



Studying root water uptake of wheat genotypes in different soils using water $\delta^{18}\text{O}$ stable isotopes

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ABSTRACT

The ability of plants to access water and nutrients is a key aspect of crop production and it is mainly through modified root growth that plants can optimize their access to those resources. Although genetics play a main role in shaping root traits, other factors such as soil physical characteristics and the distribution of water and nutrients in the soil profile can also modify root architecture.

Here we used an isotope-based approach to determine the contribution of different soil depths to water uptake of four wheat genotypes (249, Bellaroi, F6 and Suntop) grown in two soil types (clayey vertosol and loamy-sand kandosol) in Narrabri (NSW), Australia. The proportional contribution of each soil depth to plant water uptake was determined at the vegetative stage using oxygen stable isotopes in soil and plant water ($\delta^{18}\text{O}$), and available N and root structure were measured at different soil depths. In both soil types most of the available N, and the majority of roots (both in length and weight) were in the top 10 cm, while the plant water extraction profile from different soil depths varied with soil type. In the kandosol, genotype 249 had a higher probability of extracting water from shallower dry soil layers, while F6 and Suntop of relying on deeper soil layers. In the vertosol, by contrast, Suntop and F6 had a higher root branching intensity in the top 0–10 cm and a higher probability of relying on this layer for much of its water extraction. In the kandosol genotypes with greater average depth of water extraction led to higher yield, suggesting that the ability to extract water from deeper layers at the vegetative stage can provide an early indication of plant productivity. The plasticity in root traits among genotypes and their variable water uptake strategy in different soil types illustrate the challenges with identifying root traits important for water extraction.

1. Introduction

Plant productivity depends on the ability to access water and nutrients, and roots represent one of the main organs that plants can modify to access these resources (Durand et al., 2007; Lopez-Bucio et al., 2003; Sharp and Davies, 1985). The ability of plants to allocate root structures for uptake of either surface water or deep water depends on soil environmental conditions and edaphic factors (Ehleringer and Dawson, 1992). For instance, when water in the surface soil is limited, plants respond by growing deeper roots to access water at deeper soil layers (Hoekstra et al., 2014; Kirkegaard et al., 2007). However, the distribution of roots in a soil profile depends not only on how soil moisture, but also nutrients, pH and bulk density vary with soil depth. Assessment of the coupling between plant water uptake mechanisms and root structure allows for a better understanding of the strategies

that plants adopt to maximize use of the available resources and of how plant roots adapt to changing environmental conditions.

In recent years the stable isotopes of oxygen (and hydrogen) in water have been successfully used to study the water uptake profiles of grasses (Corbin et al., 2005; Durand et al., 2007; Hoekstra et al., 2014; Prechsl et al., 2015), tree species (Ehleringer and Dawson, 1992; Thorburn and Ehleringer, 1995) and contrasting perennial and annual plant communities (Asbjornsen et al., 2008). The use of water stable isotopes to determine depth of water uptake requires soil water to differ isotopically at different depths within the soil profile (Dawson and Pate, 1996). Water at the soil surface is often enriched in the heavy oxygen isotope (^{18}O) because H_2^{18}O has a lower evaporation rate than H_2^{16}O , but differences in soil water oxygen isotope composition ($\delta^{18}\text{O}$) may also occur via lateral movement of ground water of non-local origin. Furthermore, as there is no isotopic fractionation during root water

Abbreviations: RLD, root length density; RBI, root branching intensity; RWD, root weight density; NH_4^+ , ammonium; NO_3^- , Nitrate; N, nitrogen; SWC, soil water content; WU, water uptake

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uptake (Thorburn and Walker, 1993; Thorburn and Ehleringer, 1995), the isotopic signature of water collected at the plant stem base reflects the isotopic signature of the soil layers from which the plant extracted its water. A comparison between $\delta^{18}\text{O}$ in soil water at different depths and plant stem water can therefore be used to assess the depth of water uptake of individual genotypes grown in different soil types. This approach was also used to assess seasonal patterns of water uptake from different soil depths of crops including corn, cotton, rice and wheat (Bing et al., 2016; Fei et al., 2016; Shen et al., 2015; Wang et al., 2010). However, this method has not been used to assess water uptake of different genotypes that vary in root traits or to examine how the relationship between root traits and water uptake is affected by soil type.

A previous study showed that wheat relies on surface water in the early plant developmental stage and that the depth of water uptake increases from vegetative to grain filling stage (Fei et al., 2016). However, the root architecture of cereals is impacted not only by water availability in the soil profile, but also by nutrient availability, soil chemical, physical properties (Paez-Garcia et al., 2015; Rich and Watt, 2013), and by interactions among plant physiology and environmental conditions (Paez-Garcia et al., 2015). Variation in root architecture among genotypes is therefore expected to depend on their interaction with soil type and environmental conditions. The majority of soil nutrients are concentrated in the topsoil (Jobbágy and Jackson, 2001), suggesting that the shallower layers might be the soil region from which plants preferentially extract nutrients. For instance, when water limits wheat growth in the upper soil layers, wheat plants rely on water stored at deeper layers, but still require surface roots for uptake of nitrogen (N) in the topsoil (Bakhshandeh et al., 2016). Root traits can be modified to adapt to the new conditions and optimize resource use, and root plasticity plays an essential role in plant adaptation to changes in resources in the soil profile (Araki and Iijima, 2005; Bakhshandeh et al., 2016; Engels et al., 1994). However, changes in wheat root traits are not always related to the depth of water uptake (Fei et al., 2016), as the presence of roots is not in itself an indicator of water uptake at a specific depth (Thorburn and Ehleringer, 1995), suggesting that other soil factors influence root growth and distribution in the soil profile.

In this study four wheat genotypes from different genotypic groups were grown in the field in two different soil types. Our aim was to determine whether genotypes adapted their root architecture to soil water and nutrient availability, and consequently used different water uptake strategies in the different soils. Furthermore, we aimed at determining whether uptake strategies at the vegetative stage could be a proxy of plant productivity. Plant and soil samples were collected at the vegetative stage, and available N and root traits associated with the different genotypes were characterised. The measurement of $\delta^{18}\text{O}$ in water was used to determine the water uptake strategies of different wheat genotypes in the two soil types. Furthermore, relationships between available N, root structure, water uptake and grain yield were determined. At the vegetative stage plants are expected to be less N and water limited and therefore differences in root distribution and water uptake could be attributed to plant-soil interactions. We hypothesise that wheat genotypes would adapt their root traits to the availability of N in the soil profile, impacting on plant root water uptake strategies. Furthermore, we hypothesise that different wheat genotypes that vary in root characteristics would adopt different strategies depending on the soil type, with further effects on grain yield.

2. Material and methods

2.1. Germplasm selection

Wheat genotypes (*Triticum* spp.) with different genetic background were chosen from a collection of the Grains Research and Development Corporation (GRDC, Australia). Four wheat genotypes were chosen including three bread genotypes and one durum wheat genotype. Bread wheat genotypes included 249 and F6 Janz/Syn110–42 (PBICR-06-002-

42), which in a previous field study were associated with lower and higher available NO_3^- respectively, although having similar topsoil root diameter (Corneo et al., 2016). We further included a commercial variety, Suntop, with higher specific root length (Bakhshandeh et al., under review), and a durum wheat genotype (commercial variety EGA Bellaroi), which in a previous field study had different physiological traits (e.g., lower water use efficiency compared to 22 bread wheat genotypes) (Corneo et al., 2017). In the text we refer to the different genotypes as 249, Bellaroi, F6 and Suntop.

2.2. Study area and fertilization treatment

The experiment was conducted at the I.A. Watson Grains Research Centre, Narrabri, NSW, Australia (149.8E/30.3S). Two different soil types were chosen: a medium-clay grey vertosol (40.3% sand, 14.6% silt and 45.1% clay) with pH 7.5, C content of 5.5 g kg^{-1} , and N content of 0.4 g kg^{-1} in the topsoil (0–10 cm), and a loamy-sand kandosol (79.3% sand, 10.6% silt, 10.1% clay) with pH 7.8, C content of 3.8 g kg^{-1} , and N content of 0.1 g kg^{-1} . The soil orders were classified according to the Australian Soil Classification (Isbell, 2002).

The four wheat genotypes were planted at the end of May 2014 in four randomized blocks ($6 \text{ m} \times 8 \text{ m}$) that were subdivided into $6 \text{ m} \times 2 \text{ m}$ plots for individual genotypes containing 6 plant rows. All blocks were mechanically fertilized 28 days after sowing (DAS) with $10 \text{ kg ha}^{-1} \text{ P}$ and 100 kg N ha^{-1} in the kandosol. Because of higher available N concentrations at the start of the growing season, only 50 kg N ha^{-1} was applied to the vertosol. During the growing season (24th of May to 11th of November) 136 mm of rain was recorded (Fig. A1) and monthly mean maximum temperature ranged between 19.4°C in July and 35.4°C in November, while monthly mean minimum temperature ranged between 15.3°C in June and 27.4°C in November. Water was supplemented through sprinkler irrigation at 83 DAS (40 mm) and 130 DAS (30 mm).

2.3. Plant and soil sampling

Plant and soil samples were collected at vegetative stage 73 DAS (no irrigation was applied in the period preceding sample collection and the last rain event of 0.2 mm before sampling was recorded 64 DAS) (Fig. A1). Three individual plants were collected from each plot to measure plant biomass. Plant stem bases (up to 1.5 cm above soil level) were collected from three to five tillers, depending on tiller weight within each plot. The outer sheath was removed to avoid collecting photosynthetically active material that could alter the $\delta^{18}\text{O}$ signature (Durand et al., 2007). Stem bases were immediately stored in glass vials with screw caps (Exetainer, Labco Limited, USA) for $\delta^{18}\text{O}$ stem water analysis and kept at -20°C until water extraction.

Two soil cores (4.4 cm diameter \times 100 cm long) were collected within each plot with a hydraulic corer mounted on a tractor; the first core next to the plant stem bases and the second core just below the stem bases. Each core was then sectioned into eight layers (0–5, 5–10, 10–20, 20–30, 30–40, 40–50, 50–70, 70–100 cm). From the first core, soil sub-samples from each layer were immediately stored in glass vials with screw caps (Exetainer, Labco Limited, USA) for $\delta^{18}\text{O}$ analysis of soil water and stored at -20°C , while another set of sub-samples was stored at 4°C and then analysed for available N. Care was taken to minimize evaporation loss during sampling and therefore isotopic fractionation. Layers from the second core were sealed in plastic bags and stored at -20°C for subsequent analysis of root structure.

Roots from each soil layer were soaked in a 10% sodium hexametaphosphate solution buffered at pH 8.5 (Amato and Pardo, 1994) for twelve hours to disperse the soil particles and facilitate root washing. Samples were then washed on a 0.5 mm sieve placed on top of a $53 \mu\text{m}$ sieve to reduce loss of the finer root fraction. Roots were preserved in 50% ethanol at 4°C . The roots were then scanned and the images were analysed using STD4800 WinRhizo software (Regent Instrument Inc.,

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