Review

Roots, water, and nutrient acquisition: let's get physical

Nick Chapman[1,2], Anthony J. Miller[1,3], Keith Lindsey[2], and W. Richard Whalley[1]

[1] Rothamsted Research, West Common, Harpenden, Hertfordshire, AL5 2JQ, UK
[2] The School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, UK
[3] John Innes Centre, Norwich Research Park, Norwich, NR4 7UH, UK

Improved root water and nutrient acquisition can increase fertiliser use efficiency and is important for securing food production. Root nutrient acquisition includes proliferation, transporter function, exudation, symbioses, and the delivery of dissolved nutrients from the bulk soil to the root surface via mass flow and diffusion. The widespread adoption of simplified experimental systems has restricted consideration of the influence of soil symbiotic organisms and physical properties on root acquisition. The soil physical properties can directly influence root growth and explain some of the disparities obtained from different experimental systems. Turning this to an advantage, comparing results obtained with the same model plant *Arabidopsis* (*Arabidopsis thaliana*) in different systems, we can tease apart the specific effects of soil physical properties.

The need to enhance root nutrient acquisition

The challenge of securing sufficient food for an estimated global population of 9 billion people by 2050 requires a significant increase in global agricultural productivity [1]. This will not be easy given the adverse effects of climate change on crop production, and the pressure to devote land to bio-fuel production, together contributing to an intensified burden on land-use. Severe flooding and drought episodes currently occur more frequently, devastating crop yields throughout the world [2]. At current productivity there are over 1 billion inadequately fed people in the world [3] and agriculture is under political pressure to improve its sustainability [4]. A significant improvement in agricultural productivity is therefore needed to establish food security.

Enhancements in future agriculture range from better access to water and soil management to improved plant breeding and efficient nutrient acquisition [1]. One promising target is the improvement of crop nutrient acquisition under changing environmental conditions [5–7]. The efficiency by which plants acquire nutrients from the soil is a major determinant of crop yield. Root nutrient acquisition includes root proliferation and transporter function, exudates to mobilise sparingly available nutrients, symbiotic associations with other organisms, mass flow of water to the root and diffusion of nutrient ions to the root surface (see Glossary) [8]; all of which depend on both plant traits and soil physical characteristics (Figure 1). Through a better understanding of root nutrient acquisition under variable water and nutrient availability, it may be possible to modify root traits to improve nutrient acquisition in specific environmental conditions and increase agricultural productivity.

Root growth demonstrates a high degree of plasticity in response to changes in the supply of vital nutrients [9], which has not been lost in crop plants and offers some future possibilities for the improvement of nutrient acquisition. Given the potential productivity gains, it is not surprising that roots are the subject of much research and the physiological processes that underpin nutrient acquisition are frequently reviewed [5,9–21]. Although the movement of nutrients and water in soil is well understood [22,23], the investigation of root acquisition using model systems may not accurately reflect the interaction between the root and soil physical components [9,24].

In this review, we aim to dissect the soil physical properties that influence root proliferation, transporter function, and the delivery of nutrients to the root by mass flow and diffusion. The quantitative contribution of soil physical properties to each of these different root functions is identified. The limitations and strengths of different

Glossary

Diffusion: the movement of dissolved ions along a concentration gradient towards the root, driven by net influx of ions at the root surface.
Hydraulic conductivity: this characterises the ability of a soil to transmit water and depends on pore size and the water content. Empirical relationships exist which allow it to be expressed as a function of water content for a given soil.
Mass flow: the convective transport of dissolved ions from bulk soil towards the root, driven by water potential gradients from leaf to bulk soil that is initiated by the 'transpirational influx' of water.
Matric potential: the capillary pressure of water held between substrate (e.g., soil) particles [137].
Mechanical impedance: the physical resistance to root growth of a 'strong' soil.
Osmotic potential: largely determined by dissolved solutes within the soil solution. They are negative, with low potentials being more negative and high potentials less negative.
Root proliferation: dependent on the continued growth and branching of the root in response to internal and external cues that determines root system architecture (RSA).
Soil strength: mechanical resistance of a soil to root growth, and usually determined by water content and soil structure.
'Strong' soil: soil with increased strength, usually as a result of decreased water content and increasing bulk density.
Water potential: the difference between the chemical potential of water in a material and the chemical potential of pure water at defined reference conditions of pressure and temperature.
'Weak' soil: soil with decreased strength, usually as a result of increased water content and decreasing bulk density.

Corresponding author: Miller, A.J. (tony.miller@jic.ac.uk).
Keywords: mass flow; diffusion; architecture; soil physics; hydraulic; matric potential; nitrogen; nitrate; particle size.

 http://dx.doi.org/10.1016/j.tplants.2012.08.001

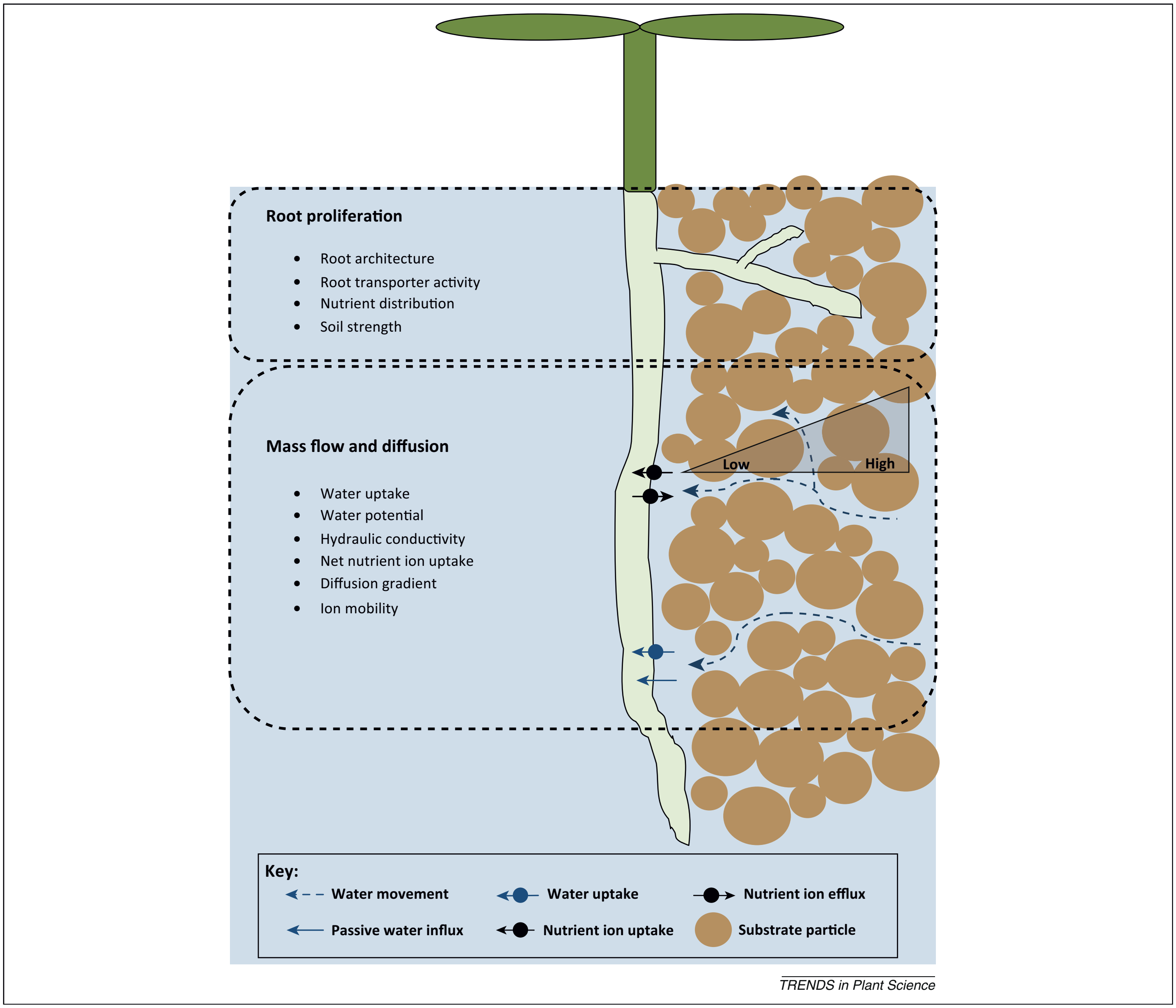

Figure 1. Nutrient acquisition depends on root proliferation and transporter function, exudation, symbioses, and diffusion of nutrient ions and mass flow of water to the root surface. These processes can be facilitated by root exudates to mobilise sparingly soluble nutrients and symbiotic associations with other organisms such as bacteria. Note that for root proliferation, soil strength is a biophysical factor while the other three listed are all biotic. These components are regulated by plant physiology and the physical properties of the substrate.

experimental systems in facilitating the study of these processes are reviewed, pointing out potential problems associated with translating laboratory understanding to the field. The major nutrient nitrogen (N) has been identified as one of the most important targets for improving root acquisition efficiency [5,6,12,25–27] and will be used here to illustrate root nutrient acquisition processes. The contribution of soil physical characteristics to N availability is varied due to the presence of both mobile and immobile forms in the soil. This is particularly true for the delivery of nutrients to the root and the consequent root responses.

Delivery of nutrients to the root surface

Mass flow and diffusion are responsible for the fluxes of water and dissolved nutrients to the root surface from bulk soil and are inextricably linked to its physical properties (or those of the growth substrate). The water potential gradient from the atmosphere to the bulk soil initiates the 'transpirational influx' that is responsible for mass transport of dissolved nutrient ions [8] and can have large effects on root growth and development [28]. A diffusion gradient of dissolved ions within the soil solution towards the root surface is generated by the influx of ions causing localised depletion at the root surface [8]. Therefore, the flux of water and dissolved ions from the soil towards the root is determined by differences in water potential, soil hydraulic conductivity and the shoot-transpiration demand.

These processes have been modelled [29], but the transport processes occurring in laboratory experimental systems are often different from those which occur in soil. Hydraulic conductivity and diffusivity are non-linear functions of matric potential and the shape of these functions, although similar in form, differs greatly between different soil types. Hydraulic conductivity in sandy soils can drop