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The introduction is based on a Teaching Tool
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Introduction

Plants can not simply walk to more favorable environments.

Behind this statement hides a complex and fascinating truth. Despite their immobility, plants still need to access soil resources such as water and nutrients to survive in environments that are becoming more challenging every day. To do so, they have evolved extensive and highly plastic root systems to forage in the surrounding heterogeneous soil. As such, roots are considered a central component of plant productivity. However technical constraints have long confined root research in its infancy.

Nowadays, the worldwide root researchers community is growing and more active than ever. In the past few years, researchers have combined the latest technologies to image and quantify root systems (e.g. digital photography, X-ray computed tomography, transparent soils, high-throughput 3D reconstructions, or fluorescence-based imaging systems), opening an exciting landscape of new research strategies. In addition, recent collaborative efforts have lead to the design of a common language for the description and storage of root architecture information. The establishment of new techniques and robust standards open the door for a new era in root research. Here we will review the most recent advances in root system architecture quantification and to provide a comprehensive introduction to computational approaches that are becoming the new standards in root research.

Root system anatomy, architecture, and

development

Single root anatomy



[Bouché, Frédéric \(2017\) figshare](#)

A single root is a relatively simple organ, compared to a human brain, for example. At its extremity (the apex, or root tip) lies the root apical meristem, a small pool of undifferentiated stem cells. The root apical meristem continuously produces new cells both behind and in front of it (the columella and the root cap) to

protect its integrity against the soil particles. The cells produced behind the root apical meristem, in the quiescent center, will differentiate and elongate, leading to the growth of the root. Cell differentiation leads to a tightly controlled arrangement of tissues with various functions. In the model plant *Arabidopsis*, the center of the root, the stele, contains both xylem vessels (that are responsible for the transport of water and nutrient from the root to the shoot) and phloem vessels (are responsible for the carbohydrates from the shoot to the root). The outermost layer of the stele is the called the endodermis (from the greek endon, within, and déрма, skin). The endodermis usually develops secondary structures (Caspary strips and suberin lamellae) to prevent water and ions from flowing across cell walls (the apoplast) but rather forces them through the cellular fluid (the symplast). Outside of the endodermis lies the cortex, composed mainly of parenchyma cells. The outermost limit of the cortex is surrounded by the epidermis, that can also present the same type of hydrophobic structures as the endodermis. After differentiation, the different cells will elongate, to reach their final size. The process of elongation is finely controlled by the apex, in order to define the growth direction and rate of the root. Indeed, the root apex can sense any deviation from the vertical orientation, through the re-distribution of dense starch particles (statoliths) within the root cap. As the root growth deviates from the vertical direction, the root apex will induce an asymmetric growth of the elongating cells, leading to re-direction of the root (gravitropism).

While a single root is a relatively simple biological object, root systems aggregate many roots into a complex network. Root system development is an iterative process. The first root that emerges from the seed (the primary or tap root) will quickly form branches (lateral roots). The frequency of formation of these lateral roots is defined by localised pulses of the plant hormone auxin within the inner root tissues. The first lateral root emerges at a given distance from the root apex (this distance is known as the Length of the Apical Unbranched Zone, or LAUZ), and the subsequent lateral roots form at given distances from the previous lateral root (called the interbranch distance). Lateral roots also emerge at a given angle with respect to their parent roots (called the insertion angle). The same process is repeated, both on the primary root and on the each of the lateral roots (to produce higher-order laterals), leading to the formation of a complex tree-like structure (described by root system architecture). A direct consequence of these dynamics is that the root system as a whole is composed of a large range of root ages, types and developmental stages. This leads to a great heterogeneity in functional properties within each single root system.

Similar to their differences aboveground, monocots and dicots have distinct root system architectures. In dicot root systems, the primary root and first order laterals generally form the backbone, however basal roots originating from the hypocotyl can be important in some dicot species. Monocot root systems, on the other hand, tend to be more complex. While both dicots and monocots can form adventitious or shoot-borne roots that originate from the stem, these roots are relatively uncommon in dicots while they are essential to the structure and function of monocot root systems. In monocots, a specific type of adventitious root generally forms on belowground stems on the same nodes from which leaves arise, so are called nodal roots. As a monocot develops, more nodal roots emerge from subsequent nodes, and also from tillers that emerge from nodes. Through this process, nodal roots generally dominate the axial roots of monocot root systems. They follow roughly the same developmental program as the primary root, although some specific genetic determinisms have been identified for them. Whereas, dicot roots undergo secondary growth,

leading to a thickening (and sometimes suberisation) of the older parts of the root system, this is absent in monocots. Because of the lack of secondary growth in monocots, newly emerging nodal roots tend to be thicker than the previous set with more capacity for water flow.