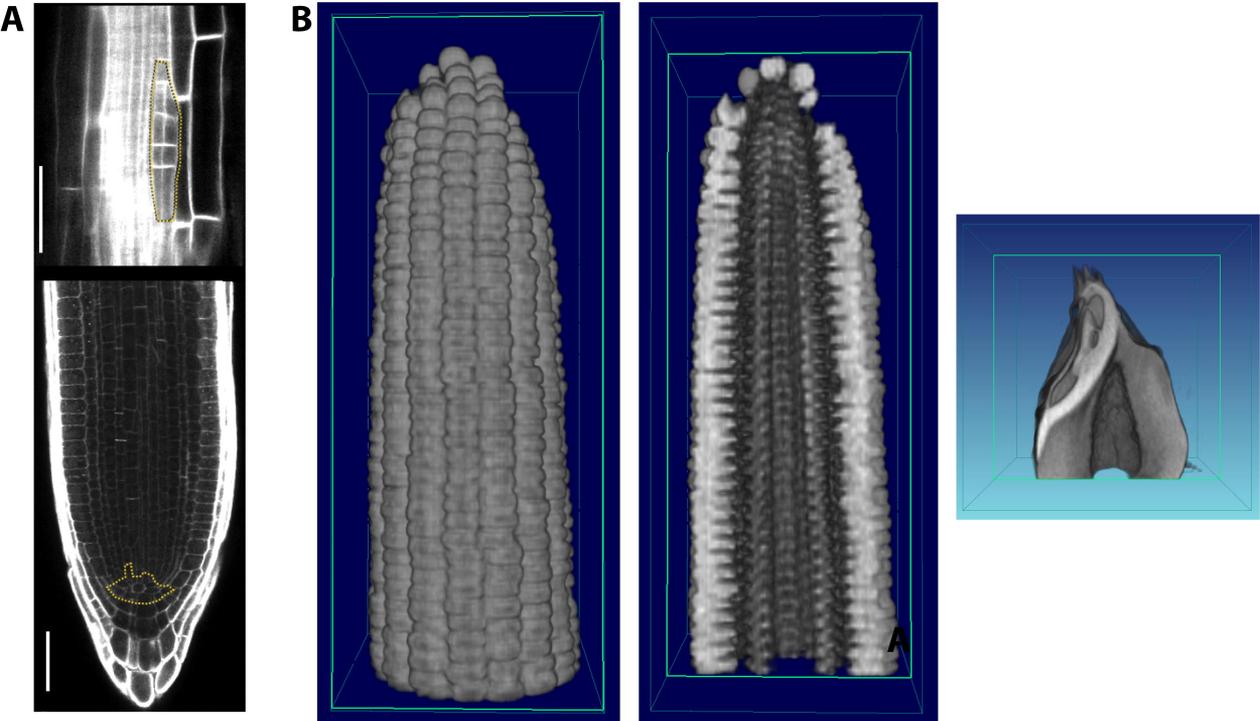
2180 **Figure 7: Modeling the interaction between plant morphology and fluid dynamics. A)**
2181 3D immersed boundary simulations of flow past a flexible rectangular sheet (left) and disk
2182 with a cut from the center to edge (right). Both structures are attached to a flexible petiole,
2183 and the flow is from left to right. The contours show the magnitude of vorticity (the
2184 rotation in the air). The circular disk reconfigures into a cone shape, similar to many broad
2185 leaves. **B)** Reconfiguration of tulip poplar leaves in 3 m/s (left) and 15 m/s flow (right). The
2186 leaves typically flutter at lower wind speeds and reconfigure into stable cones at high wind
2187 speeds. **C)** A cluster of redbud leaves in wind moving from right to left. The wind speed is
2188 increased from 3 m/s (left) to 6 m/s (middle) and 12 m/s (right). Note that the entire
2189 cluster reconfigures into a cone shape. This is different from the case of tulip poplars and
2190 maples where each leaf individually reconfigures into a conic shape. Images provided by
2191 Laura Miller (University of North Carolina, Chapel Hill).

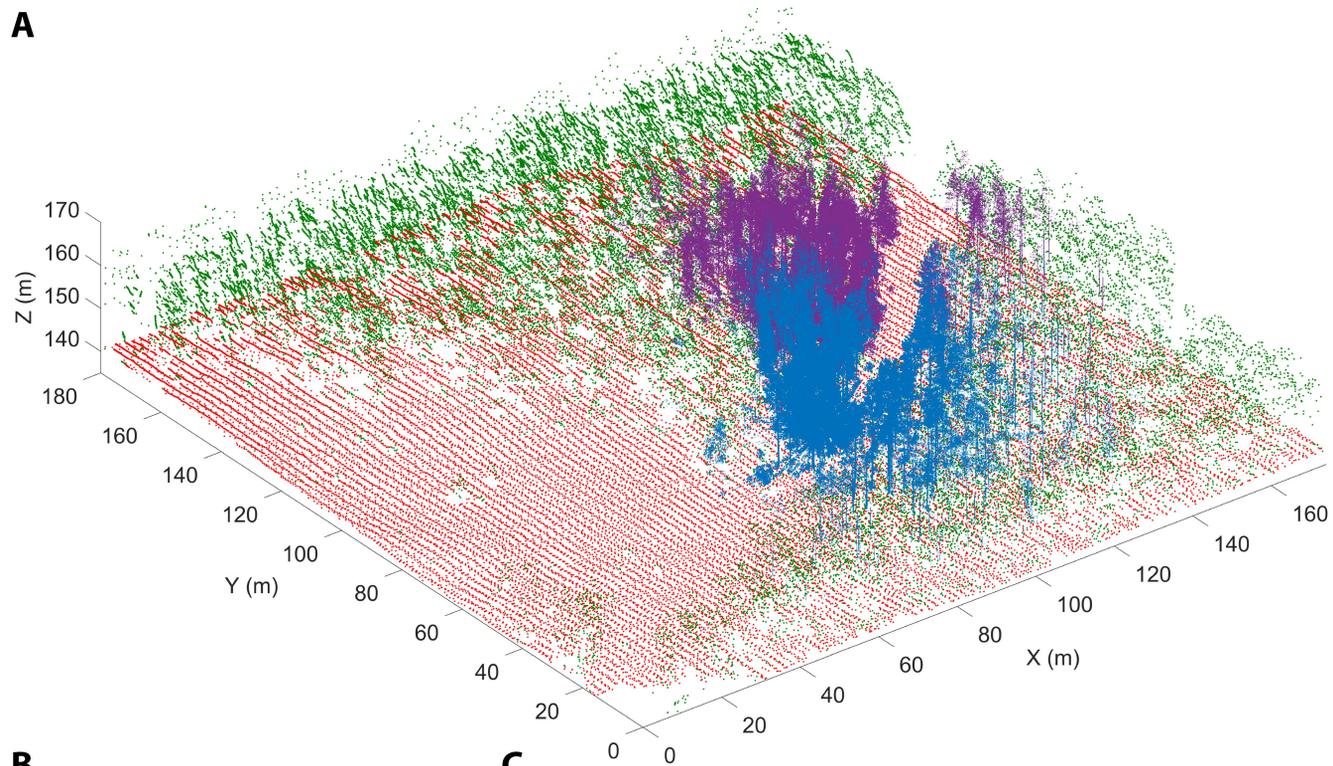
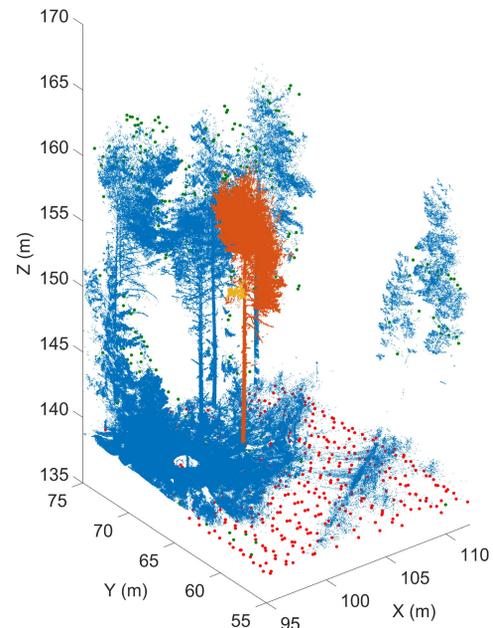
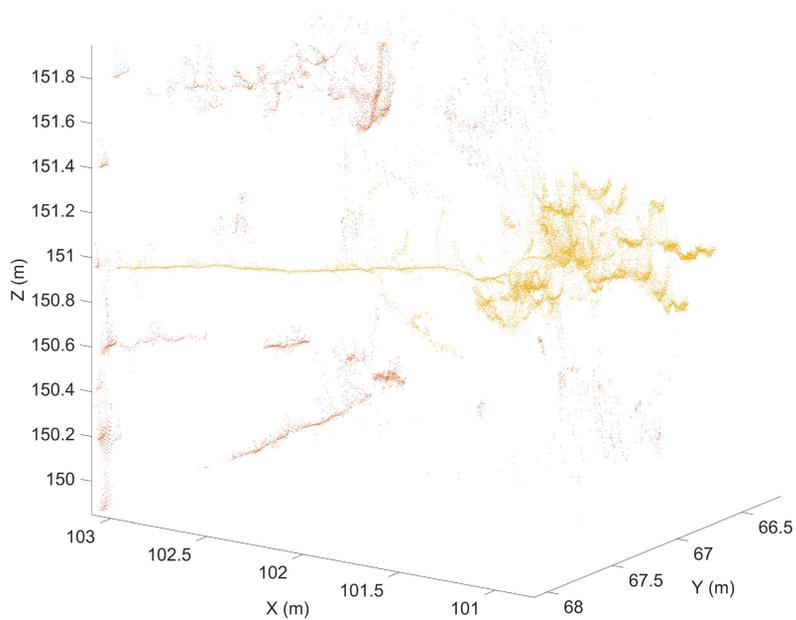
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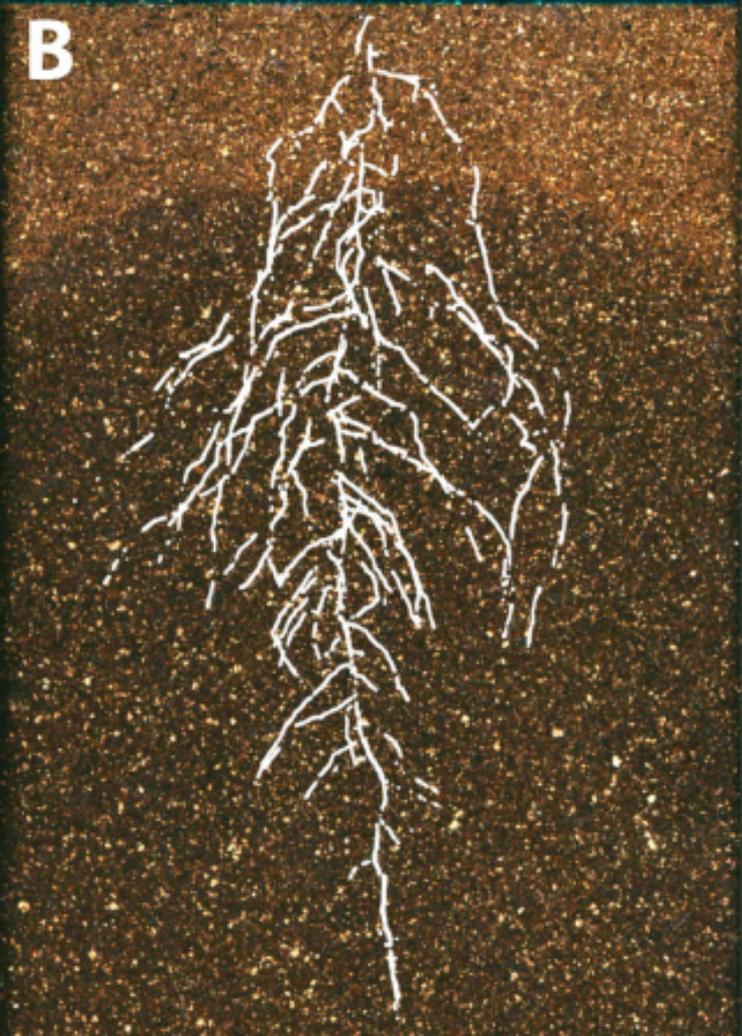
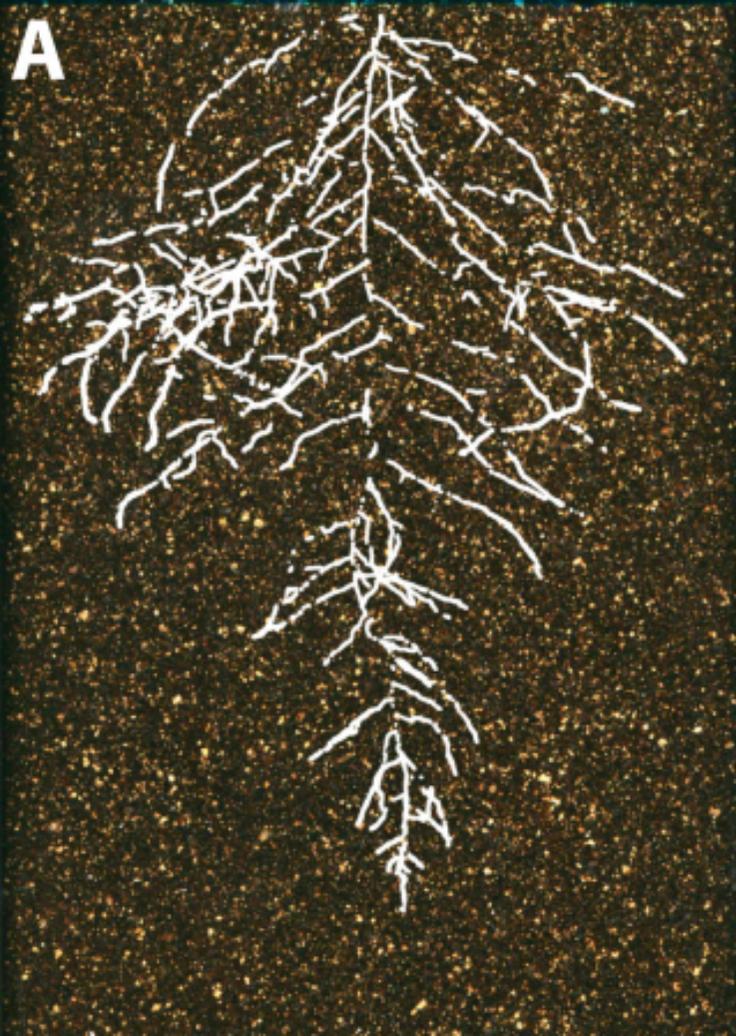
2193 **Figure 8: Milestones to accelerate the infusion of math into the plant sciences.** Group
2194 photo of the authors from the National Institute for Mathematical and Biological Synthesis
2195 (NIMBioS) meeting on plant morphological models (University of Tennessee, Knoxville,
2196 September 2-4, 2015) that inspired this manuscript. Workshops such as these, bringing
2197 mathematicians and plant biologists together, will be necessary to create a new synthesis
2198 of plant morphology.

A**B****C**





A**B****C**



ATotal force on a vertex i

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

Spring force on a wall a

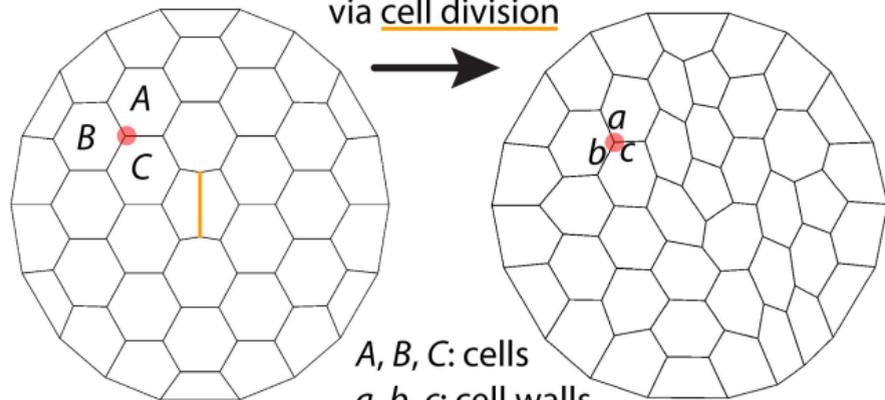
$$\vec{F}_s^a = -K(l_a - l_0)$$

Turgor pressure 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

$$\vec{x}_i(t + \Delta t) = \vec{x}_i(t) + \vec{F}_i^T \Delta t$$

Tissue growth
via cell division

A, B, C : cells
 a, b, c : cell walls
 ● vertex: i

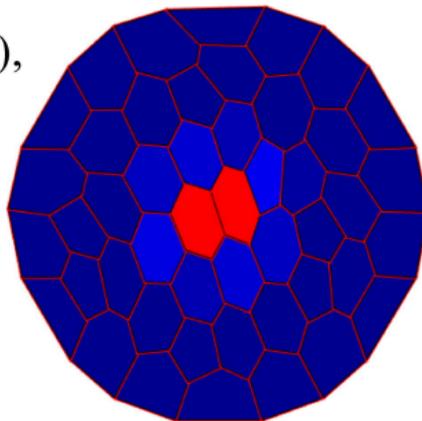
B

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

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

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

WUSCHEL



CLAVATA

