

The root system of plants: from the shadows to the light

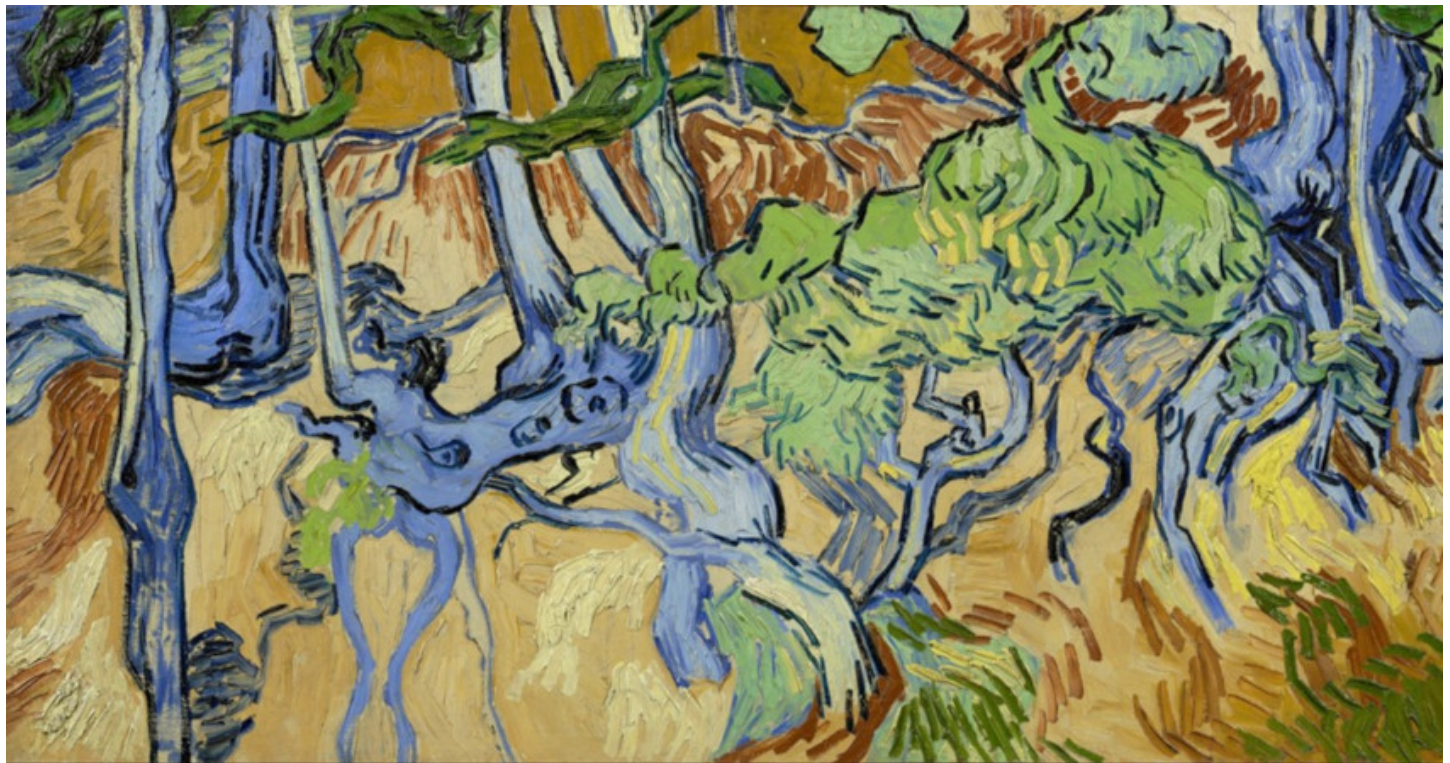
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Roots are a prime target for crop improvement towards a more frugal and environmentally friendly agriculture. However, root traits have long been neglected in breeding programs, especially because the first green revolution was based on massive use of water and fertilizers. Global changes are now encouraging a more rational use of agricultural inputs in order to reduce soil degradation, water and air pollution, and resource depletion. Meeting production needs while limiting the use of water and mineral elements is a major challenge. What role can roots, the plant's nourishing organs, play in the development of a more sustainable and resilient agriculture in the face of current and future climates? An essential role, as shown by recent research that allows us to better understand root system development, functions, diversity and adaptations to the environment, bringing roots from the shadows to the light.

1. Roots capture water and nutrients for the plant

Roots are organs of higher plants that are specialized in exploring the soil and taking up water and mineral ions (See [How to feed plants while polluting less?](#)). They play an essential role in plant survival and development. Each plant has several categories of roots organized in a **root system**. This set of roots anchors the plant in the soil and communicates with the stem(s), which carry the leaves, flowers and fruits. The root system develops through the repeated formation of new roots and their growth in length. Roots form and grow in tight relation to the plant's environment. In doing so, roots allow plant adaptation to the heterogeneous and variable soil resources and constraints of its living environment (See [The fixed life of plants and its constraints](#), [The tireless quest for water by plants](#) & [Water needs of plants: how to satisfy them?](#)).

1.1. Architecture and anatomy of the root system

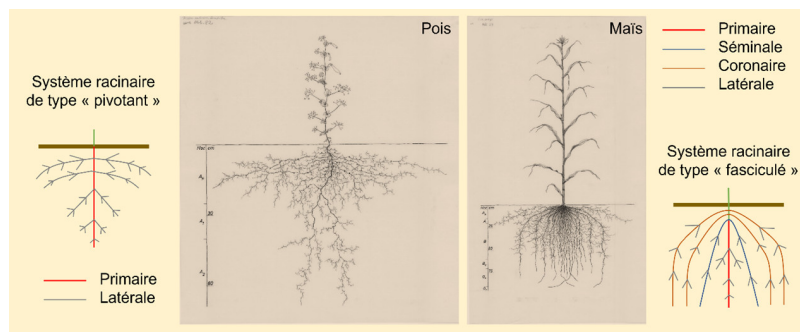


Figure 1: Diagram of a taproot system in pea (*Pisum sativum*) and a fibrous root system in maize (*Zea mays*) with their different root types. [Source: authors' diagram adapted from ref [2], CC BY-NC-ND 4.0]

The root system has a branched **architecture** and a specialized **anatomy** that influence its soil exploration and exchange properties. During germination, the first so-called seminal roots develop from the embryo located in the seed. Later, and throughout the life of the plant, other so-called post-embryonic roots develop from existing roots or stems. There is great variation in the proportions of the different categories of roots that contribute to the root system, as well as in their rate of growth and branching. Thus, there is a great diversity of root systems.

However, two main types of root systems can be distinguished [1]. The "**taproot**" system, found in dicotyledonous Angiosperms (such as rapeseed or pea) and Gymnosperms (such as pine), is most often characterized by the formation of lateral roots on a main seminal root that grows in the soil like a pivot (Figure 1a) [2]. The majority of monocotyledonous Angiosperms (such as wheat or rice) have a "**fibrous**" root system characterized by several seminal roots and numerous so-called crown roots that are relatively equivalent in size and form from the base of the stems (Figure 1b). These roots themselves carry lateral roots. Some plants with a "fibrous" root system can develop more than a hundred crown roots.

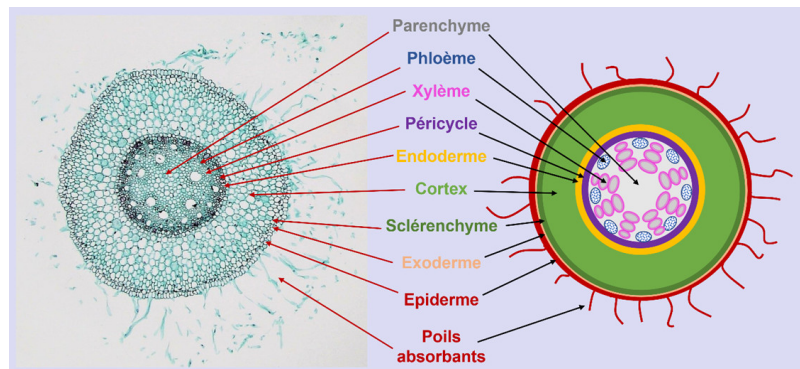


Figure 2. Typical anatomical organization of a maize (monocot) root cross section. [Source: adapted by the authors from a micrograph from Berkshire Community College, Public Domain]

Exploration of the internal structure of roots reveals different types of tissues organized in concentric layers. The typical anatomical organization of a young root contains from the outside in: the epidermis and root hairs that are in contact with the soil, the cortex that may contain air cavities called aerenchyma, the endodermis, and in the center, the stele which contains the vascular tissues [1] (Figure 2).

The specific properties of these different root tissues allow the root to **modulate its exchange capacities with the soil**:

In particular, the root hairs drastically increase the exchange surface of the root and facilitate the acquisition of water and nutrients.

More or less impermeable barriers surrounding the cells in the outer cortex and the endodermis regulate the flow of water and nutrients to the conducting vessels [3].

The vascular tissues channel sap **exchanges between the roots and the aerial organs**:

The xylem vessels contain the raw sap composed of water and mineral elements that circulates from the roots to the aerial organs.

The phloem vessels contain the elaborated sap rich in photosynthesis products that circulates from the aerial organs to the roots.

In perennial species, old roots enlarge over the years by adding new layers of tissues. These so-called secondary tissues form, among other things, cork in the periphery and wood in the center of the root.

1.2. Development and plasticity of the root system

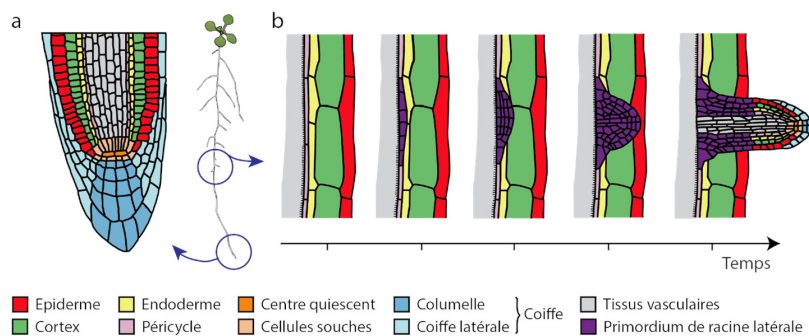


Figure 3. Anatomical organization of root zones involved in root length growth (a) and root branching (b) in the dicot model plant *Arabidopsis thaliana*. The identity of the different root tissues is indicated by the color code. [Source: © IRD Soazig Guyomarc'h. Reproduced with permission]

Root length growth is ensured by a set of specialized cells located near the tip of the growing root: the **meristem** [4] (Figure 3a). This root apical meristem is protected by a cap containing cells that are sensitive to Earth's gravity. Meristematic cells can multiply by cell division, commit some of their daughter cells to the formation of new root tissues, or conversely maintain these daughter cells in the undifferentiated stem cell state. These multiple states are controlled by complex processes involving many factors such as regulatory proteins and plant hormones, including auxin [5]. New root formation involves the formation of a new root meristem by the accumulation of auxin in some existing root or stem cells (Figure 3b).

Root development in the soil is very sensitive to the environment. Root growth, development, and functional properties are influenced by signals circulating within the plant and stimuli perceived from the soil. These modifications of the root system in response to changing environmental conditions are crucial for plant adaptation and are referred to as **root plasticity**.

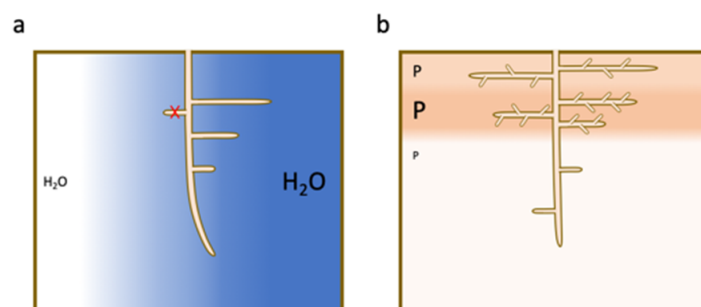


Figure 4. Plastic root development in response to water (a; H_2O) and phosphorus (b; P) availability in the soil. The size of the letters (for H_2O and P) represents larger or smaller quantities of these molecules. [Source: © IRD Alexandre Grondin, reproduced with permission]

For example, local water availability can influence root growth rate and direction. Researchers have identified a biological mechanism in maize that specifically stimulates lateral root formation and growth in regions of the soil where water is most available [6] (Figure 4a):

auxin accumulates preferentially in the zones of the root in contact with the humid soil and stimulates the formation of a new

root meristem.

abscisic acid, a hormone involved in plant responses to water stress, accumulates preferentially in tissues in front of dry soil regions and suppresses the formation of lateral roots.

As with water, a high local accumulation of phosphorus and nitrate in poor soils induces a preferential proliferation of lateral roots in these particular areas [7] (Figure 4b).

Thus, the plant root system is a complex structure that develops continuously in the soil and adapts dynamically to it. Adaptive root plasticity is favorable for plant nutrition under resource-limited conditions. Moreover, through their activity, these roots interact with the soil and modify its characteristics.

2. Roots interact with the soil and its microbial communities

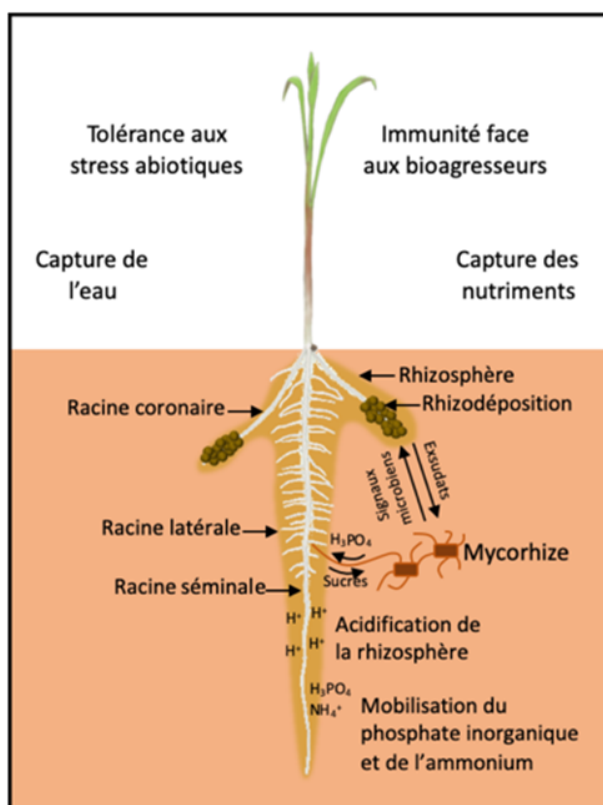


Figure 5: Beneficial effects of the rhizosphere on hydromineral nutrition and plant health. [Source: © IRD Alexandre Grondin, reproduced with permission]

The soil in contact with the roots is referred to as the **rhizosphere** [8] (Figure 5). This zone plays a crucial role for the hydromineral nutrition of the plant and its characteristics are actively influenced by the roots. In particular, the roots secrete specific molecules (or exudates) into this rhizosphere in a process called **root exudation**. This phenomenon can represent a very important energetic investment for the plant: between 17 and 40% of the total carbon produced by photosynthesis can be “exported” by the plant to the soil. These exuded molecules can, depending on their nature, change the physico-chemical properties of the soil and improve the availability and mobility of certain nutrients. They can also influence the diversity of microorganisms able to interact with the plant.

2.1. Influence of roots on soil characteristics

Some nutrients are present in the soil in a chemical form inaccessible to the plant. **Root exudation** contributes to make these elements more available to the roots. Mechanisms of soil acidification by the exudation of protons or phytosiderophores [9] promote the acquisition of iron in certain plants [10]. Root exudation is also a plastic process and depends on the environment in which the root develops. White lupin plants growing in phosphorus-poor soil, for example, produce short and dense root clusters called “**proteoid roots**” [11]. These roots secrete large amounts of acidic molecules capable of lowering the soil pH, making phosphorus ions more assimilable. In this plant species adapted to nutrient-poor soils, this plasticity of root activity is a major adaptation mechanism. In one experiment, it was shown that a lupin plant growing on phosphorus-poor soil can secrete up to 25 times more exudates than a plant growing on phosphorus-rich soil [12].

Exudation also contributes to the formation of a **rhizosheath**. This rhizosheath corresponds to the aggregation, around the roots,

of a soil rich in mucilage and other carbonaceous molecules, which facilitates water acquisition by the plant. In chickpea, a large rhizosheath has been associated with a better capacity of the plant to tolerate water stress [13]. This aggregation of particles around the roots could increase soil moisture in contact with the root epidermis and help maintain the contact and exchange zone between the soil and the root under drought conditions. In addition, this aggregated soil rich in exudates represents an important source of carbon for microorganisms potentially able to establish beneficial interactions with the plant.

2.2. Mobilization of microorganisms by the roots

The rhizosphere is generally microbiologically very active. Some root exudates act as attractive signals for microorganisms [14]. Strigolactone molecules [15], secreted by the plant into the rhizosphere stimulate the germination of spores of **arbuscular mycorrhizal fungi**. The molecules produced by the fungus in turn promote the initiation of root processes that allow the establishment of a symbiosis between the plant and the fungus (Figure 6). During this symbiosis, the exploration of a very large volume of soil by the mycelial hyphae of the fungus contributes to the supply of water, phosphorus and other mineral elements to the plant. In return, the fungus benefits from the carbon molecules produced by plant photosynthesis.

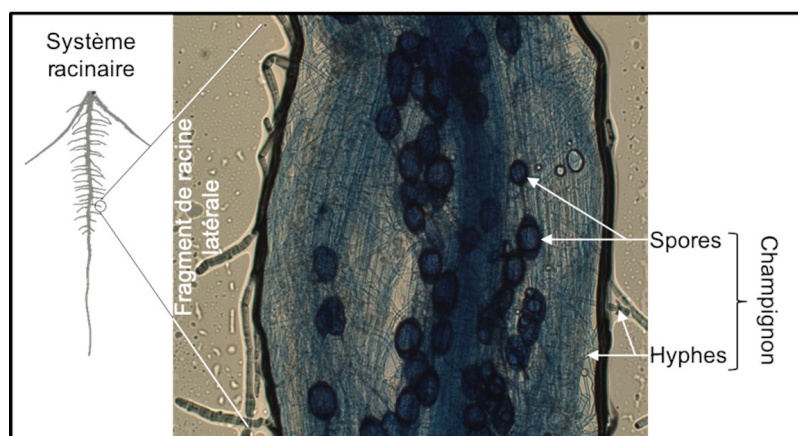


Figure 6: Image of a maize root interacting with arbuscular endomycorrhizal fungi. [Source: © IRD Branly Effa Effa. Reproduced with permission]

Fabaceae, or legumes, produce flavonoids that stimulate symbiotic interactions with **nitrogen-fixing soil bacteria** according to similar principles (See [Plants that live on air](#)). These symbioses are characterized by the formation of new root organs, called **nodules**, where the bacteria are hosted and carry out the transformation of atmospheric nitrogen into a form of nitrogen that is assimilable by the plant. Furthermore, other exudates can act, on the contrary, as repulsive signals for pathogenic microorganisms or soil parasites.



Figure 7. Cowpea plants with roots growing in a poor substrate in the absence (left) or presence (right) of a symbiotic nitrogen-fixing bacteria. [Source: © IRD Clémence Chaintreuil, reproduced with permission]

By improving water and nutrient acquisition by roots, beneficial soil microorganisms contribute to better plant growth, which can translate into better agronomic crop yields (Figure 7). In maize, root colonization by an **endomycorrhizal fungus** is thought to be responsible for about one-third of grain production in the field [16]. Some soil bacteria, in synergy or not with fungi, can also improve plant tolerance to drought, salt stress or heavy metal pollution in the soil. In addition, by interacting with the roots, these microorganisms can stimulate the plant's immune system and improve its protection against pathogens.

By their continuous and plastic development, their adaptable properties and their beneficial actions on the rhizosphere, roots promote the nutrition and health of the plant. Improving the characteristics of the root system of cultivated plants allows to optimize these properties in increasingly constrained agronomic contexts.

3. The root system: a target for plant improvement

3.1. Diversity and complexity of root systems

The root development of a single plant develops and **adapts dynamically** to environmental conditions. A great **diversity** in the way root systems develop and adapt to different environments can be observed between individuals of the same plant species. This diversity of root systems between varieties of the same species is the result of a progressive selection, over the course of evolution, of certain genetically controlled adaptive traits.

In rice, distinct root architectural traits have been identified in varieties adapted to different growing systems:

Varieties adapted to **irrigated** cultivation (where the field is permanently covered with water) have a root system that tends to colonize the superficial layers of the soil;

Varieties adapted to **rainfed** cultivation (where the water supply depends only on intermittent rainfall) develop a deeper root system.



Figure 8. Roots of the millet variety IP-8187 (a) and IP-10539 (b) showing contrasting root insertion angles. [Source: © ISRA/IRD Alexandre Grondin, reproduced with permission]

In pearl millet, variations in the angle that roots form with the stem bases (called insertion angle; Figure 8) have been observed between different varieties. In maize, a great diversity of anatomical characters could also be observed between plants adapted to different environments, especially in the formation of aerenchyma [17], air cavities present in the root cortex (see Figure 2). This diversity of root traits between plants of the same species can be exploited for **plant breeding**. The transfer of beneficial root traits from one variety to another by crossing is an improvement strategy.

This diversity of root traits between plants of the same species can be exploited for **varietal improvement**. The transfer of beneficial root traits from one variety to another by crossing is an improvement strategy.

Following this principle, Japanese researchers have been able to improve the drought tolerance of the rice variety IR64. This variety is very productive and its grains have desirable quality traits. Nevertheless, its shallow root system does not allow the plant to take up enough water when the first few centimeters of soil dry out. In contrast, another rice variety, called Kinandang Patong, is less productive but better adapted to drought thanks to the ability of its root system to capture water from deep soil layers. A cross between these two varieties was conducted to introduce the “deep root system” trait in IR64 [18]. A new rice variety combining the agronomic characteristics of IR64 with the deep root system and drought tolerance of Kinandang Patong was then created.

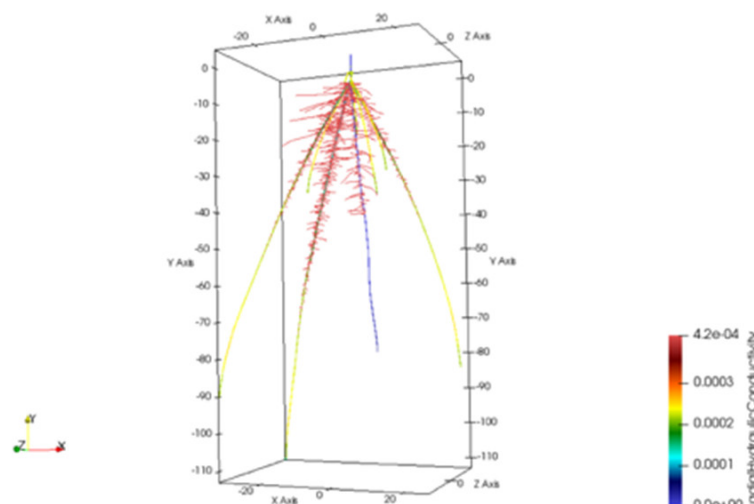


Figure 9. Simulation of millet root growth in sandy soil. The colors indicate the ability of the roots to conduct water from the epidermis to the xylem vessels. [Source: © IRD/ISRA Sokhatil Ndoye, with permission of the author]

However, roots are **complex systems** and their performance depends on how architectural and anatomical features combine and function synergistically. Improving a trait without considering the overall functioning of the root system in its environment can produce detrimental effects. The development of deep roots, for example, may promote the acquisition of water when it is more

abundant at depth. However, more roots at depth may hinder phosphorus acquisition. Indeed, phosphorus, that is an essential element for the plant, generally accumulates in the shallow soil.

In silico models of root systems interacting with soil models have been developed and allow simulating root system structure and functions as a whole (Figure 9). These models facilitate the identification of root traits that will, ultimately, show beneficial effects on plant nutrition and development in a given environment.

3.2. Utility of root systems for plant breeding

Powerful methods are now available to visualize and describe quantitatively the characteristics of the root system of plants without disturbing them. Nevertheless, these data are generally collected using laboratory experimental set-ups that poorly reflect the conditions of plants grown in the field. To meet the need of characterizing plant root systems under agronomic conditions and to facilitate their consideration in plant breeding programs, several methods for studying root systems in field have been developed.

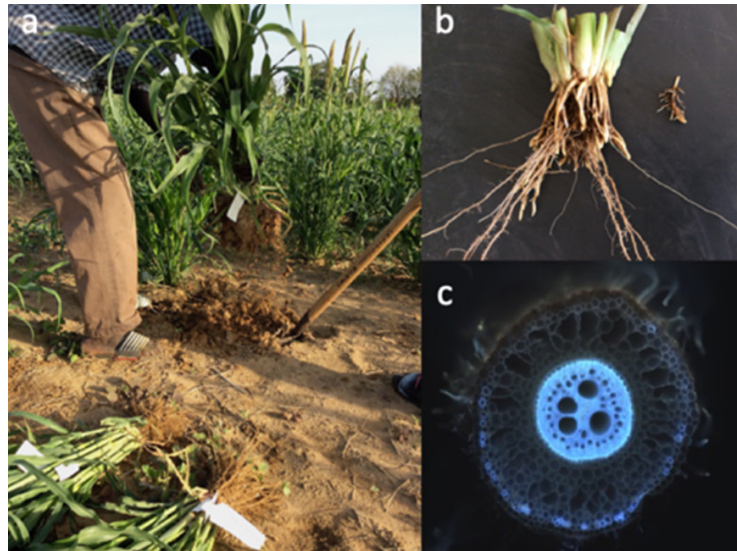


Figure 10. Root samples using the "shovelomics" method (a) and images of roots for the study of architecture (b) and anatomy (c); [Source: © IRD/ISRA/UoN Jimmy Burridge (a, b) and Darren Wells (c), reproduced with permission of the authors].

The so-called "**shovelomics**" method [19] allows the characterization of the root architecture of some cereals in the field, by mechanically excavating the root system of the plant (Figure 10a). The main part of the root system of the plants is removed to a depth of 15-20 centimeters with a simple shovel. After a quick washing, an image of the roots is taken to measure some architectural characteristics such as the insertion angle or the density of lateral roots (Figure 10b). Although not exhaustive, these rapid and relatively accessible measurements allow sufficient statistical characterization of some root system traits in the field. In addition, measurements of some simple traits allow the evaluation of more complex characters, which are correlated to the former. For instance, root insertion angle is a good indicator of the depth of the root system; roots with sharper angles generally tend to grow deeper. Root samples can also be collected and preserved for detailed analysis in the laboratory: histological sections, or tomographic imaging after laser ablation, can be used to study the anatomical organization of these root samples [20] (Figure 10c).

By increasing the number of observations and collected data, the development of these new methods of root exploration in the field are decisive to:

characterize the diversity of root traits and their plasticity

and identify the regions of the genome involved in the control of these traits.

4. Take home messages

Root **architectural** and **anatomical** traits influence the ability of plants to acquire water and nutrients and to adapt to certain

stresses including drought.

The development and functioning of the root system respond dynamically to the environment. This phenomenon called **root plasticity** strongly contributes to the adaptation capacities of the plant to environmental constraints.

The exudation of carbon compounds by the roots in the soil allows to modify the physical, chemical and biological characteristics of the **rhizosphere**. It facilitates the acquisition of water and nutrients and is involved in the establishment of symbiotic interactions with soil microorganisms.

Not all plants have the same root system. There is great **diversity**, between species and between plants of the same species in the way roots develop, function, adapt to the environment and interact with the soil. This diversity, linked to differences in genetic heritage between plants, can be exploited in plant breeding.

In research efforts targeting plant root performance, the whole root system and its complex relationships with its environment need to be considered. For this purpose, efficient **characterization methods** in the field and **modelling strategies** are useful.

Selection of crop varieties with favourable root traits has improved the performance of several species of agronomic interest, such as wheat, maize, and soybean. This research strategy contributes to a more sustainable agriculture, aiming to improve the food security of populations.

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Cover image. Tree Roots (1890), last painting by Van Gogh (1853-1890), Van Gogh Museum, Amsterdam. [Source: Vincent van Gogh, Public domain, via Wikimedia Commons]

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