Genotype by environment (GxE) interactions for root depth of wheat: Associations and implications

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Abstract

A significant proportion of arable land is susceptible to subsoil compaction or soil physical constraint, which limits root access to water and nutrients at depth. This paper reviews recent research on root traits for hardpan penetration and water extraction. The ability of roots to penetrate a compacted soil layer was simulated experimentally by growing plants in soil columns containing a thin paraffin wax-petroleum jelly layer. The objective was to assess temporal variation of root growth of Australian wheat cultivars in terms of their penetration ability with or without a thin wax layer and/or contrasting water regimes, and relate this to performance on contrasting soils in the field. GxE for root depth in the field was examined, and its association with various soil parameters and other root and shoot traits. Cranbrook/Halberd doubled-haploid lines (DHL) were phenotyped for hardpan penetration in the laboratory, and the root depth of contrasting DHLs was assessed in different soils in the field. Quantitative trait loci (QTL) for hardpan penetration were identified. This research established root penetration may be screened using the wax layer system, and that root penetration benefits root depth in the field. Cultivars with enhanced root penetration should be advantageous in many situations.

Key Words

Soil physical constraint, root depth, hardpan penetration ability, water deficit, screening, wheat, review

Introduction

Australian subsoils are often hostile to roots, with numerous chemical and physical constraints. Of the 17.8 million hectares of cropping land in the Western Australian wheatbelt, 24% has high susceptibility for subsoil compaction and 43% has moderate susceptibility, while duplex soils total around 60%. Soils that compact easily or had a high clay content that set hard on drying, or abruptly changed in bulk density at depth, constrain root growth and water movement. Roots are instead distorted and thickened radially. Without penetration, root growth was restricted to the soil layer above the hardpan or clay subsoil, and rapid depletion of soil nitrogen and water there promoted the early onset of water deficit, poor shoot growth and reduced grain yield. In contrast, root depth is relatively uninhibited in deep sands, but these soils drain freely and have poor water-storage capacity per unit depth. In all cases, soil remediation for improved root growth is needed, together with deeper roots that can penetrate hostile subsoils. This paper reviews recent research on root traits for hardpan penetration and water extraction, and the implications for agronomy and crop improvement.

Validation of the thin wax layer technique for evaluating hardpan penetration ability

The ability of roots to penetrate hard soil was simulated experimentally using soil columns containing a thin paraffin wax-petroleum jelly layer. A series of experiments were undertaken to assess the effect of wax-layer strength and soil water deficit (above and below the wax-layer) on root penetration during vegetative growth of wheat (Acuna and Wade 2005). Partitioning of the soil column by the wax layer made it possible to examine the interaction between hardpan strength and soil water deficit.

Wheat cultivars differ in root penetration of a wax layer and of field soils

Following the successful technical experimentation just discussed, the ability of seminal and nodal root to penetrate through thin wax layers was evaluated in 24 Australian wheat entries (cultivars and breeding lines) in soil columns (Acuna et al 2007). Nodal roots ceased growth early under soil water deficit, and water uptake was instead dependant on seminal roots under conditions imposed in columns. Plants were then reliant on the ability of seminal roots to penetrate the wax layer. Eight entries (Camm, Carnamah, Bonnie Rock, Halberd, Janz, Machete, Stiletto and Wilgoyne) had superior root penetration in both well-watered and drought-stressed conditions, with water deficit promoting faster and greater exploration of soil below the wax layer (Fig. 1). Roots of two other entries (C18 and Cranbrook) failed to penetrate the wax layer, and could not maintain their water requirements (Fig. 2).



Fig. 1. Root DM below the wax layer for four wheat cultivars: A) Bonnie Rock; B) C18; C) Cranbrook; and D) Halberd in well-watered (WW) and water stress (WS) conditions through time. (Acuna and Wade 2005).



Fig. 2. Daily water use over time of selected entries under drought-stress in controlled conditions. ●, Bonnie Rock; ○, Halberd; ▼, C18; and △, Cranbrook. (Acuna et al 2007).

Our research was the first attempt in wheat to relate cultivar differences in root penetration ability through thin wax layers to field performance in contrasting soil types, including a sandy duplex that contained a hardpan and a red clay that increased in soil strength with depth (Acuna et al 2007). Four of the eight superior entries also showed superior root penetration at both sites in the field. GxE was hypothesised to relate to differences in root traits, should these confer an ability to penetrate a sudden versus gradual increase in soil hardness or adaptation to drought. Alternatively, a cultivar with a greater root front velocity may be able to grow roots to depth before penetration resistance rises on subsequent soil drying. A more vigorous cultivar may have more dry matter to allocate to roots, and this may be important where thicker roots were observed to be beneficial for root penetration to depth. There was overall consistency among genotypes in root penetration between a wax layer in soil columns and a hardpan in the field, but there were some exceptions at individual field sites.

$\mathbf{G}\times\mathbf{E}$ for root depth is significant

Numerous studies in various crops have reported on G x E interactions for yield and components of yield, but none to our knowledge have attempted to use this approach for root depth in wheat. A G × E approach was used to determine the basis of adaptive response in root depth of the same 24 wheat entries in 6 environments with contrasting soil physical characteristics. For root depth, genotype accounted for only 12% of total variance compared with 40% for G × E interaction. Cluster analysis on the mean-polish standardised residuals was used to identify five environment and five genotype groups (Fig. 3). The results were consistent with the hypothesis that different soil conditions would require a different combination of traits for effective root growth, water extraction and nutrient uptake. Greater dry matter accumulation was generally associated with greater root growth. In the absence of physical constraint, faster root front velocity was important, especially on deep sands of low water-holding capacity. When physical constraint was present, however, root penetration ability was essential for greater exploitation of soil resources below the topsoil.



Fig. 3. Principal component analysis (mean polished) for the environment x genotype interaction for AX1 and AX2 for root depth for 6 environments and 24 wheat cultivars. Refer to Table for genotype (G) abbreviations and site, soil and year abbreviations for environments (E). The G x E interaction for AX1 and AX2 accounted for 69.9% of the sum of squares. (Botwright-Acuna and Wade 201_ Field Crops Res. submitted).

Substantial variation among DHLs in root depth below the wax layer and in the field

Study of the genotypic variation in hardpan penetration ability within the same genetic background was undertaken using a doubled haploid population (N = 143) of the cross between Halberd (good) and Cranbrook (poor). Nodal root DM above the wax layer was the same for the two parents, with little variation among the DHLs. In contrast, seminal roots of the Cranbrook parent and around half of the DHL population failed to penetrate the wax layer, while seminal root DM below the wax layer of the Halberd parent was

exceeded in around 15 of the DHLs (Fig. 4). Root growth of a subset of the DHL population (N = 16) plus the parents and check cultivars was assessed on contrasting soil types at 90 days after sowing at Merredin in 2008. Consistent with previous observations, root exploration of Cranbrook and C18 was constrained in the sandy soil that contained a hardpan. Root depth of two of the DHLs was similar to the Halberd parent, which reached 55 cm on the sandy soil by 90 DAS. QTL analysis identified complex genetic control for root traits, but with significant genotype contributions associated with chromosomes 1B, 1D, 2B and 6D (not shown).



Fig. 4. Frequency of response of root characteristics for 145 Cranbrook (CBK) x Halberd (HAL) DHLs and the parents for: A) Nodal root DM above the wax layer; and, B) Seminal root DM below the wax layer. (Botwright-Acuna et al 201_ Field Crops Res. submitted).

Conclusions

Results from soil column and field studies indicated that genetic variation existed in root traits that were required to penetrate uniformly hard soil, dry soil or soil containing a hardpan. Screening for hardpan penetration ability of wheat in soil columns with a wax layer was reasonably correlated with root depth and root growth in field soils. GxE interactions for root depth in field soils were large, reflecting complex root-soil interactions, with different trait combinations required for different target environments. Cultivars with enhanced root penetration should be advantageous in many situations.

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