Article

A Statistical Description of Plant Shoot Architecture

Highlights

- We analyzed 557 3D plant architectures to study how branches distribute in space

- Branch density was separable, self-similar, and described by a truncated Gaussian

- These three properties are shared by dendritic and axonal morphologies in the brain

Authors

Adam Conn, Ullas V. Pedmale, Joanne Chory, Charles F. Stevens, Saket Navlakha

Correspondence

navlakha@salk.edu

In Brief

Conn et al. analyze 557 3D plant shoot architectures and discover that the distribution of branches in space is well approximated by a truncated 3D Gaussian density function. This result highlights a new principle guiding growth and adaptation of plants, and it raises new questions about the molecular mechanisms driving pattern formation.

CellPress

Article

CellPress

A Statistical Description of Plant Shoot Architecture

Adam Conn,[1] Ullas V. Pedmale,[2,4] Joanne Chory,[2] Charles F. Stevens,[3] and Saket Navlakha[1,5,*]

[1]Integrative Biology Laboratory, Salk Institute for Biological Studies, La Jolla, CA 92037, USA
[2]Howard Hughes Medical Institute and Plant Biology Laboratory, Salk Institute for Biological Studies, La Jolla, CA 92037, USA
[3]Molecular Neurobiology Laboratory, Salk Institute for Biological Studies, La Jolla, CA 92037, USA
[4]Present address: Cold Spring Harbor Laboratory, Cold Spring Harbor, New York, NY 11724, USA
[5]Lead Contact
*Correspondence: navlakha@salk.edu
http://dx.doi.org/10.1016/j.cub.2017.06.009

SUMMARY

Plant architectures can be characterized statistically by their spatial density function, which specifies the probability of finding a branch at each location in the territory occupied by a plant. Using high-precision 3D scanning, we analyzed 557 plant shoot architectures, representing three species, grown across three to five environmental conditions, and through 20–30 developmental time points. We found two elegant properties in the spatial density functions of these architectures: all functions could be nearly modified in one direction without affecting the density in orthogonal directions (called "separability"), and all functions shared the same underlying shape, aside from stretching and compression (called "self-similarity"). Surprisingly, despite their striking visual diversity, we discovered that all architectures could be described as variations on a single underlying function: a Gaussian density function truncated at roughly two SDs. We also observed systematic variation in the spatial density functions across species, growth conditions, and time, which suggests functional specialization despite following the same general design form.

INTRODUCTION

One central challenge in plant biology is to identify general principles guiding growth and adaptation of plant architectures [1]. Plant architectures are highly complex, developing meticulously over time and constantly adjusting to challenges from the environment [2]. These adjustments include modulation of growth rates, the size and number of branching elements and leaves, and flowering times [3, 4]. Growth strategies also vary across species in terms of the number of seed leaves generated, the presence of secondary growth, and leaf patterning [5].

Over the last several decades, many principles describing plant form have been discovered [6], including phyllotaxis (spatial arrangement of leaves) [7], bifurcation planarity [8], fractal branching [9–11], and allometric scaling of several other plant properties, including plant height, stem diameter, and

leaf biomass [12–15]. These insights have led to many models of plant architectures, including Lindenmayer systems [16] and its many variants [17–19], the metabolic theory of ecology [20], and functional-structural models [21–25], used to simulate how different physiological or ecological factors influence plant structure. These models have had wide applications in agriculture [26], plant engineering [27, 28], and computer graphics [16, 29].

Here, we study the spatial density function of plant architectures and ask, for each point in the 3D territory or volumetric space occupied by a plant (defined as the convex hull of the cloud points representing the plant's architecture), what is the probability of finding a branch at that point? The spatial density function characterizes how plants distribute branches in space and can reveal growth strategies that may not be apparent by eye. Indeed, it is not clear a priori how many different forms of the density function are used. For example, the functional form may be class specific (monocots versus dicots), species specific, or even condition specific; the form may even depend on growth and developmental timing. Understanding which forms are used and in what context may help guide plant biologists studying similarities and differences in the biological mechanisms that produce these structures, including how they may have evolved.

Our goals here are to characterize plant spatial density functions using statistical moments, to test these functions for two mathematical properties (separability and self-similarity), and to determine the form of the density function. "Separability" means that branch density is independent in the x, y, and z directions. "Self-similarity" means that architectures of different sizes have the same underlying shape, modulo compression and stretching along one or more directions. The form of the function is not designed to be used to reconstruct an individual plant's architecture but rather to highlight statistical properties shared by a large collection of architectures.

Compared to prior work, we offer the following contributions:

(1) Analysis of an extensive dataset of 557 juvenile plant 3D architectures from three species, scanned across various growth conditions for the same species, and several early developmental time points for the same individual plant.

(2) Quantification of separability and self-similarity of plant spatial density functions. Whereas fractal branching has long been appreciated by mathematical biologists [9–11], there has been little formal analysis of the *degree*