Resource acquisition, one of the major functions of roots, can contribute to crop growth and mitigating environmental impacts. The spatio-temporal distribution of roots in the soil in relation to the dynamics of the soil resources is critical in resource acquisition. Root distribution is determined by root system development. The root system consists of many individual roots of different types and ages. Each individual root has specific development, resource acquisition, and transport traits, which change with root growth. The integration of individual root traits in the root system could exhibit crop performance in the various environments via root distribution in the soil. However, the relationship between individual root traits and the pattern of root distribution is complicated. To understand this complicated relationship, we need to evaluate enormous numbers of individual root traits and understand the relationship between individual root development and root distribution as well as the integrated functions of individual root traits along with dynamics of resources in the soil.

Key Words: crop growth, environmental impact, individual root, resource acquisition, root distribution, root system, root traits.

Introduction

Unlike aboveground plant parts, most roots are hidden in the soil, and we cannot directly observe their way of life. Scientists have been able to uncover relatively little about root biology compared to other plant parts and processes because examining roots is often time-consuming and labor-intensive (Gewin 2010). Because of this, roots are known as the “hidden half” of plants (Eshel and Beeckman 2013), and have been a fascinating object for many scientists (de Kroon and Visser 2003). Roots are gradually becoming more visible thanks to emerging technologies such as computed tomography (Rogers et al. 2016, Teramoto et al. 2020) and computer simulation modeling (see Dunbabin et al. 2013), and our understanding of them is improving.

Roots play an important role in crop growth because roots are the plant part that absorbs water and nutrients from the soil. One would expect that roots play a critical role in various environments based on these functions. In fact, deeper roots (higher deep root ratio and rootig depth) seem to uptake more water from the soil, and higher root length densities seem to absorb more nutrients. Depending on individual crop species and environments, the results of some studies have agreed with these expectations (e.g., Kawata et al. 1978, Nemoto et al. 1998).

These characteristics of root system and even the evaluation of the whole root system such as topological index (Fitter and Stickland 1991) are often taken to be the root traits of the root system. The term ‘root traits’ encompasses various physical, chemical, and biological properties of roots. However, in this review, the term ‘root traits’ will be used to denote the traits of individual roots because the traits of the root system are the integrated indicators of individual root traits.

In this review, the common and important functions of roots in crop production and environmental impacts are firstly discussed. Next, the basic information of resource acquisition of roots from the soil are confirmed to understand the importance of root distribution. Then, the development of individual roots as a basic unit of the root system is described and the relationship between individual root traits and root distribution is examined.

Resource acquisition and root functions

Resource acquisition is the most essential role of roots, although other abilities such as nutrient storage and plant anchorage are also important (Lynch 2007). For healthy crop growth, crops must absorb adequate amounts of 14 essential mineral elements from the soil via the roots (see White and Brown 2010). Crops also absorb sodium (Na) and silicon (Si) as beneficial elements. In particular, rice
plants actively absorb Si and their yield is expected to increase under high concentrations of Si in the plant (Ma et al. 2001). Therefore, in Japan, Si application is encouraged in paddy fields. Crops change the morphological and anatomical structures of their roots to acquire more of these elements during root development. Various breeding and management practices enhance or sometimes inhibit these changes to improve crop yield and quality.

Resource acquisition can also impact the environment in important ways. The direct effects of mitigating environmental impacts through improving crop roots are reductions in nutrient leaching, runoff, and volatilization. For example, nitrate, which has the potential to pollute water sources, easily leaches out of soils via vertical water flow (Jobbágy and Jackson 2001). If roots forage in the soil immediately or the uptake capacity of the roots is high, they can catch these nutrients that are susceptible to escaping from the soil (Lynch and Wojciechowski 2015).

The indirect effects of crop root improvement include fertilizer reduction and water conservation. If resource acquisition is increased, additional fertilization and irrigation are not required. For example, decreasing phosphorus (P) application to croplands has a significant positive effect on the global environment because P fertilizers are made from limited resources such as phosphate rocks found in only a few countries (Dawson and Hilton 2011). Crop cultivation in a suboptimal environment with higher root resource acquisition can also indirectly mitigate potential environmental impacts. If crops can be grown in drought conditions and fertile fields, no additional deforestation is needed to obtain fertile land, and natural habitats can be allowed to remain and support biodiversity (Folberth et al. 2020).

Furthermore, the supply of inorganic and organic matter from roots plays an important role in agricultural eco-systems. Crops release many substances, including biologically active compounds, as root exudates (Baetz and Martinoia 2014). These could change the nutrient cycle in soils through microbial activity. For example, Subbarao et al. (2009) found that Brachiaria humidicola and sorghum released a biological nitrification inhibitor that inhibits ammonium (NH$_4^+$) conversion to nitrate (NO$_3^-$), which is a process in the soil nitrogen cycle. Root turnover, as the replacement of a particular standing stock caused by the growth and death of roots maintains resource acquisition for a longer period of time. In root turnover, organic matter from the death of roots is released into the soil. In addition, roots remain in the soil after annual crops are harvested. These add to the soil carbon cycle and could contribute to carbon sequestration, thus mitigating global warming (Kätterer et al. 2011).

In this review, the soil is taken as a small compartment continuum in order to explain the interactions between roots and the soil (Fig. 1). Each soil compartment contains root segments of some individual roots (root segments), water, inorganic and organic substances. Focusing on one compartment, water is retained in the soil aggregates or exists freely. The free water easily travels among compartments and can easily leach out of root-accessible areas by gravity. Part of the retained water is available to the roots (Strawn et al. 2015b). Even without plant roots, the behavior of nutrients in a compartment is complex, as nutrients exist in various organic or inorganic forms. Some of these nutrients dissolve in the soil solution, and some are adsorbed onto soil particles because soil particles have charges. Cations such as calcium ions (Ca$^{2+}$) and NH$_4^+$ are adsorbed to a greater extent than anions such as NO$_3^-$ and divalent ions.
are adsorbed to a greater extent than monovalent ions (Strawn et al. 2015a). Phosphorus is strongly adsorbed by active aluminum (Al) and Fe, and this process is known as specific adsorption (Nanzyo et al. 1993). In paddy fields, P release from iron-containing sorption products is affected by the redox conditions (Kirk 2004).

In a specific compartment, nutrients are transformed by microorganisms. A typical example is nitrogen transformation, as summarized by Strawn et al. (2015a). Three forms of nitrogen exist in the soil: organic nitrogen, ammonium nitrogen, and nitrate nitrogen. Organic nitrogen is broken down into ammonium nitrogen, and ammonium nitrogen is further transformed into nitrate nitrogen by microbial activity. Both ammonium nitrogen and nitrate nitrogen are readily-available to crops. Ammonium nitrogen has a positive charge and can be adsorbed onto soil particles. On the other hand, nitrate nitrogen has a negative charge and easily leaves the compartment via moving water as a result. Under redox conditions in paddy fields, most ammonium nitrogen cannot be transformed into nitrate nitrogen, and ammonium nitrogen is therefore a major nitrogen source for rice plants in paddy fields (Kyuma 2004).

Root segments can acquire part of the water retained by soil aggregates and free water in compartments. In addition, the root segments can absorb some of the nutrients when the nutrient concentrations in the soil solution in the compartment reach an available level. To increase the absorption capacity of the root segments, plants make various efforts to decrease this threshold available level. A large number of root segments in a particular area, high root hair density, long root hair on the roots, and symbiosis of arbuscular mycorrhizal fungi are some such mechanisms (Brown et al. 2013a, Cavagnaro et al. 2005, Postma et al. 2014). In addition, activating the ion transporters on the roots could lead to effective absorption at low concentrations of nutrients (Mudge et al. 2002). Another way to increase absorption is to increase the availability of nutrients in a compartment, such as using root exudates (Baetz and Martinhoia 2014). For example, roots release phosphatases, the enzyme removing phosphate ion from the proteins in the rhizosphere of various plants (Tarafdar and Jungk 1987).

The behaviors of soil resources and the absorption of root segments affect the movement of water and nutrients among compartments. When the difference in nutrient concentration between adjacent compartments occurs through resource absorption by the root segments, fertilization, and irrigation, the resources diffuse along the concentration gradient. When water absorption caused by the roots, irrigation, or rainfall generates soil water flow, water and nutrients in the water travel between compartments; this is known as mass flow. Resources move to the root surface in these two ways (diffusion and mass flow), and are loaded into the roots (Barber 1984). The importance of diffusion or mass flow depends on the types of mineral elements available in the soil, as summarized by White et al. (2013).

Diffusion is more important in P and potassium (K) acquisitions, and mass flow is more important in nitrogen (N), sulfur (S), calcium (Ca), and magnesium (Mg) acquisitions because the concentrations of these elements are relatively high in the soil solution.

Root distribution in the soil (how much root segments of individual roots exist in each soil compartment) is the most crucial factor in resource acquisition from the soil. Therefore, in field observations, root weight or length densities in the soil compartments could be useful indicators of root distribution, even if data is only collected for part of the root system. In addition, the aim of setting targets for root distribution in various croplands needs the input from agronomy and soil science (Lynch 2019).

If crops distribute their roots suitably in relation to the spatio-temporal dynamics of resources, crops can efficiently uptake water and nutrients. However, it is not easy. One root distribution pattern in the soil is not uniquely defined by one type of root system. There may be many different methods of root development that achieve similar root distributions. For example, to achieve higher root length density at the deep part of the soil, the consequence of the growth angles of some nodal roots becoming larger and root length increasing could be the same as that of when the primary root becomes longer and has a greater number of longer lateral roots. Therefore, understanding the development of individual roots is essential for constructing ideal root system in various conditions.

**Individual root development**

Crops cannot freely place their roots in the soil because crops have the evolutionary constraint of sequentially developing roots one-by-one from the seed (Robinson et al. 2003). The individual root is defined as the basic unit of root development. Root system consists of many individual roots of different types and ages. Each individual root has specific traits, which change with the growth. Therefore, this section of the review will focus on the development of individual roots as the basic unit of the root system.

**Root types**

Individual roots can be classified as seed-borne, shoot-borne, or root-borne (Zobel 1991). Seed-borne roots are known as primary and seminal roots. At the early growth stage, primary and seminal roots play important roles in both resource acquisition and as the framework of the root system in most crops; however, after growth, their importance depends on the specific crop species.

Shoot-borne roots include nodal roots, basal roots, and adventitious roots. Nodal roots are important in gramineous crops such as rice, maize, and wheat because the framework of the root system composed of nodal roots in these crops (Morita 2000). Basal roots emerging from the base of the hypocotyl are important in leguminous crops in the same way as nodal roots in gramineous crops. In the common...
bean, the angle and number of basal roots are linked to biomass and yield in P-deficient conditions (Miguel et al. 2013, Rubio et al. 2003). In soybean, adventitious roots are formed when potting the soil on the base of the plants. Lee et al. (2003) indicated that adventitious roots may play an important role in nitrogen uptake during flooding injury.

Root-borne roots, known as lateral roots, are the most abundant of all root types in all crops (Doussan et al. 1998). Many studies have indicated that lateral roots are key players in resource acquisition (e.g., Doussan et al. 1998, Postma et al. 2014). In rice, Kono et al. (1972) documented two types of lateral roots: L-type, which is relatively thick and long and has lateral roots, and S-type, which is thin and short and does not have lateral roots. The morphological and anatomical structures and functions of individual roots differ depending on their type (e.g., Tajima et al. 2008, Watanabe et al. 2020).

**Growth direction**

The growth direction of individual roots is almost exclusively determined by the root emergence angle and gravitropism after emergence. In rice, the emergence angle of nodal roots changes depending on the time of emergence and the root diameter of the nodal root (Morita 2000, Yamazaki et al. 1981). Several studies have indicated that root growth direction is closely associated with vertical root distribution in the soil. In rice, a near-isogenic line characterized by increased emergence angle and gravitropic curvature of the primary root in laboratory experiments was found to have a deeper root distribution than the parental cultivar in the field (Uga et al. 2013). In the common bean, the weaker growth direction of basal roots makes for a shallower root system (Rubio et al. 2003).

**Root elongation**

Root elongation is determined by cell division at the root apical meristem and by cell elongation in both the root apical meristem and the cell elongation zone, as described in Ishikawa and Evans (1995). Root elongation occurs on an extremely small zone. For example, in the primary root of maize, root elongation occurs only 12 mm from the root apex (Sharp et al. 2004). The root elongation rate is easily affected by environmental conditions such as water deficit (Sharp et al. 1988) and soil compaction (Bengough et al. 2006).

**Age**

As individual root development progresses from emergence to death, several events occur, such as root hair and lateral root formation. Each lateral root generated on the parent root becomes a new individual root. Anatomical transformations, such as secondary thickening in dicot roots and root cortical aerenchyma formation, also occur during development. Root cortical aerenchyma, which convert cortical tissues into air volume through cell death, form in several major crops such as rice, wheat, barley, and maize (Jackson and Armstrong 1999). In maize, root cortical aerenchyma formation has been linked to improved N capture (Saengwilai et al. 2014). Furthermore, the resource acquisition capacity of individual roots changes with development. These changes are caused by the expansion of root surface area by root elongation, thickening, root hair formation, symbiosis of mycorrhizal fungi, as well as by the abilities per unit root surface area, such as hydraulic conductivity (Ma and Peterson 2003). For example, several studies indicate the distance between root hair formation and root tip changes depending on the elongation rate of the individual root (e.g., Schmidt et al. 2013, Watt et al. 2003). Even the release of root exudates changes depending on the individual root development (Baetz and Martinho 2014).

**Individual root traits**

The major and common traits of individual roots are shown in Table 1. Single traits or combinations of traits contribute to the forms or functions of roots. For example, the root length of individual roots is obtained by multiplying the root elongation rate by growth duration (Morita 2000). The theoretical effects of root hair length, density, and longevity on P acquisition are estimated in Brown et al. (2013b), and increasing root hair length enhances P uptake ability (Okano et al. 2020). The number of individual roots is also important (e.g., Morita et al. 1995), but is not an individual root trait.

These traits can be measured in laboratory experiments

| Table 1. Individual root traits |
|--------------------------------|
| **Trait**                   | **Remarks**                                                                 |
| Type                        | Primary root, seminal root, nodal root, basal root, adventitious root, and lateral root |
| Elongation rate             | Cell division × cell elongation at the root apical meristem               |
| Emergence angle             | Vertical and horizontal angles of the root generated from the seed, shoot, and root |
| Gravitropism                | The curvature per unit time in gravity                                    |
| Root thickness              | The size of radial direction i.e. diameter                                |
| Growth duration             | The time from emergence to cessation of elongation                        |
| Longevity                   | The time from emergence to root death                                     |
| Lateral root density        | The number of root-generated roots per unit of the parent root length     |
| Root hair properties        | Density, length, and longevity                                           |
| Resource acquisition capacity| The activity of ion transporters etc.                                     |
such as hydro cultures. Even the contributions of cell division and elongation at the root apical meristem to root elongation rate can be estimated (Beemster and Baskin 1998). However, the characteristics observed in laboratory experiments are not the same as in field conditions. In fact, root elongation rate varies depending on physical properties of the soil such as water status and compaction (Bengough et al. 2006, Sharp et al. 1988). Even measuring a single root in the field is not easy. However, the new technologies that can measure the root system of standing plants in the soil are emerging (e.g., Teramoto et al. 2020). Using these technologies, it could become possible to measure enormous numbers of individual roots of different types and ages in the soil at the same time. The datasets of individual roots help to understand the integration of individual root development in the field combined with the knowledge of individual roots in the laboratory experiments.

It is challenging to build root traits like blocks when targeting crop root distribution because the interactions among root traits are complicated; as few as two root traits could have synergistic or antagonistic effects (York et al. 2013) and compete for limited metabolic energy in crops (Lynch and Ho 2005), and each trait exhibits plasticity in response to environmental variables (Suralta et al. 2018). To solve this problem, a root growth model with a soil model, as introduced in Dunbabin et al. (2013), should be developed based on datasets from past and future root studies, which will provide insights and support crop breeders to predict how improving individual root traits changes the crop performance via root distribution in the soil and what traits are useful in various environments.

**Concluding remarks**

Roots play a key role in resource acquisition, which impacts crop growth and the environment. In this context, the importance of root distribution in relation to the dynamics of the resources in the soil cannot be overstated. As for the integration of individual roots, the basic unit of the root system, the root system determines root distribution as depicted in Fig. 1, but the relationships among individual root traits and the pattern of root distribution is complex. Accelerating the studies to understand the complex relationship will provide insights and support crop breeders to improve root performance in specific environments.

**Author Contribution Statement**

RT wrote the manuscript.

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