

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

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73 **Abstract**

74

75 Plant morphology is inherently mathematical in that morphology describes plant form and
76 architecture with geometrical and topological descriptors. The geometries and topologies
77 of leaves, flowers, roots, shoots and their spatial arrangements have fascinated plant
78 biologists and mathematicians alike. Beyond providing aesthetic inspiration, quantifying
79 plant morphology has become pressing in an era of climate change and a growing human
80 population. Modifying plant morphology, through molecular biology and breeding, aided by
81 a mathematical perspective, is critical to improving agriculture, and the monitoring of
82 ecosystems with fewer natural resources. In this white paper, we begin with an overview of
83 the mathematical models applied to quantify patterning in plants. We then explore
84 fundamental challenges that remain unanswered concerning plant morphology, from the
85 barriers preventing the prediction of phenotype from genotype to modeling the movement
86 of leaflets in air streams. We end with a discussion concerning the incorporation of plant
87 morphology into educational programs. This strategy focuses on synthesizing biological
88 and mathematical approaches and ways to facilitate research advances through outreach,
89 cross-disciplinary training, and open science. This white paper arose from bringing
90 mathematicians and biologists together at the National Institute for Mathematical and
91 Biological Synthesis (NIMBioS) workshop titled “Morphological Plant Modeling: Unleashing
92 Geometric and Topological Potential within the Plant Sciences” held at the University of
93 Tennessee, Knoxville in September, 2015. Never has the need to quantify plant
94 morphology been more imperative. Unleashing the potential of geometric and topological
95 approaches in the plant sciences promises to transform our understanding of both plants
96 and mathematics.

97

98 **I. Introduction**

99

100 *A. Morphology from the perspective of plant biology*

101

102 The study of plant morphology interfaces with all levels of biological organization (**Figure**
103 **1**). Plant morphology can be descriptive and categorical, as in systematics, which focuses
104 on biological homologies to discern groups of organisms (Mayr, 1981; Wiens, 2000). In
105 plant ecology, the morphology of communities defines vegetation types and biomes,
106 including their relationship to the environment. In turn, plant morphologies are mutually
107 informed by other fields of study, such as plant physiology, the study of the functions of
108 plants, plant genetics, the description of inheritance, and molecular biology, the underlying
109 gene regulation (Kaplan, 2001).

110

111 Plant morphology is more than an attribute affecting plant organization, it is also dynamic.
112 Developmentally, morphology reveals itself over the lifetime of a plant through varying
113 rates of cell division, cell expansion, and anisotropic growth (Esau, 1960; Steeves and
114 Sussex, 1989; Niklas, 1994). Response to changes in environmental conditions further
115 modulate the abovementioned parameters. Development is genetically programmed and
116 driven by biochemical processes that are responsible for physical forces that change the
117 observed patterning and growth of organs (Green, 1999; Peaucelle et al., 2011; Braybrook
118 and Jönsson, 2016). In addition, external physical forces affect plant development, such as
119 heterogeneous soil densities altering root growth or flows of air, water, or gravity
120 modulating the bending of branches and leaves (Mouliia & Fournier, 2009). Inherited
121 modifications of structure or development, either incrementally or abruptly, over
122 generations results in the evolution of plant morphology (Niklas, 1997). A record of these
123 changes over geologic time is preserved through fossils and correlates with the
124 paleoclimate, which contributes to our understanding of morphology in extant plants
125 today (Bailey and Sinnott, 1915). Development and evolution are the biological
126 mechanisms through which plant morphology arises, regardless of whether in a systematic,
127 ecological, physiological, or genetic context (**Figure 1**).

128

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

130

131 In 1790 Johann Wolfgang von Goethe pioneered a perspective that transformed the way
132 mathematicians think about plant morphology: the idea that the essence of plant
133 morphology is an underlying repetitive process of deformation (Goethe, 1790; Friedman
134 and Diggle, 2011). The modern challenge that Goethe's paradigm presents is to
135 quantitatively describe deformations resulting from differences in the underlying genetic,
136 developmental, and environmental cues. From a mathematical perspective, the challenge is
137 how to define shape descriptors to compare, and generation processes to simulate, plant
138 morphology with topological and geometrical techniques.

139

140 *1. Mathematics to describe plant shape and morphology*

141 Several areas of mathematics can be used to extract quantitative measures of plant shape
142 and morphology. One intuitive representation of the plant form relies on the use of skeletal
143 descriptors that reduce the branching morphology of plants to a set of intersecting lines or
144 curve segments, constituting a mathematical graph. These skeleton-based mathematical
145 graphs can be derived from manual measurement (Godin et al., 1999; Watanabe et al.,
146 2005) or imaging data (Bucksch et al., 2010; Bucksch 2011; Bucksch, 2014a; Aiteanu and
147 Klein, 2014). Such skeletal descriptions can be used to derive quantitative measurements
148 of lengths, diameters, and angles in tree crowns (Bucksch and Fleck, 2011; Raunonen et al.,
149 2013; Seidel et al., 2015) and roots, at a single time point (Fitter, 1987; Danjon et al., 1999;
150 Lobet et al., 2011; Galkovskyi et al., 2012) or over time to capture growth dynamics
151 (Symonova et al., 2015). Having a skeletal description in place allows the definition of
152 orders, in a biological and mathematical sense, to enable morphological analysis from a
153 topological perspective (**Figure 2A**). Topological analyses can be used to compare shape
154 characteristics independently of events that deform and transform plant shape
155 geometrically, providing a framework by which plant morphology can be modeled. The
156 relationships between orders, such as degree of self-similarity (Prusinkiewicz, 2004) or
157 self-nestedness (Godin and Ferraro, 2010) are used to quantitatively summarize patterns
158 of plant morphology. Persistent homology (**Figure 2B**), an extension of Morse theory
159 (Milnor, 1963), deforms a given plant shape gradually to define self-similarity (MacPherson

160 and Schweinhardt, 2012) and morphological properties (Edelsbrunner and Harer, 2010)
161 on the basis of topological event statistics. In the example in **Figure 2B**, topological events
162 are represented by the geodesic distance at which branches are “born” and “die” along the
163 length of the structure.

164

165 Traditionally, descriptors that compare outlines of plant organs independently of scale,
166 rotation, and translation have been used to quantify morphologies. However, in the 1980s,
167 David Kendall defined an elegant alternative statistical framework to these descriptors
168 (Kendall, 1984). His idea was to compare the outline of shapes in a transformation-
169 invariant fashion, which fulfills the parameters of the mathematical concept of shape. This
170 concept infused rapidly as morphometrics into biology (Bookstein, 1997) and is
171 increasingly carried out using machine vision techniques (Wilf et al., 2016). Kendall’s idea
172 inspired the development of methods such as elliptical Fourier descriptors (Kuhl and
173 Giardina, 1982) and new trends employing the Laplace Beltrami operator (Reuter et al.,
174 2009), both relying on the spectral decompositions of shapes (Chitwood et al., 2012a;
175 Chitwood et al., 2012b; Laga et al. 2014; Rellán-Álvarez et al., 2015). Beyond the organ
176 level, such morphometric descriptors were used to analyze cellular expansion rates of
177 rapidly deforming primordia into mature organ morphologies (Rolland-Lagan et al., 2003;
178 Remmler and Rolland-Lagan, 2012; Das Gupta and Nath, 2015).

179

180 Parallel to strictly mathematical descriptions of plant morphology, Ronald Fisher
181 developed a statistical framework to partition variance into different sources of variability
182 (Fisher, 1925). Specifically, with respect to plant morphology, the *Iris* flower dataset
183 (Fisher, 1936) was used to develop novel methods to differentiate three *Iris* species based
184 on the length and width of sepals and petals.

185

186 From a geometric perspective, developmental processes construct surfaces in a three-
187 dimensional space. Yet, this space in which development is embedded imposes constraints
188 on plant forms observed. Awareness of these constraints has led to new interpretations of

189 plant morphology (Prusinkiewicz and DeReuille, 2010; Bucksch et al., 2014b) that might
190 provide avenues to explain symmetry or asymmetry in leaf shape (Martinez et al., 2016) or
191 the occurrence of plasticity in leaf shape as the morphological response of plants to
192 environmental changes over developmental and evolutionary timescales (Royer et al.,
193 2009; Chitwood et al., 2016).

194

195 *2. Mathematics to simulate plant morphology*

196 Computer simulations use principles from graph theory, such as graph rewriting, to model
197 plant morphology over developmental time by successively augmenting a graph with
198 vertices and edges as plant development unfolds using observed rules (Hallé, 1971). These
199 rules unravel the differences between observed plant morphologies across plant species
200 (Kurth, 1994; Prusinkiewicz et al., 2001; Barthélémy and Caraglio, 2007) and are capable of
201 modeling fractal descriptions that reflect the repetitive and modular appearance of
202 branching structures (Horn, 1971, Hallé, 1986). Recent developments in graph theory
203 abstract the genetic mechanisms driving the developmental program of tree crown
204 morphology into a computational framework (Runions et al., 2007; Palubicki et al., 2009;
205 Palubicki, 2013). Equivalently, functional-structural models of roots can be utilized to
206 simulate the efficiency of nutrient and water uptake following developmental programs
207 (Nielsen et al., 1994; Dunabin et al., 2013).

208

209 Alan Turing, a pioneering figure in twentieth-century science, had a longstanding interest
210 in phyllotactic patterns. Turing's approach to the problem was twofold: first, a detailed
211 geometrical analysis of the patterns (Turing, 1992), and second, an application of his
212 theory of morphogenesis through local activation and long-range inhibition (Turing, 1952),
213 which defined the first reaction-diffusion system for morphological modeling. Combining
214 physical experiments with computer simulations, Douady and Couderc (1996)
215 subsequently modeled a diffusible chemical produced by a developing primordium that
216 would inhibit the initiation of nearby primordia, successfully recapitulating known
217 phyllotactic patterns in the shoot apical meristem (Bernasconi, 1994; Meinhardt, 2004;

218 Hohm et al., 2010; Fujita et al., 2011), the number of floral organs (Kitazawa and Fujimoto,
219 2015), the regular spacing of root hairs (Meinhardt and Gierer, 1974), and the
220 establishment of specific vascular patterns (Meinhardt, 1976).

221

222 **II. Emerging questions and barriers in the mathematical analysis of plant** 223 **morphology**

224

225 A true synthesis of plant morphology, which comprehensively models observed biological
226 phenomena and incorporates a mathematical perspective, remains elusive. In this section
227 we highlight current focuses in the study of plant morphology, including the technical
228 limits of acquiring morphological data, phenotype prediction, responses of plants to the
229 environment, models across biological scales, and the integration of complex phenomena,
230 such as fluid dynamics, into plant morphological models.

231

232 *A. Technological limits acquiring plant morphological data*

233

234 There are several technological limits to acquiring plant morphological data that must be
235 overcome to move this field forward. One such limitation is the acquisition of quantitative
236 plant images. Traditionally, many acquisition systems do not provide morphological data
237 with measurable units. Approaches that rely on the reflection of waves from the plant
238 surface can provide quantitative measurements for morphological analyses. Time of flight
239 scanners, such as terrestrial laser scanning, overcome unit-less measurement systems by
240 recording the round-trip time of hundreds of thousands of laser beams sent at different
241 angles from the scanner to the first plant surface within the line of sight (Vosselman and
242 Maas, 2010) (**Figure 3**). Leveraging the speed of light allows calculation of the distance
243 between a point on the plant surface and the laser scanner. Laser scanning and the
244 complementary approach of stereovision both produce surface samples or point clouds as
245 output. However, both approaches face algorithmic challenges encountered when plant
246 parts occlude each other, since both rely on the reflection of waves from the plant surface

247 (Bucksch, 2014a). Radar provides another non-invasive technique to study individual tree
248 and forest structures over wide areas. Radar pulses can either penetrate or reflect from
249 foliage, depending on the selected wavelength (Kaasalainen et al., 2015). Most radar
250 applications occur in forestry and are being operated from satellites or airplanes. Although
251 more compact and agile systems are being developed for precision forestry above- and
252 below-ground (Feng et al., 2016), their resolution is too low to acquire the detail in
253 morphology needed to apply hierarchy or similarity oriented mathematical analysis
254 strategies.

255

256 Image techniques that utilize penetration of the plant tissue to resolve occlusions are
257 possible with X-ray (Kumi et al., 2015) and magnetic resonance imaging (MRI; van
258 Dusschoten et al., 2016). While both technologies resolve occlusions and can even
259 penetrate soil, their limitation is the requirement of a closed imaging volume. Thus,
260 although useful for a wide array of purposes, MRI and X-ray are potentially destructive if
261 applied to mature plant organs such as roots in the field or tree crowns that are larger than
262 the imaging volume (Fiorani et al., 2012). Interior plant anatomy can be imaged using
263 confocal microscopy and laser ablation (**Figure 4**) or nano- or micro-CT tomography
264 techniques, that are limited to small pot volumes, to investigate the first days of plant
265 growth.

266

267 *B. The genetic basis of plant morphology*

268

269 One of the outstanding challenges in plant biology is to link the inheritance and activity of
270 genes with observed phenotypes. This is particularly challenging for the study of plant
271 morphology, as both the genetic landscape and morphospaces are complex: modeling each
272 of these phenomena alone is difficult, let alone trying to model morphology as a result of
273 genetic phenomena (Benfey and Mitchell-Olds, 2008; Lynch and Brown, 2012; Chitwood
274 and Topp, 2015). Although classic examples exist in which plant morphology is radically
275 altered by the effects of a few genes (Doebley, 2004; Clark et al., 2006; Kimura et al., 2008),

276 many morphological traits have a polygenic basis (Langlade et al., 2005; Tian et al., 2011;
277 Chitwood et al., 2013; 2014b).

278

279 Quantitative trait locus (QTL) analyses can identify the polygenic basis for morphological
280 traits that span scales from the cellular to the whole organ level. At the cellular level, root
281 cortex cell number (Ron et al., 2013), the cellular basis of carpel size (Frary et al., 2000),
282 and epidermal cell area and number (Tisne et al., 2008) have been analyzed. The genetic
283 basis of cellular morphology ultimately affects organ morphology, and quantitative genetic
284 bases for fruit shape (Monforte, et al., 2014; Paran and van der Knaap, 2007), root
285 morphology (Zhu et al., 2005; Clark et al., 2011; Topp et al., 2013; Zurek, et al., 2015), shoot
286 apical meristem shape (Thompson et al., 2015; Leiboff et al., 2015), leaf shape (Langlade et
287 al., 2005; Ku et al., 2010; Tian et al., 2011; Chitwood et al., 2013; 2014a; 2014b; Zhang et al.,
288 2014; Truong et al., 2015), and tree branching (Kenis and Keulemans, 2007; Segura et al.,
289 2009) have been described.

290

291 Natural variation in cell, tissue, or organ morphology ultimately impacts plant physiology.
292 For example, root cortical aerenchyma formation reduces the metabolic costs of soil
293 exploration, thereby improving plant growth under conditions of suboptimal availability of
294 water and nutrients (Zhu et al. 2010; Postma and Lynch, 2011; Lynch et al., 2013). Maize
295 genotypes with greater root cortical cell size or reduced root cortical cell file number also
296 have reduced metabolic costs, and therefore root deeper to increase water capture under
297 drought (Chimungu et al., 2015). The radial distribution of auxin in the rice root leads to
298 differential cell expansion and deeper root angles, resulting in greater water capture in
299 soils with retracting water tables (Uga et al., 2013).

300

301 High-throughput phenotyping techniques are increasingly used to reveal the genetic basis
302 of natural variation. In doing so, phenotyping techniques complement classic approaches of
303 reverse genetics and often lead to novel insights, even in a well-studied species like
304 *Arabidopsis thaliana*. Phenotyping techniques have revealed a genetic basis for such

305 dynamic traits as root growth (Slovack et al., 2014). Similarly, high-resolution sampling of
306 root gravitropism has led to an unprecedented understanding of the dynamics of the
307 genetic basis of plasticity (Miller et al., 2007; Brooks et al., 2010; Spalding and Miller,
308 2013).

309

310 *C. The environmental basis of plant morphology*

311

312 Plasticity is defined as the ability of one genotype to produce different phenotypes based
313 on environment (Bradshaw 1965; DeWitt and Scheiner, 2004) and adds to the phenotypic
314 complexity created by genetics and development. Trait variation in response to the
315 environment has been defined classically using reaction norms (originally
316 “Reaktionsnorm”) where the value of a certain trait is plotted against different
317 environments (Woltereck, 1909). If the reaction norm line is flat, the trait is not plastic and
318 can be considered canalized across environments; if the reaction norm varies across the
319 environment the trait is plastic and the slope of the reaction norm line will be a measure of
320 the plasticity. Significant differences in slopes among genotypes indicate a genotype by
321 environment (GxE) interaction (Via and Lande, 1985).

322

323 Seminal work by Clausen, Keck, and Hiesey (1941) demonstrated using several clonal
324 species in a series of reciprocal transplants that, although heredity exerts the most
325 measureable effects on plant morphology, environment is also a major source of
326 phenotypic variability. Research continues to explore the range of phenotypic variation
327 expressed by a given genotype in the context of different environments, which has
328 important implications for many fields, including conservation, evolution, and agriculture
329 (Nicotra et al., 2010; DeWitt, 2016). Many studies examine phenotypes across latitudinal or
330 altitudinal gradients, or other environmental clines, to characterize the range of possible
331 variation and its relationship to local adaptation processes (Cordell et al. 1998; Díaz et al.,
332 2016).

333

334 Below-ground, plants encounter diverse sources of environmental variability, including
335 water availability, soil chemistry, and physical properties like soil hardness and movement.
336 These factors vary between individual plants (Razak et al., 2013) and within an individual
337 root system, where plants respond at spatio-temporal levels to very different granularity
338 (Drew, 1975; Robbins and Dinneny, 2015). Plasticity at a micro-environmental scale has
339 been linked to developmental and molecular mechanisms (Bao et al., 2014). The scientific
340 challenge here is to integrate these effects at a whole root system level and use different
341 scales of information to understand the optimal acquisition in resource limited conditions
342 (Rellán-Álvarez, et al., 2016) (**Figure 5**).

343

344 *D. Integrating models from different levels of organization*

345

346 Since it is extremely difficult to examine complex interdependent processes occurring at
347 multiple spatio-temporal scales, mathematical modeling can be used as a complementary
348 tool with which to disentangle component processes and investigate how their coupling
349 may lead to emergent patterns at a systems level (Hamant, 2008; Band and King, 2012;
350 Jenzen and Fozard 2015; Band et al. 2012). To be practical, a multiscale model should
351 generate well-constrained predictions despite significant parameter uncertainty
352 (Gutenkunst et al., 2007, Hofhuis et al., 2016). It is desirable that a multiscale model has
353 certain modularity in its design such that individual modules are responsible for modeling
354 specific spatial aspects of the system (Baldazzi et al., 2012). Global sensitivity analysis can
355 be applied to reveal how individual modules function when other modules are perturbed
356 (Sudret, 2008). Most importantly, a multiscale model must be tested against available data
357 (Gordon et al. 2009, Chickarmane et al. 2010, Sahlin et al. 2011, Shapiro et al. 2013, Willis
358 et al. 2016).

359

360 To illustrate the challenges of multi-scale modeling, we highlight an example that
361 encompasses molecular and cellular scales. At the molecular scale, models can treat some
362 biomolecules as diffusive, but others, such as membrane-bound receptors, can be spatially

363 restricted (Fujita et al., 2011; Battogtokh and Tyson, 2016). Separately, at the cellular scale,
364 mathematical models describe dynamics of cell networks where the mechanical pressures
365 exerted on the cell walls are important factors for cell growth and division (Jensen and
366 Fozard, 2015) (**Figure 6A**). In models describing plant development in a two-dimensional
367 cross-section geometry, cells are often modeled as polygons defined by walls between
368 neighboring cells. The spatial position of a vertex, where the cell walls of three neighboring
369 cells coalesce, is a convenient variable for mathematical modeling of the dynamics of
370 cellular networks (Prusinkiewicz and Lindenmayer, 2012). A multiscale model can then be
371 assembled by combining the molecular and cellular models. Mutations and deletions of the
372 genes encoding the biomolecules can be modeled by changing parameters. By inspecting
373 the effects of such modifications on the dynamics of the cellular networks, the relationship
374 between genotypes and phenotypes can be predicted. For example, Fujita et al. (2011)
375 model integrates the dynamics of cell growth and division with the spatiotemporal
376 dynamics of the proteins involved in stem cell regulation and simulates shoot apical
377 meristem development in wild type and mutants plants (**Figure 6B**).

378

379 *E. Modeling the impact of morphology on plant function*

380

381 Quantitative measures of plant morphology are critical to understand function. In one
382 example, leaf shape and material properties that alter the boundary layer of the fluid over
383 the surface of the leaf or enhance passive movement can potentially augment gas and heat
384 exchange. For example, it has been proposed that the broad leaves of some trees flutter for
385 the purpose of convective and evaporative heat transfer (Thom, 1968; Grant, 1983).

386 Fluttering may also allow more light to penetrate the canopy (Roden and Pearcy, 1993).

387

388 The morphology and mechanical properties of leaves can alter the boundary layer. For
389 example, trichomes, the hair-like protrusions on the surfaces of leaves, can effectively
390 thicken the boundary layer around a leaf under some conditions (Benz and Martin, 2006)
391 and increase turbulence (Schreuder et al., 2001). Any movement of the leaf relative to the

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

396

397 Vogel (1989) was the first to provide quantitative data on drag reduction in plants. He
398 found that single broad leaves reconfigure at high flow velocities into cone shapes that
399 reduce flutter and drag when compared to paper cut-outs of similar shape and flexibility
400 (**Figure 7A-B**). Subsequent experimental studies on broad leaves, compound leaves, and
401 flowers also support rapid repositioning in response to strong currents as a general
402 mechanism to reduce drag (Vogel, 1989; Niklas, 1992; Ennos, 1997; Etnier and Vogel, 2000;
403 Vogel, 2006) (**Figure 7C**).

404

405 **III. Milestones in education and outreach to accelerate the infusion of math into the** 406 **plant sciences**

407

408 In a world increasingly geared towards a quantitative mindset and with dwindling natural
409 resources both mathematics and plant biology are timely disciplines. These disciplines
410 need to come together through opportunities to interact, including cross-disciplinary
411 training, workshops, meetings, and funding opportunities. Both fields can immediately
412 benefit from more open approaches to science. In this section, we outline perspectives for
413 enhancing the crossover between mathematics and plant biology.

414

415 *A. Education*

416

417 Mathematics has been likened to “biology’s next microscope”, because of the insights into
418 an otherwise invisible world it has to offer. Conversely, biology has been described as
419 “mathematics’ next physics”, stimulating novel mathematical approaches because of the
420 hitherto unrealized phenomena that biology studies (Cohen, 2004). The scale of the needed

421 interplay between mathematics and plant biology is enormous and may lead to new science
422 disciplines at the interface of both: ranging from the cellular, tissue, organismal, and
423 community levels to the global; touching upon genetic, transcriptional, proteomic,
424 metabolite, and morphological data; studying the dynamic interactions of plants with the
425 environment or the evolution of new forms over geologic time; and spanning
426 quantification, statistics, and mechanistic mathematical models.

427
428 Research is becoming increasingly interdisciplinary, and undergraduate, graduate, and
429 post-graduate groups are actively trying to bridge the archaic separation between
430 mathematics and biology skillsets. While many graduate programs have specialization
431 tracks under the umbrella of mathematics or biology-specific programs, more frequently
432 departments are forming specially designed graduate groups for mathematical biology. We
433 emphasize the need for more of these graduate groups and the incorporation of
434 mathematics into biology graduate education. This will necessitate team-teaching across
435 disciplines to train the next generation of mathematical biologists.

436
437 *B. Public outreach: Citizen science and the maker movement*

438
439 Citizen science, which is a method to make the general public aware of scientific problems
440 and employ their help in solving them¹, is an ideal platform to initiate a synthesis between
441 plant biology and mathematics because of the relatively low cost and accessibility of each
442 field. Arguably, using citizen science to collect plant morphological diversity has already
443 been achieved, but has yet to be fully realized. In total, it is estimated that the herbaria of
444 the world possess greater than 207 million voucher specimens², representing the diverse
445 lineages of land plants collected over their respective biogeographies over a timespan of
446 centuries. Digital documentation of the millions of vouchers held by the world's botanic
447 gardens is actively underway, allowing for researchers and citizens alike to access and

¹ 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)

² List of herbaria, https://en.wikipedia.org/wiki/List_of_herbaria (retrieved May 29, 2016)

448 study for themselves the wealth of plant diversity across the globe and centuries (Smith et
449 al., 2003; Corney et al., 2012; Ryan, 2013).

450

451 The developmental changes in plants responding to environmental variability and
452 microclimatic changes over the course of a growing season can be analyzed by studying
453 phenology. Citizen science projects such as the USA National Phenology Network³ or
454 Earthwatch⁴ and associated programs such as My Tree Tracker⁵ document populations and
455 individual plants over seasons and years, providing a distributed, decentralized network of
456 scientific measurements to study the effects of climate change on plants.

457

458 Citizen science is also enabled by low-cost, specialized equipment. Whether programing a
459 camera to automatically take pictures at specific times or automating a watering schedule
460 for a garden, the maker movement—a do-it-yourself cultural phenomenon that intersects
461 with hacker culture—focuses on building custom, programmable hardware, whether via
462 electronics, robotics, 3D-printing, or time-honored skills such as metal- and woodworking.
463 The focus on programming is especially relevant for integrating mathematical approaches
464 with plant science experiments. The low-cost of single-board computers (like Raspberry Pi,
465 Hummingboard, or Cubieboard) makes tinkering more permissive for a greater population
466 of citizen scientists than previously feasible.

467

468 *C. Workshops and funding opportunities*

469

470 Simply bringing mathematicians and plant biologists together to interact, to learn about
471 tools, approaches, and opportunities in each discipline that researchers may not be aware
472 of, is a major opportunity for the full integration of these two disciplines. This white paper
473 itself is a testament to the power of bringing mathematicians and biologists together,
474 resulting from a National Institute for Mathematical and Biological Synthesis (NIMBioS)

³ <https://www.usanpn.org/#> (retrieved May 29, 2016)

⁴ <http://earthwatch.org/scientific-research/special-initiatives/urban-resiliency> (retrieved May 29, 2016)

⁵ <http://www.mytreetracker.org/cwis438/websites/MyTreeTracker/About.php?WebSiteID=23> (retrieved May 29, 2016)

475 workshop titled “Morphological Plant Modeling: Unleashing Geometric and Topologic
476 Potential within the Plant Sciences”, held at the University of Tennessee, Knoxville
477 September 2-4, 2015⁶ (**Figure 8**). Other mathematical institutes such as the Mathematical
478 Biology Institute (MBI) at Ohio State University⁷, the Statistical and Applied Mathematical
479 Sciences Institute (SAMSI) in Research Triangle Park⁸, the Institute for Mathematics and Its
480 Applications at University of Minnesota⁹, and the Centre for Plant Integrative Biology at the
481 University of Nottingham¹⁰ have also hosted workshops for mathematical and quantitative
482 biologists from the undergraduate student to the faculty level.

483
484 There are efforts to unite biologists and mathematics through initiatives brought forth
485 from The National Science Foundation, including Mathematical Biology Programs¹¹ and the
486 Joint DMS/NIGMS Initiative to Support Research at the Interface of the Biological and
487 Mathematical Sciences¹² (DMS/NIGMS). Outside of the Mathematics and Life Sciences
488 Divisions, the Division of Physics houses a program on the Physics of Living Systems.
489 Societies such as The Society for Mathematical Biology and the Society for Industrial and
490 Applied Mathematics (SIAM) Life Science Activity Group¹³ are focused on the dissemination
491 of research at the intersection of math and biology, creating many opportunities to present
492 research and provide funding. We emphasize the importance that funding opportunities
493 have had and will continue to have in the advancement of plant morphological modeling.

494
495 *D. Open Science*

496

⁶ http://www.nimbios.org/workshops/WS_plantmorph (retrieved May 29, 2016)

⁷ <https://mbi.osu.edu/> (retrieved May 29, 2016)

⁸ <http://www.samsi.info/> (retrieved May 29, 2016)

⁹ <https://www.ima.umn.edu/> (retrieved May 29, 2016)

¹⁰ <https://www.qpic.ac.uk/outreach/qpic-summer-school/> (retrieved May 29, 2016)

¹¹ https://www.nsf.gov/funding/pgm_summ.jsp?pims_id=5690 (retrieved May 29, 2016)

¹² http://www.nsf.gov/funding/pgm_summ.jsp?pims_id=5300&org=DMS (retrieved May 29, 2016)

¹³ <https://www.siam.org/activity/life-sciences/> (retrieved May 29, 2016)

497 Ultimately, mathematicians, computational scientists, and plant biology must unite at the
498 level of jointly collecting data, analyzing it, and doing science together. Open and timely
499 data sharing to benchmark code is a first step to unite these disciplines along with building
500 professional interfaces to bridge between the disciplines (Bucksch et al, 2016).

501
502 A number of platforms provide open, public access to datasets, figures, and code that can be
503 shared, including Dryad¹⁴, Dataverse¹⁵, and Figshare¹⁶. Beyond the ability to share data is
504 the question of open data formats and accessibility. For example, in remote sensing
505 research it is unfortunately common that proprietary data formats are used, which
506 prevents their use without specific software. This severely limits the utility and community
507 building aspects of plant morphological research. Beyond datasets, making code openly
508 available, citable, and user-friendly is a means to share methods to analyze data. Places to
509 easily share code include web-based version controlled platforms like Bitbucket¹⁷ or
510 Github¹⁸ and software repositories like Sourceforge¹⁹.

511
512 Meta-analysis datasets provide curated resources where numerous published and
513 unpublished datasets related to a specific problem (or many problems) can be accessed by
514 researchers²⁰. The crucial element is that data is somehow reflective of universal plant
515 morphological features, bridging the gap between programming languages and biology, as
516 seen in the Root System Markup Language (Lobet et al., 2015) and OpenAlea (Pradal et al.,
517 2008). Bisque is a versatile platform to store, organize, and analyze image data, providing
518 simultaneously open access to data and analyses as well as the requisite computation
519 (Kvilekval et al., 2010). CyVerse²¹ (formerly iPlant) is a similar platform, on which

¹⁴ <http://datadryad.org/> (retrieved May 29, 2016)

¹⁵ <http://dataverse.org/> (retrieved May 29, 2016)

¹⁶ <https://figshare.com/> (retrieved May 29, 2016)

¹⁷ <https://bitbucket.org/> (retrieved May 29, 2016)

¹⁸ <https://github.com/> (retrieved May 29, 2016)

¹⁹ <https://sourceforge.net/> (retrieved May 29, 2016)

²⁰ BAAD: a Biomass And Allometry Database for woody plants, <https://github.com/dfalster/baad> (retrieved May 29, 2016)

²¹ <http://www.cyverse.org/> (retrieved August 20, 2016)

520 academic users get 100 GB storage for free and can create analysis pipelines that can be
521 shared and reused (Goff et al., 2011). For example, DIRT²² is an automatic, high throughput
522 computing platform (Bucksch et al., 2014c; Das et al., 2015) that the public can use hosted
523 on CyVerse using the Texas Advanced Computing Center²³ (TACC) resources at UT Austin
524 that robustly extracts root traits from digital images. We emphasize the importance of
525 adopting open science policies at the individual investigator and journal level to continue
526 expanding the field of mathematical biology.

527

528 **IV. Conclusion: Unleashing geometric and topological potential within the plant** 529 **sciences**

530

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

538

539 Never have the resources to study plant morphology been more plentiful. Burgeoning
540 imaging technologies—innovative confocal microscopy, laser ablation tomography, X-ray
541 imaging, MRI, radar, terrestrial laser scanning, among many others—have made detailed
542 3D models of plants feasible (**Figures 3-4**). Interest in the hidden half of plant
543 morphology—the root system—has only recently seen a renaissance with technologies
544 capable of penetrating soil and visualizing roots *in situ* (**Figure 5**).

545

22 <http://dirt.iplantcollaborative.org/> (retrieved August 20, 2016)

23 <https://www.tacc.utexas.edu/> (retrieved August 20, 2016)

546 Integrating observations at different scales is a persistent challenge, such as shoot apical
547 meristem development or the movement of leaves within a tree canopy (**Figures 6-7**).
548 Modifying plant morphology through molecular biology and breeding is key to develop
549 agricultural outputs and sustainability. Monitoring the morphology of plants in response to
550 a shifting environment is necessary to model global responses to climate change. Cross-
551 disciplinary training of scientists, citizen science, and open science are all necessary
552 components to address these needs (**Figure 8**). Unleashing the potential of geometric and
553 topological approaches in the plant sciences promises to transform our understanding of
554 both plants and mathematics, and to meet the challenges posed by a future with dwindling
555 and uncertain natural resources.

556

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1211

1212 **Figure Legends**

1213

1214 **Figure 1: Plant morphology from the perspective of biology.** Adapted from Kaplan
1215 (2001). Plant morphology interfaces with all disciplines of plant biology—plant physiology,
1216 plant genetics, plant systematics, and plant ecology—influenced by both developmental
1217 and evolutionary forces.

1218

1219 **Figure 2: Plant morphology from the perspective of mathematics. A)** The topological
1220 complexity of plants requires a mathematical framework to describe and simulate plant
1221 morphology. Shown is the top of a maize crown root 42 days after planting. Color
1222 represents root diameter, revealing topology and different orders of root architecture.
1223 Image provided by Jonathan Lynch and Johannes Postma (Pennsylvania State University).
1224 **B)** Persistent homology deforms a given plant morphology using functions to define self-
1225 similarity in a structure. In this example, a geodesic distance function is traversed to the
1226 ground level of a tree (that is, the shortest curved distance of each voxel to the base of the
1227 tree), as visualized in blue in successive images. The branching structure, as defined across
1228 scales of the geodesic distance function is recorded as an H_0 (zero-order homology)
1229 barcode, which in persistent homology refers to connected components. As the branching
1230 structure is traversed by the function, connected components are “born” and “die” as
1231 terminal branches emerge and fuse together. Each of these components is indicated as a
1232 bar in the H_0 barcode, and the correspondence of the barcode to different points in the
1233 function is indicated by vertical lines, in pink. Images provided by Mao Li (Danforth Plant
1234 Science Center).

1235

1236 **Figure 3: Terrestrial laser scanning creates a point cloud reconstruction of a Finnish**
1237 **forest. A)** Structure of a boreal forest site in Finland as seen with airborne (ALS) and
1238 terrestrial (TLS) laser scanning point clouds. The red (ground) and green (above-ground)
1239 points are obtained from National Land Survey of Finland national ALS point clouds that
1240 cover hundreds of thousands of square kilometers with about 1 point per square meter
1241 resolution. The blue and magenta point clouds are results of two individual TLS
1242 measurements and have over 20 million points each within an area of about 500 square
1243 meters. TLS point density varies with range but can be thousands of points per square
1244 meter up to tens of meters away from the scanner position. **B)** An excerpt from a single TLS
1245 point cloud (blue). The TLS point cloud is so dense that individual tree point clouds
1246 (orange) and parts from them (yellow) can be selected for detailed analysis. **C)** A detail

1247 from a single TLS point cloud. Individual branches (yellow) 20 meters above ground can be
1248 inspected from the point cloud with centimeter level resolution to estimate their length
1249 and thickness. Images provided by Eetu Puttonen (Finnish Geospatial Research Institute in
1250 the National Land Survey of Finland). ALS data was obtained from the National Land
1251 Survey of Finland Topographic Database, 08/2012 (National Land Survey of Finland open
1252 data licence, version 1.0).

1253

1254 **Figure 4: Imaging techniques to capture plant morphology. A)** Confocal sections of an
1255 Arabidopsis root. The upper panel shows a new lateral root primordium at an early stage of
1256 development (highlighted in yellow). At regular intervals new roots branch from the
1257 primary root. The lower panel shows the primary root meristem and the stem cell niche
1258 (highlighted in yellow) from which all cells derive. Scale bars: 100 μ m. Images provided by
1259 Alexis Maizel (Heidelberg University). **B)** Computational tomographic (CT) x-ray sections
1260 through a reconstructed maize ear (left and middle) and kernel (right). Images provided by
1261 Chris Topp (Donald Danforth Plant Science Center). **C)** Laser ablation tomography (LAT)
1262 image of a nodal root from a mature, field-grown maize plant, with color segmentation
1263 showing definition of cortical cells, aerenchyma lacunae, and metaxylem vessels. Image
1264 provided by Jennifer Yang (Penn State).

1265

1266 **Figure 5: The environmental basis of plant morphology.** Root system architecture of
1267 Arabidopsis Col-0 plants expressing ProUBQ10:LUC2o growing in **A)** control and **B)** water-
1268 deficient conditions using the GLO-Roots system (Rellán-Álvarez et al., 2015). Images
1269 provided by Ruben Rellán-Álvarez (Laboratorio Nacional de Genómica para la
1270 Biodiversidad, CINVESTAV).

1271

1272 **Figure 6: Integration of tissue growth and reaction-diffusion models. A)** Vertex model
1273 of cellular layers (Prusiniewicz and Lindenmayer, 2012). K , l_α and l_0 are the spring
1274 constant, current length, and rest length for wall α . K_P is a constant and S_A is the size of cell
1275 A . Δt is time step. Shown is a simulation of cell network growth. **B)** Reaction diffusion

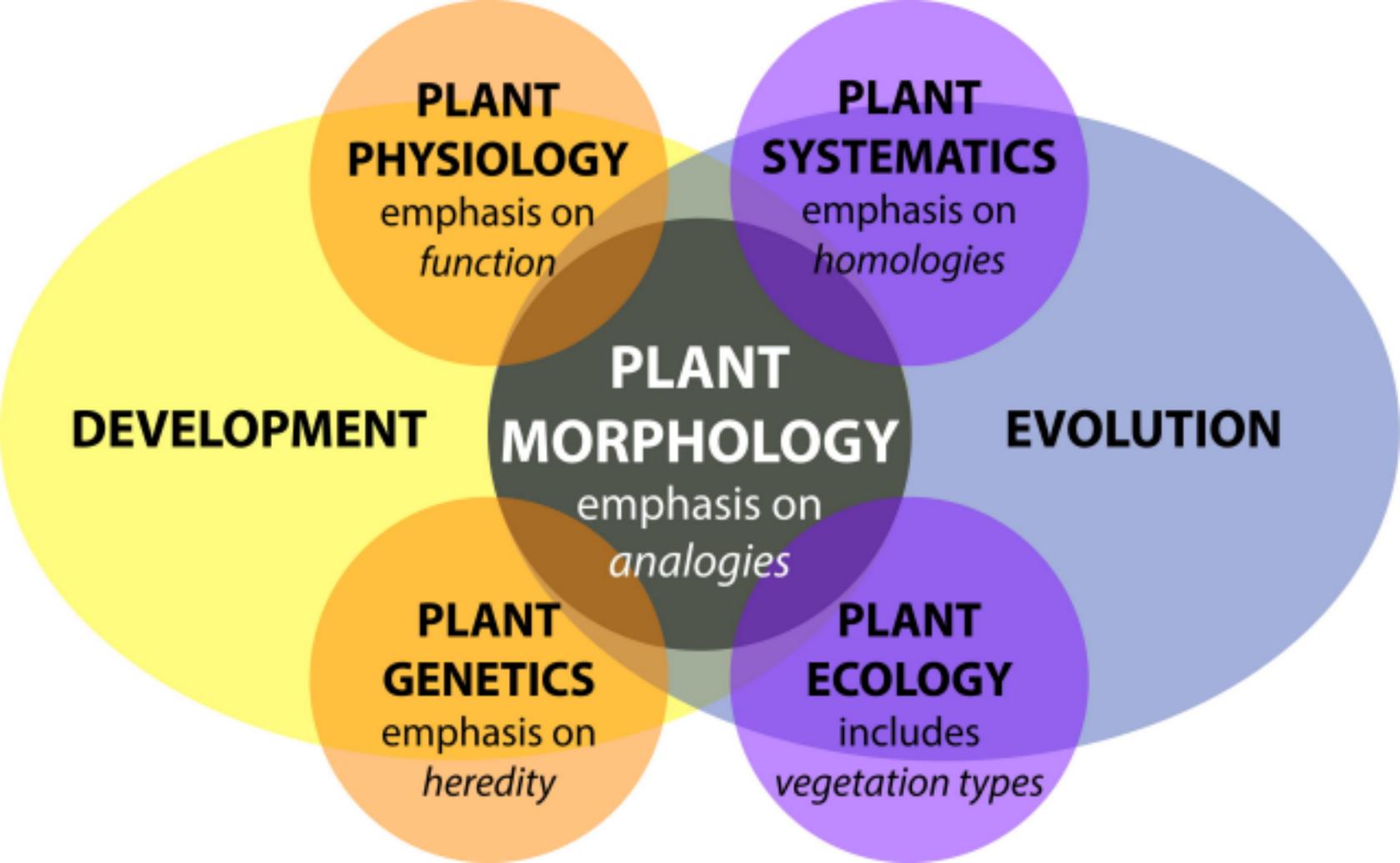
1276 model of the shoot apical meristem for WUSCHEL and CLAVATA interactions (Fujita et al.,
1277 2011). $u=WUS$, $v=CLV$, i =cell index, Φ is a sigmoid function. $E, B, A_s, A_d, C, D, u_m, D_u, D_v$ are
1278 positive constants. Shown are the distributions of WUS and CLV levels within a dynamic
1279 cell network. Images provided by Dorjsuren Battogtokh (Virginia Tech).

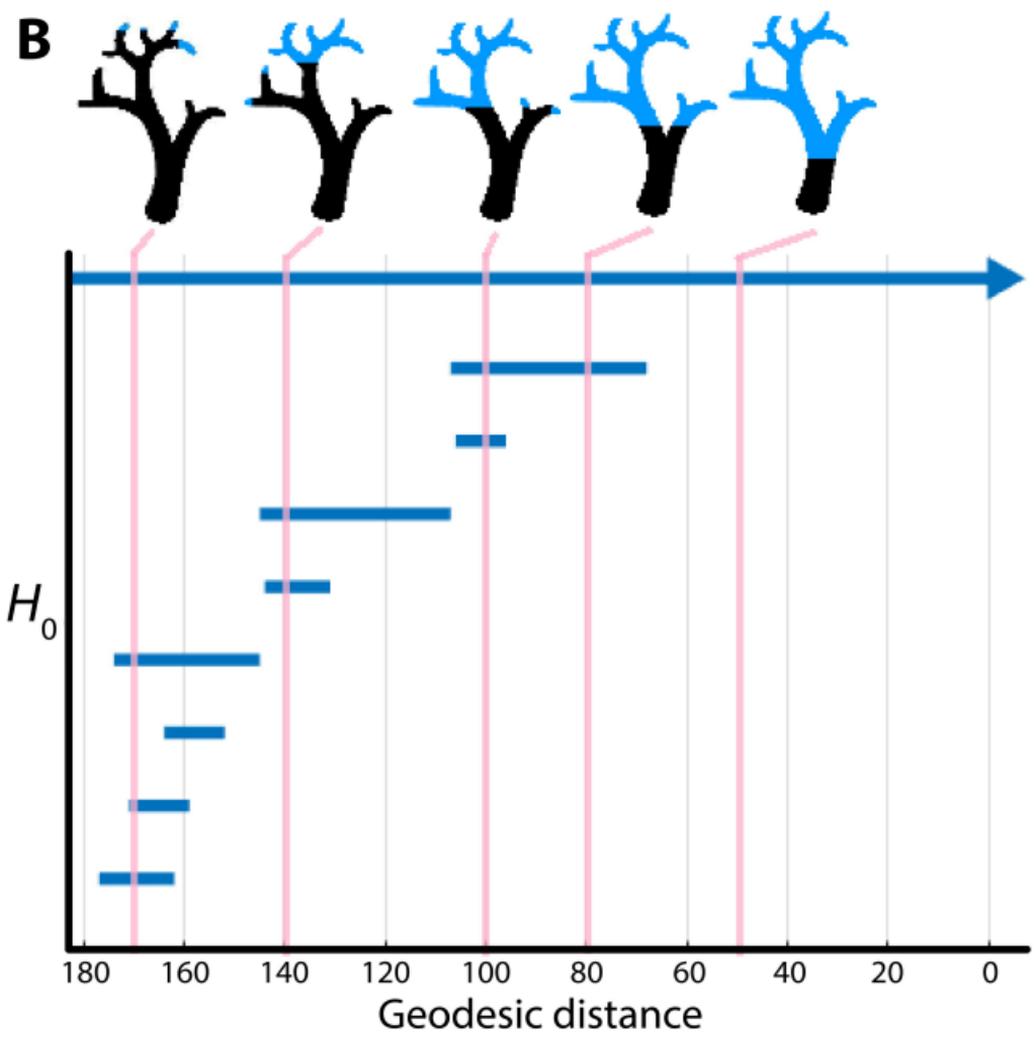
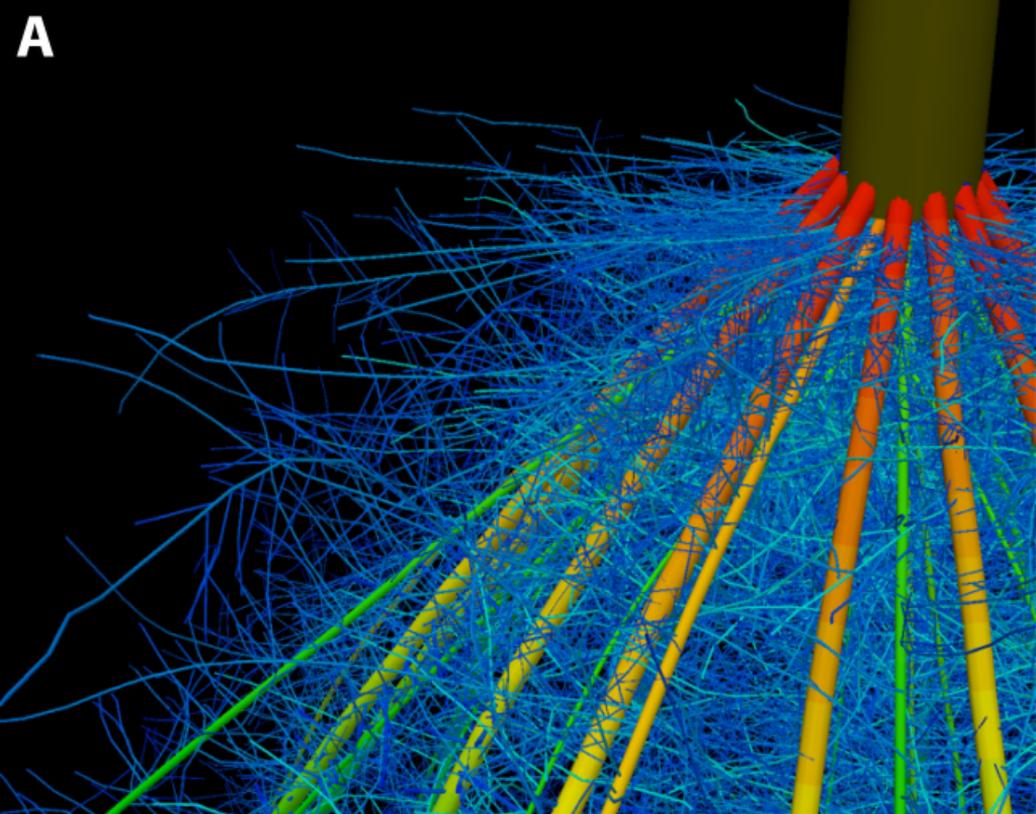
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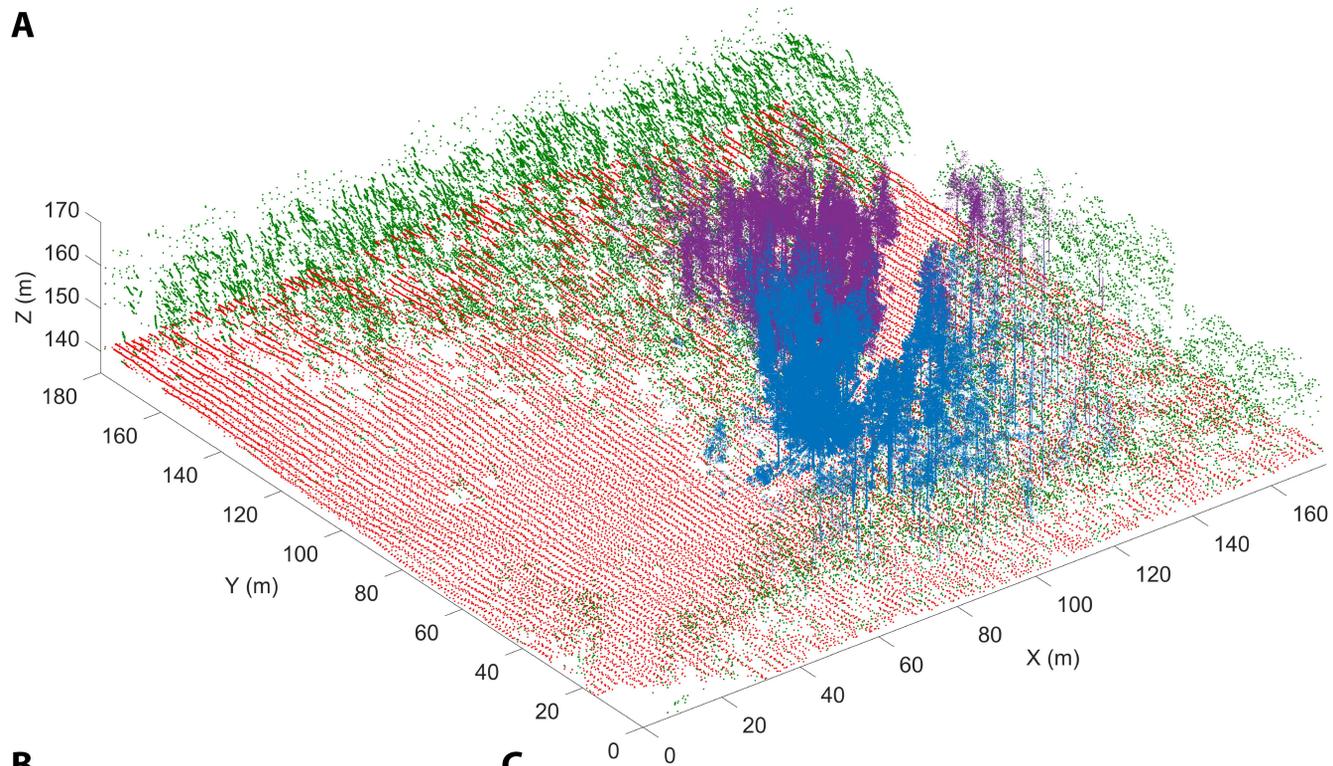
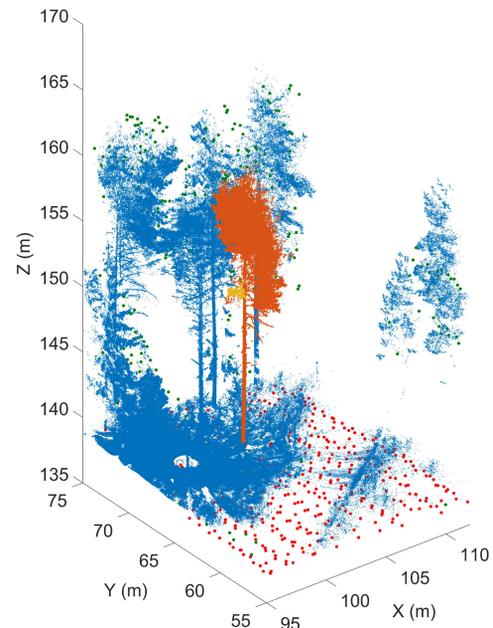
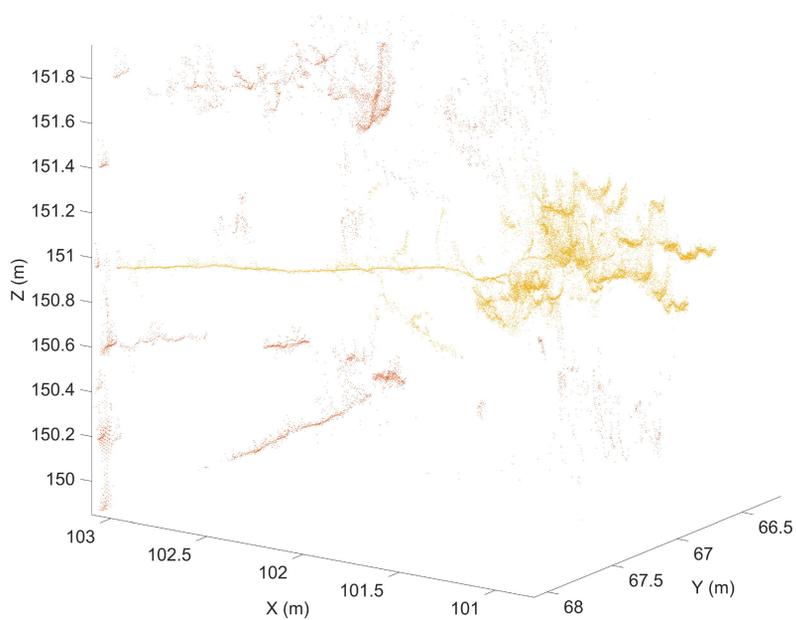
1281 **Figure 7: Modeling the interaction between plant morphology and fluid dynamics. A)**
1282 3D immersed boundary simulations of flow past a flexible rectangular sheet (left) and disk
1283 with a cut from the center to edge (right). Both structures are attached to a flexible petiole,
1284 and the flow is from left to right. The contours show the magnitude of vorticity (the
1285 rotation in the air). The circular disk reconfigures into a cone shape, similar to many broad
1286 leaves. **B)** Reconfiguration of tulip poplar leaves in 3 m/s (left) and 15 m/s flow (right). The
1287 leaves typically flutter at lower wind speeds and reconfigure into stable cones at high wind
1288 speeds. **C)** A cluster of redbud leaves in wind moving from right to left. The wind speed is
1289 increased from 3 m/s (left) to 6 m/s (middle) and 12 m/s (right). Note that the entire
1290 cluster reconfigures into a cone shape. This is different from the case of tulip poplars and
1291 maples where each leaf individually reconfigures into a conic shape. Images provided by
1292 Laura Miller (University of North Carolina, Chapel Hill).

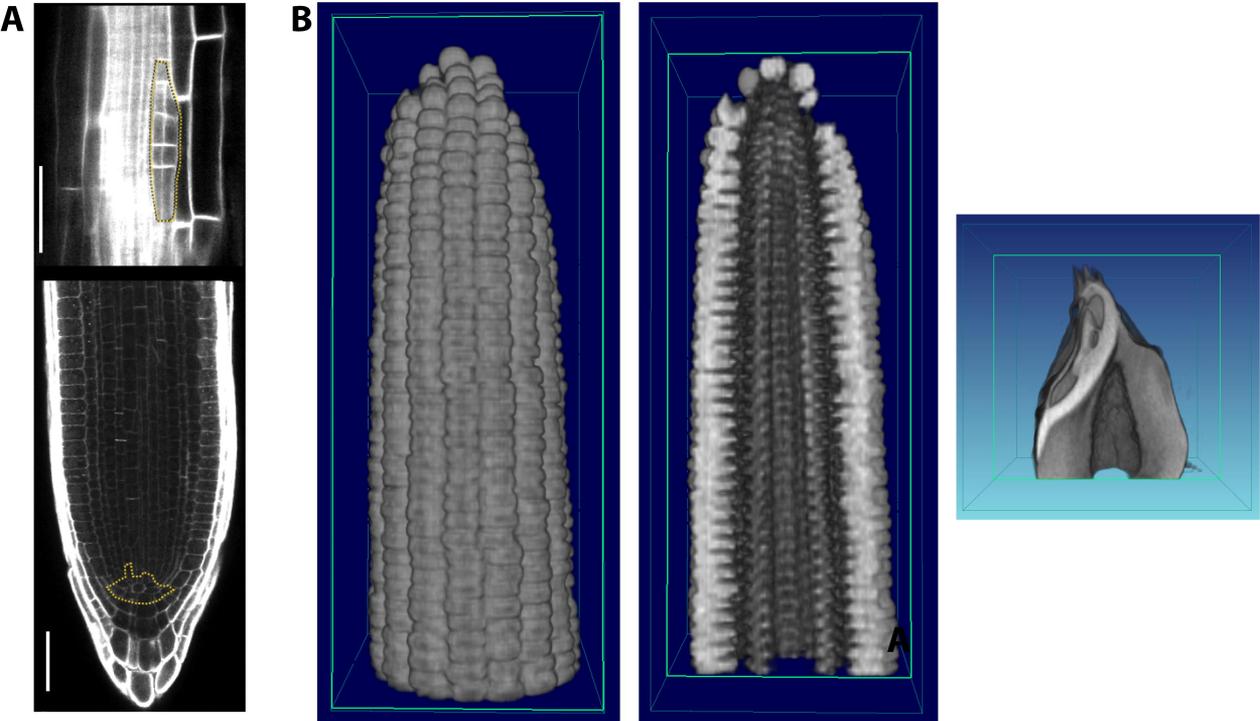
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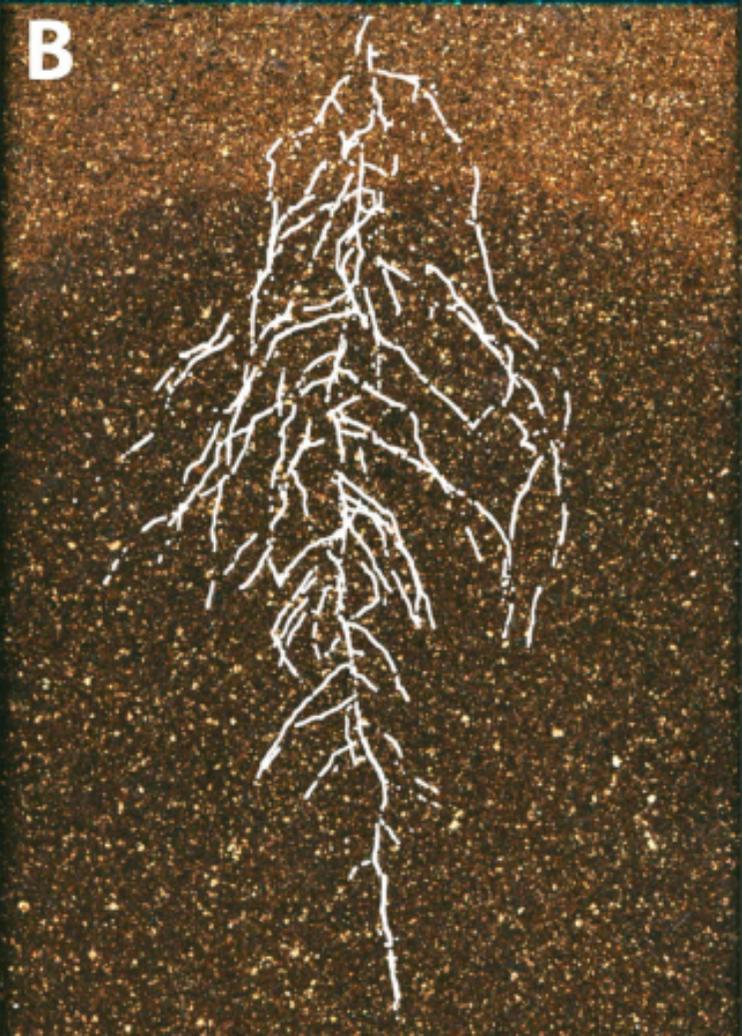
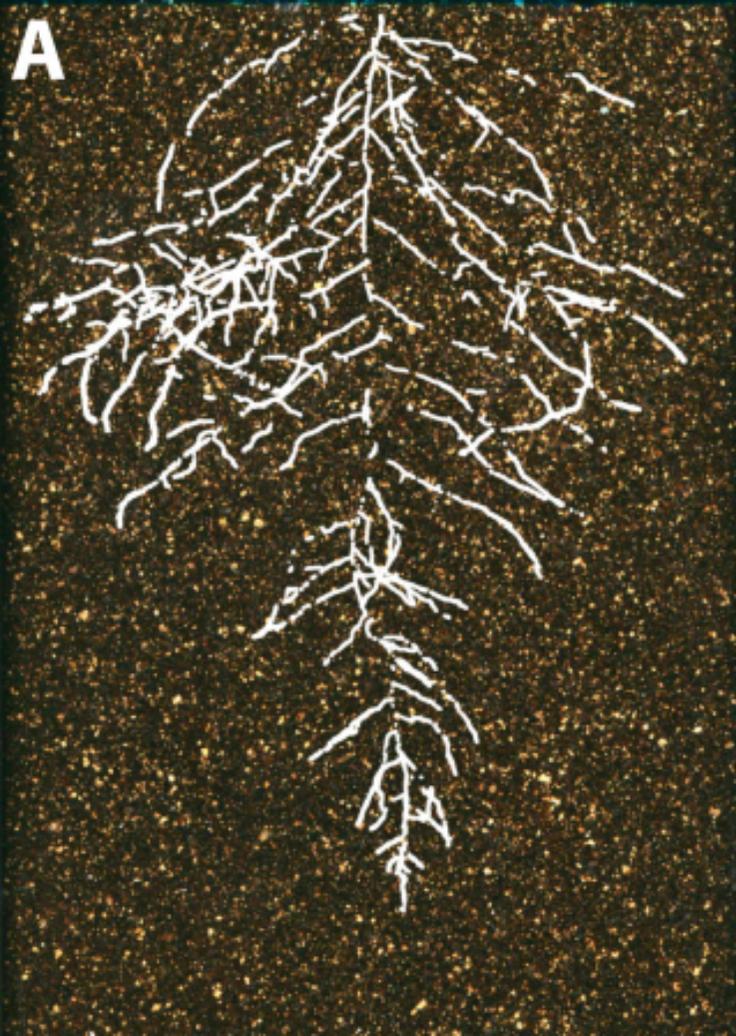
1294 **Figure 8: Milestones to accelerate the infusion of math into the plant sciences.** Group
1295 photo of the authors from the National Institute for Mathematical and Biological Synthesis
1296 (NIMBioS) meeting on plant morphological models (University of Tennessee, Knoxville,
1297 September 2-4, 2015) that inspired this manuscript. Workshops such as these, bringing
1298 mathematicians and plant biologists together, will be necessary to create a new synthesis
1299 of plant morphology.





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

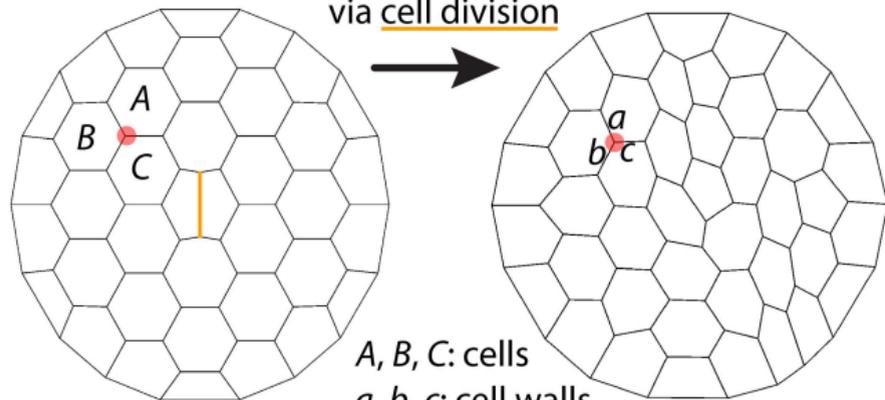
$$\vec{F}_s^a = -K(l_a - l_0)$$

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

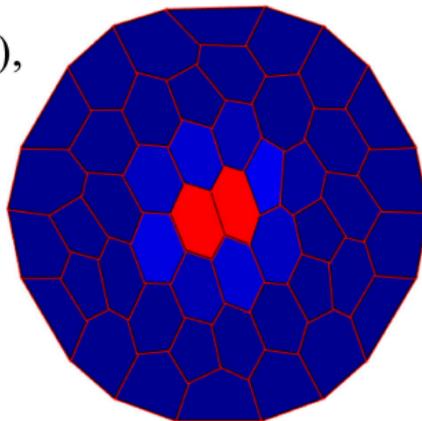
B

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

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

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

WUSCHEL



CLAVATA

