

## Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (*Triticum aestivum* L.)

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**Abstract** Root system characteristics are of fundamental importance to soil exploration and below-ground resource acquisition. Root architectural traits determine the in situ space-filling properties of a root system or root architecture. The growth angle of root axes is a principal component of root system architecture that has been strongly associated with acquisition efficiency in many crop species. The aims of this study were to examine the extent of genotypic variability for the growth angle and number of seminal roots in 27 current Australian and 3 CIM-

MYT wheat (*Triticum aestivum* L.) genotypes, and to quantify using fractal analysis the root system architecture of a subset of wheat genotypes contrasting in drought tolerance and seminal root characteristics. The growth angle and number of seminal roots showed significant genotypic variation among the wheat genotypes with values ranging from 36 to 56 (degrees) and 3 to 5 ( $\text{plant}^{-1}$ ), respectively. Cluster analysis of wheat genotypes based on similarity in their seminal root characteristics resulted in four groups. The group composition reflected to some extent the genetic background and environmental adaptation of genotypes. Wheat cultivars grown widely in the Mediterranean environments of southern and western Australia generally had wider growth angle and lower number of seminal axes. In contrast, cultivars with superior performance on deep clay soils in the northern cropping region, such as SeriM82, Baxter, Babax, and Dharwar Dry exhibited a narrower angle of seminal axes. The wheat genotypes also showed significant variation in fractal dimension ( $D$ ). The  $D$  values calculated for the individual segments of each root system suggested that, compared to the standard cultivar Hartog, the drought-tolerant genotypes adapted to the northern region tended to distribute relatively more roots in the soil volume directly underneath the plant. These findings suggest that wheat root system architecture is closely linked to the angle of seminal root axes at the seedling stage. The implications of genotypic variation in the seminal root characteristics and fractal dimension for specific

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adaptation to drought environment types are discussed with emphasis on the possible exploitation of root architectural traits in breeding for improved wheat cultivars for water-limited environments.

**Keywords** Cluster analysis · Digital imaging · Fractal dimension · Root architecture · Seminal roots · Drought environments

## Introduction

Drought is generally regarded as the most widespread limitation to wheat (*Triticum aestivum* L.) productivity and yield stability in rain-fed production systems. Consequently, developing wheat cultivars with enhanced drought adaptation and higher yield has been the focus of many crop improvement programs. Root system characteristics are of fundamental importance to soil exploration and below-ground resource acquisition, and hence are strongly related to plant adaptation to sub-optimal conditions such as drought stress. In a comprehensive review of traits likely to improve yield in water-limited environments, Ludlow and Muchow (1990) placed rooting depth and density high in their list of priorities of drought-adaptive attributes to be exploited in crop improvement programs.

There is widespread evidence for genotypic variation in the root characteristics of many crop species (O'Toole and Bland 1987; Ludlow and Muchow 1990). In wheat, such traits include the depth of rooting, root elongation rate, root distribution at depth, xylem vessel diameter, and root to shoot dry matter ratio (Hurd 1968; O'Brien 1979; Richards and Passioura 1989; Siddique et al. 1990; Gregory 1994; Hoad et al. 2001; Manske and Vlek 2002; Manschadi et al. 2006). Compared to shoot-related traits, integration of drought-adaptive root characteristics in breeding for drought-tolerant wheat cultivars has been relatively less successful (Sinclair et al. 2004; Richards 2006). Genetic modification of the diameter of xylem vessels to increase root hydraulic resistance is the only example where targeted selection for a specific root trait was linked with attempts to breed wheat varieties with improved yield under dry conditions (Passioura 1972; Richards and Passioura 1989). The reasons for neglecting traditional drought-

adaptive root traits, such as greater depth of rooting and increased distribution of root length at depth, lie in the difficulties involved in accessing and evaluating mature root systems in soil, large phenotypic plasticity of root traits in response to various soil conditions, and lack of rapid and cost-effective screening methods. Given the obstacles to selection for traditional root traits, architectural root properties that are expressed at early stages of crop development and determine the growth and functioning of the mature root system later in the season may be more suitable as selection criteria in crop improvement programs (Manschadi et al. 2006).

Root architectural traits can be divided into geometric properties, such as the growth angle of root axes, and topological properties that describe the pattern of root branching. Together with the extension rate of individual root axes, these traits determine the in situ space-filling properties of a root system within the soil (i.e. root architecture), with the implication that the overall geometric configuration has some functional significance for the temporal and spatial patterns of water and nutrient acquisition (Fitter 1987, 2002 #872; Lynch 1995 #884). Therefore, if the whole root system architecture is known, traits that have commonly been associated with drought tolerance such as the depth of rooting, spatial root length distribution, and root-length density, can also be estimated.

Substantial variation in root architecture has been reported both among plant species (Kutschera 1960; Fitter and Stickland 1992; Bouma et al. 2001), and within genotypes of crop species (Masi and Maranville 1998; Liao et al. 2001; Lynch and Brown 2001; McPhee 2005) including wheat (Manschadi et al. 2006). Several attempts have been made to develop quantitative methods for describing root architecture. Fitter (1987, 2002) proposed a topological approach based on the number and spatial arrangement of root links for the analysis of root branching pattern. While this approach yielded valuable parameters for quantitative characterisation of root branching (Fitter and Stickland 1991; Berntson 1997; Bouma et al. 2001), the requirement for detailed data on root links which are difficult to acquire render this method less suitable for selection purposes. Another approach involves the application of fractal geometry to architectural analysis of root systems. Fractal geometry is a quantitative method of describing complex natural objects with

non-integer dimensions (Mandelbrot 1983). Root systems appear to approximate fractal objects over a finite range of scales because the repetitive branching of roots leads to a certain degree of self-similarity which is a fundamental characteristic of fractal objects (Tatsumi et al. 1989; Fitter and Stickland 1992; Bertson 1994; Eshel 1998). Variations in fractal dimension of root architecture in response to genotype, water, and nutrient availability have been reported in a number of crop species (Eghball et al. 1993; Lynch and van Beem 1993; Masi and Maranville 1998; Nielsen et al. 1999). However, to the best of our knowledge, there has been no attempt to characterise root system architecture of wheat using fractal analysis.

The growth angle of root axes or root gravitropic response is a principal component of root system architecture which has been strongly associated with temporal and spatial acquisition efficiency of soil resources. In common bean (*Phaseolus vulgaris* L.) for instance, the angle of basal roots is the major determinant of root architecture, with genotypes exhibiting a wider basal root angle appearing to develop a shallower root system, which enhances topsoil foraging and thus phosphorous acquisition (Lynch and van Beem 1993; Nielsen et al. 1999; Liao et al. 2001; Lynch and Brown 2001). Likewise, Kato et al. (2006) demonstrated that the growth angle of nodal roots in rice (*Oryza sativa* L.) affects vertical root distribution and rooting depth, which are considered as important traits for drought adaptation in upland rice. In wheat, Nakamoto and Oyanagi (1994) demonstrated significant genotypic variation in the angular spread of seminal roots in the Japanese germplasm and argued that deeply-rooted wheat genotypes exhibit a narrower angle of seminal roots, while genotypes with a shallower root system tend to grow their seminal roots more horizontally.

In a previous study conducted in large root observation chambers, we found significant differences in root system architecture and spatial patterns of water acquisition between the high-yielding drought-tolerant wheat genotype SeriM82 and the standard wheat cultivar Hartog, with roots of SeriM82 exhibiting less lateral spread and a more uniform and deep root architecture in the post-anthesis phase (Manschadi et al. 2006). Based on these observations and the evidence available in the literature (Nakamoto and Oyanagi 1994; Araki and Iijima 2001), we hypothesised that seminal roots characteristics may

be a major determinant of the architecture of the mature root system. Consequently, the objectives of the present study were to (1) examine the extent of potential genotypic variability for the growth angle and number of seminal roots in a set of widely grown current Australian and CIMMYT wheat genotypes including Hartog and SeriM82, (2) quantify, using fractal analysis, the root system architecture of a subset of wheat genotypes contrasting in seminal roots characteristics and drought tolerance, and (3) assess the relationship between seminal root traits and adaptation of wheat genotypes to Australian regions contrasting in drought environment types.

## Materials and methods

### Plant material

The growth angle and number of seminal roots was measured for 26 wheat cultivars representing some of the most widely grown varieties in Australia and 3 CIMMYT genotypes Babax, SeriM82 and Dharwar dry (Table 1). Among these wheat genotypes were Hartog and SeriM82 which, based on our previous study (Manschadi et al. 2006), differ in root architecture and adaptation to water-limited environments. SeriM82 is a high-yielding drought-tolerant CIMMYT line (Sivapalan et al. 2001, 2003; Olivares-Villegas et al. 2007) that has been shown to yield on average 12% more than Hartog in multi-environment trials in north-eastern Australia (Peake et al. 1996; Cooper et al. 1999).

For the fractal analysis of root architecture, a subset of wheat genotypes differing in seminal root characteristics, including Hartog, SeriM82, Baxter, Rees, and Dharwar Dry, were chosen. As with SeriM82, the genotypes Baxter, Rees, and Dharwar Dry also exhibit varying degrees of drought tolerance in north-eastern Australia when compared to Hartog (Christopher et al., unpublished data). The spring barley (*Hordeum vulgare* L.) cv. Mackay was also included for comparison with wheat.

### Gel-filled chamber experiment

The number and growth angle of seminal roots of wheat seedlings was measured using gel-filled root observation chambers as described by Bengough et al.

**Table 1** Characteristics of wheat genotypes and barley cv. Mackay used in the studies of seminal root characteristics and fractal analysis of seedling root architecture

Genotype	Breeding program <sup>a</sup>	Genetic background <sup>b</sup>	Adaptation <sup>c</sup>		
			N	SE	W
Babax	CIMMYT	Veery	X		
Baxter	QDPI	CIMMYT/Cook	X		
Chara	DPI Vic	Cook/Pavon		X	X
Dharwar Dry	CIMMYT	CIMMYT	X		
Diamondbird	NSW DPI	Pavon	X		
EGA Gregory	EGA	Pelsart/Batavia	X		
EGA Hume	QDPI	Pelsart/Batavia	X		
EGA Wedgetail	EGA	Cook/Pavon		X	
EGA Wentworth	EGA	Cook	X	X	X
EGA Wylie	EGA	CIMMYT/Cook	X		
Frame	AGT	Condor/Gabo		X	
GBA Hunter	EGA	Veery	X	X	X
Giles	QDPI	Cook	X	X	X
Hartog	QDPI	Pavon	X		
Janz	QDPI	Cook	X	X	X
Kennedy	QDPI	Pavon/Veery	X	X	
Krichauff	AGT	Condor/Gabo		X	X
Lang	QDPI	Cook	X	X	
Leichhardt	QDPI	Pavon	X	X	
Petrie	QDPI	Pelsart/Batavia	X		
Rees	QDPI	Pavon	X		
Rosella	NSW DPI	Cook/Pavon		X	
SeriM82	CIMMYT	CIMMYT/Veery	X		
Silverstar	NSW DPI	Cook/Pavon		X	
Sunco	Uni Syd	Cook	X	X	
Sunvale	Uni Syd	Cook	X		
Ventura	NSW DPI	Cook/Pavon		X	
Wyalkatchem	AgWA	Condor/Gabo		X	X
Yitpi	AGT	Condor/Gabo		X	X
Barley cv. Makay	QDPI	Cameo/Kuro	X		

<sup>a</sup> Breeding program abbreviations: *QDPI* Queensland Department of Primary Industries, *DPI Vic* Department of Primary Industries Victoria, *AGT* Australian Grain Technologies, *NSW DPI* New South Wales Department of Primary Industry, *CIMMYT* International Maize and Wheat Improvement Center, *EGA* Enterprise Grains Australia, *AgWA* Western Australia department of Agriculture, *Uni Syd* University of Sydney

<sup>b</sup> Indicates cultivars or breeding lines related to the tested line. Relatedness of background lines to the tested lines varies and these are cited as a general guide to the characteristics of the test lines only. In some cases the test lines are sibs of the background line. In other cases the major parent lines from the pedigree are given. Pavon and Veery indicate lines from these two crosses made and named at CIMMYT. “CIMMYT” indicates other or unnamed breeding lines from CIMMYT.

<sup>c</sup> Cultivars are classified as adapted to regions where they can produce yields equal to or in excess of those of wheat variety Janz in the absence of biotic stresses; N, SE, and W indicate the northern, south-eastern, and western wheat cropping regions of Australia (P. Banks, personal communication; Eastwood 2001; Lush 2007; McRae et al. 2007; DAFWA 2007).

(2004). Chambers were constructed from two plates (one black Perspex and one clear glass), each measuring 210 × 300 × 3 mm. Sterilised agar (Sigma Type A; 2% w/v) was poured onto each plate and

allowed to gel before the two plates were taped together with the agar surfaces inward. Seed of each genotype were graded removing the largest and smallest seed to select a uniformly sized sample close

to the median size for each genotype. The selected seed samples ranged from  $3.1 \text{ g } 100^{-1}$  for Wyalkatchem to  $4.7 \text{ g } 100^{-1}$  for Diamondbird.

Surface sterilised wheat seed was imbibed with sterile deionised water for a few hours and then placed on wet blotting paper and kept at room temperature for 2 days to allow germination. Two germinated seeds were placed into the narrow air space of approximately 2.5 mm between the agar layers, 80 mm apart, and 50 mm from the top edge of the vertically mounted chambers. The seeds were oriented vertically with the radicle facing downwards. The gel-filled chambers were then kept in a plant growth cabinet at  $15^{\circ}\text{C}$  for 5 days in the dark until the first leaf emerged at the top of the trays and then cultured under constant temperature of  $15^{\circ}\text{C}$  at 12/12 h dark/light condition. The light intensity in the growth cabinet at plant height was  $220 \mu\text{moles photons m}^{-2} \text{ s}^{-1}$ . Light was excluded from the root observation chambers using opaque vinyl covers except during observations. The gel-filled chambers were arranged in a complete randomised block with four chambers per genotype. At 8 days after seed transfer, the seminal roots visible through the clear glass were scanned using a flat bed scanner (HP Scanjet 4670). For each wheat seedling, the growth angle of individual root axes belonging to the first and second pair of seminal roots, counting upwards from the primary seminal root (or radicle), was measured at 3 cm distance from the seed relative to a vertical line passing through the stem base. Specifically designed computer software allowed rapid measurement of seminal root angle from the digital images.

#### Soil-filled chamber experiment

Root system architecture of five wheat genotypes, Hartog, SeriM82, Dharwar Dry, Rees, Baxter, and the barley cv. Mackay was studied in soil-filled root observation chambers. The experiment was conducted in the winter growing season 2006 at the Queensland Department of Primary Industries and Fisheries, Toowoomba (27 31'58" S, 151 56'8" E), Australia. The rectangular root chambers (400 mm wide, 600 mm deep and 30 mm thick) were constructed using steel frames with Perspex sides (6 mm thick), and filled with a soil mixture consisting of brown vertosol soil, composted cattle manure, and coarse sand (50:30:20vol.%). To ensure non-limiting supply

of nutrients, pellets of Osmocote® slow release fertilizer were added to the soil mixture. Prior to planting, the soil was saturated and then allowed to drain for several days. Three seeds of each genotype were planted in the middle of each root chamber at a depth of 30 mm on June 22. Seedlings were thinned to one per chamber following emergence and water was added again until drainage was observed from the bottom of the chambers. No more water was added during the plant growth period. Light was excluded from the Perspex sides of the chambers using opaque vinyl covers except during root observations. The root chambers were arranged in a complete randomized block design with four replicates per genotype in a poly-house. The mean daily air temperature during the experimental period in the poly-house ranged from 7.9 to  $12.5^{\circ}\text{C}$ . The solarweave cover of the poly-house allowed transmission of 75% of incident photosynthetically active radiation.

At the 4–5 leaf stage (40 days after planting), plant shoots were harvested and dissected into leaf blades and stems (including leaf sheaths). The dry weight (oven-drying at  $65^{\circ}\text{C}$  for 72 h) of shoot organs was determined for each plant. The chambers were then laid on one side and the upper Perspex was removed for root sampling. A black-painted pin board with the same dimensions as the Perspex sheet was positioned onto the open chamber so that the pins penetrated the soil block. The chamber was then inverted and carefully removed to expose the soil block with intact root system on the pin board. In this way the spatial orientation of the root system was maintained. The pins within the pin board were arranged in a grid pattern with pins evenly spaced 18 mm apart. After carefully washing the soil mixture from the roots, digital photographs of each entire root system were taken with a digital camera (8Mega Pixel) mounted on a tripod. The images ( $540 \times 340 \text{ mm}$  with a resolution of  $50 \text{ pixels cm}^{-1}$ ) were converted to high-contrast black-and-white pictures using Photoshop CS2 software (Adobe Systems Incorporated, USA). Following the digital imaging, roots were removed from the pin board and oven-dried at  $65^{\circ}\text{C}$  for 72 h before determining their dry mass.

Fractal dimension was calculated from the root system images using the box-counting method (Tatsumi et al. 1989; Nielsen et al. 1997). This procedure is based on superimposing a grid on the root system image and counting the numbers of squares intercepted

by roots for various square sizes. Fractal dimension ( $D$ ) is then estimated by fitting the linear regression:

$$\log N(r) = -D \log r + \log K$$

where  $N(r)$  is the number of boxes intercepted by roots,  $r$  is the box side length and  $K$  is a constant. The slope of the regression line defines the fractal dimension  $D$ . By definition, if a two-dimensional object is fractal, the value of  $D$  must be greater than 1 and less than or equal to 2. The box side lengths used varied from 2 to 10 mm in seven steps.  $D$  was estimated both for the entire root system and for individual root system sections formed by dividing the root system images into nine ( $110 \times 180$  mm) segments. A computer program was written to automate the calculations of fractal dimension.

### Statistical analysis

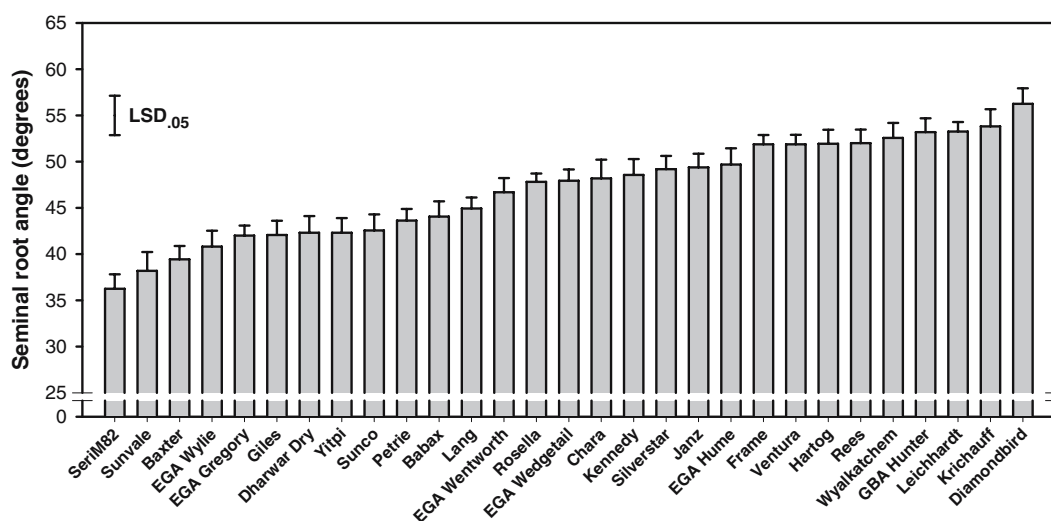
Analysis of variance was carried out using the GLM (General Linear Model) procedure of the SAS statistical package (SAS Institute Inc. 1991). Significant differences in the mean values were determined by Fisher's Least Significant Difference (LSD) test at a significance level of 0.05. A cluster analysis was also conducted to identify discrete groups of wheat genotypes with similar growth angle and number of seminal roots. Clustering was performed in S-PLUS ver. 6.1 software (Insightful Corporation, USA) using Ward's hierarchical approach based on minimum

variance linking method with Euclidean distance as the similarity measure (Hartigan 1975). Prior to cluster analysis, the seminal root data were standardized by subtracting the values for each genotype from the overall mean and then dividing by the standard deviation.

## Results

### Growth angle and number of seminal roots

In the gel-filled chambers, seedling roots grew freely in the air space between the two gel surfaces generally without penetrating the gel layers. At the time of root imaging, i.e. 8 days after seed germination, no lateral roots had emerged from the seminal axes. In wheat genotypes, the primary seminal root (radicle) appeared to grow almost vertically, while the second pair of seminal roots elongated almost horizontally. The average growth angle of the second pair of seminal roots was  $78.4 (\pm 6.79)$  and did not differ significantly among the wheat genotypes. The average growth angle of the first pair of seminal roots was generally between those measured for the radicle and second pair, and showed significant genotypic variation among the wheat cultivars (Fig. 1). As there was little difference in the angle of second pair of seminal roots these will not be discussed further. To simplify the discussion we will hereafter refer to the first pair



**Fig. 1** Growth angle (degrees) of wheat seminal roots in a set of CIMMYT and widely grown Australian genotypes. The bars indicate standard error of the mean; the vertical bar represents LSD ( $p=0.05$ ) for comparing the mean values

of seminal roots simply as the “seminal roots” unless otherwise stated. SeriM82 exhibited the smallest growth angle ( $36.2 \pm 1.57$ ) and the largest angle ( $56.3 \pm 1.68$ ) was measured for Diamondbird. The seminal roots of Hartog and Rees cultivars had significantly wider growth angle than those of SeriM82, Baxter, and Dharwar Dry.

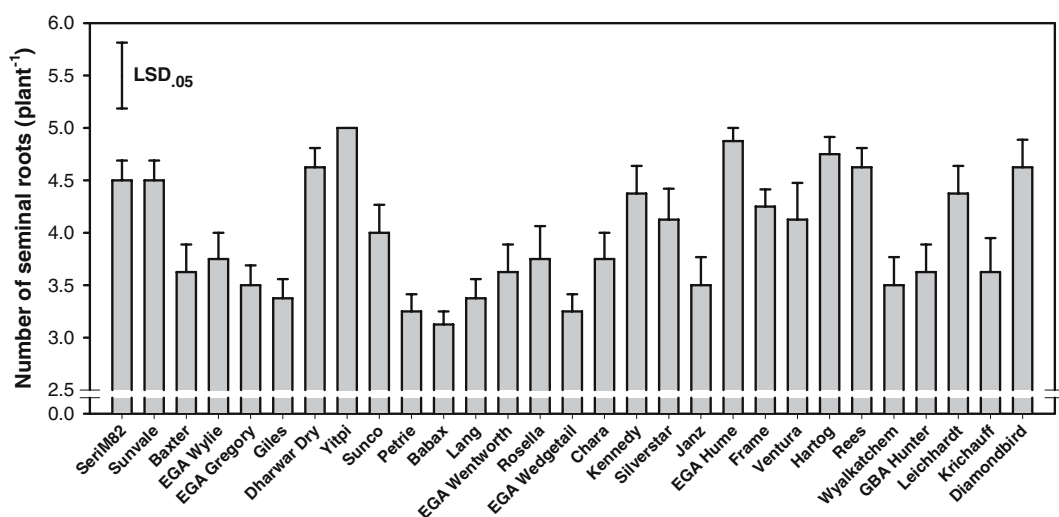
As with the growth angle, the number of seminal roots also varied between wheat genotypes (Fig. 2). While Yitpi developed consistently five seminal root axes, Petrie, EGA Wedgetail, and Babax were the genotypes with the lowest number of seminal roots ( $3.2 \pm 0.15$ ). Contrary to the finding on angle of seminal roots, the number of seminal axes did not differ significantly among the wheat cultivars Hartog, Rees, SeriM82 and Dharwar Dry. There was no correlation between the growth angle and number of seminal roots. Furthermore, the seminal root traits did not correlate with seed size in the tested wheat genotypes (data not shown).

Cluster analysis of the seminal root number and growth angle indicated that the wheat genotypes formed 4 discrete groups (Fig. 3). Groups 1 and 2 consisted of eight genotypes each, while Groups 3 and 4 included nine and four cultivars, respectively. Wheat cultivars in Groups 1 and 2 exhibited a low number of seminal roots combined with either wide or narrow root growth angle, respectively, whereas cultivars in Groups 3 and 4 comprised genotypes expressing a high number of seminal roots combined with either wide or narrow root angle (Fig. 4).

The grouping of genotypes based on their seminal root traits appeared to be only partly related to their genetic background. For instance, all Pavon-type cultivars including Hartog had wider growth angle and higher number of seminal axes and were clustered in Group 3. Similarly, the sister lines Baxter and EGA Wylie were clustered together in Group 2. Cultivars belonging to other genetic backgrounds did not show a consistent pattern of seminal root angle and number and therefore were grouped in different clusters. For example genotypes closely related to Cook are found in all groups. Adaptation to production environments seemed to also partially explain the grouping of wheat genotypes. While Group 1 was dominated by genotypes specifically adapted to the south-eastern and western wheat cropping regions of Australia, the majority of genotypes in Groups 2, 3, and 4 are predominantly grown in the northern region. One exception to this general trend was Yitpi which is adapted in south-east but clusters in Group 4.

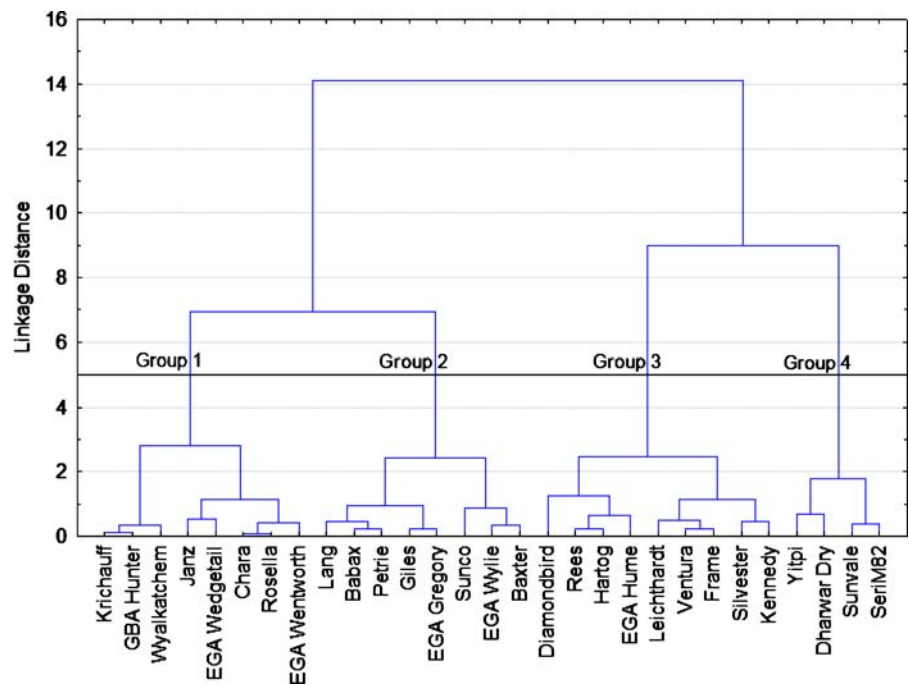
#### Fractal analysis of root architecture

At the time of harvest of the soil-filled chamber experiment (33 days after emergence), roots of all plants had reached the bottom of the chambers. Digital images of the whole root system removed from the soil onto the pin board illustrated visual differences in the lateral extension and branching intensity of roots among the genotypes tested (Fig. 5). Most of the root axes in barley cv. Mackay and wheat



**Fig. 2** Total number of wheat seminal roots ( $\text{plant}^{-1}$ ) in a set of CIMMYT and widely grown Australian genotypes. The bars indicate standard error of the mean; the vertical bar represents LSD ( $p=0.05$ ) for comparing the mean values

**Fig. 3** Clustering of 29 wheat genotypes based on their growth angle and number of seminal roots. The horizontal line indicates the cut-off used to form the four groups



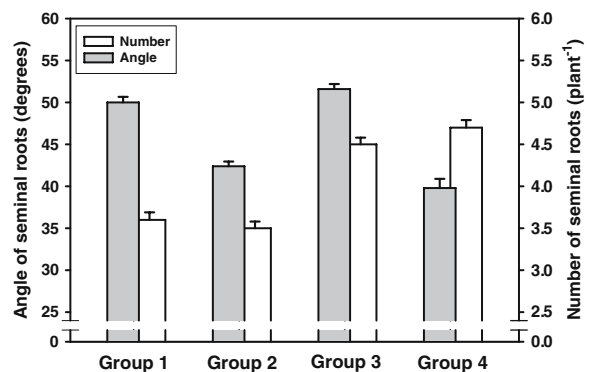
cultivars Hartog and Rees reached the sides of the root chamber at a depth of approximately 25 cm and grew thereafter down the sides of the root boxes. The drought-tolerant wheat SeriM82 exhibited the most compact root system with the main axes showing a near vertical growth orientation. Barley cv. Mackay, in contrast, had the most vigorous root system with a highly intensive branching structure.

In the calculation of fractal dimension ( $D$ ), all linear regressions had a coefficient of determination greater than or equal to 0.99 (data not shown), suggesting that within the range of resolution used in this study (2–10 mm) the root systems appeared to be fractal. The values of  $D$  calculated for the entire root system varied substantially among the genotypes. The lowest value of  $D$  ( $1.62 \pm 0.043$ ) was obtained for SeriM82 and the highest value for the barley cv. Mackay ( $1.84 \pm 0.040$ ) (Fig. 6). Among the wheat genotypes, the root system of Hartog had the greatest  $D$  and was significantly higher than that calculated for SeriM82.

The  $D$  values for the nine sections of the root systems are presented in Table 2. The data suggested that the roots of wheat genotypes Hartog and Rees and barley cv. Mackay were more uniformly distributed over the entire available soil volume, whereas SeriM82 exhibited a marked difference in spatial root distribution and branching intensity. This is evident in

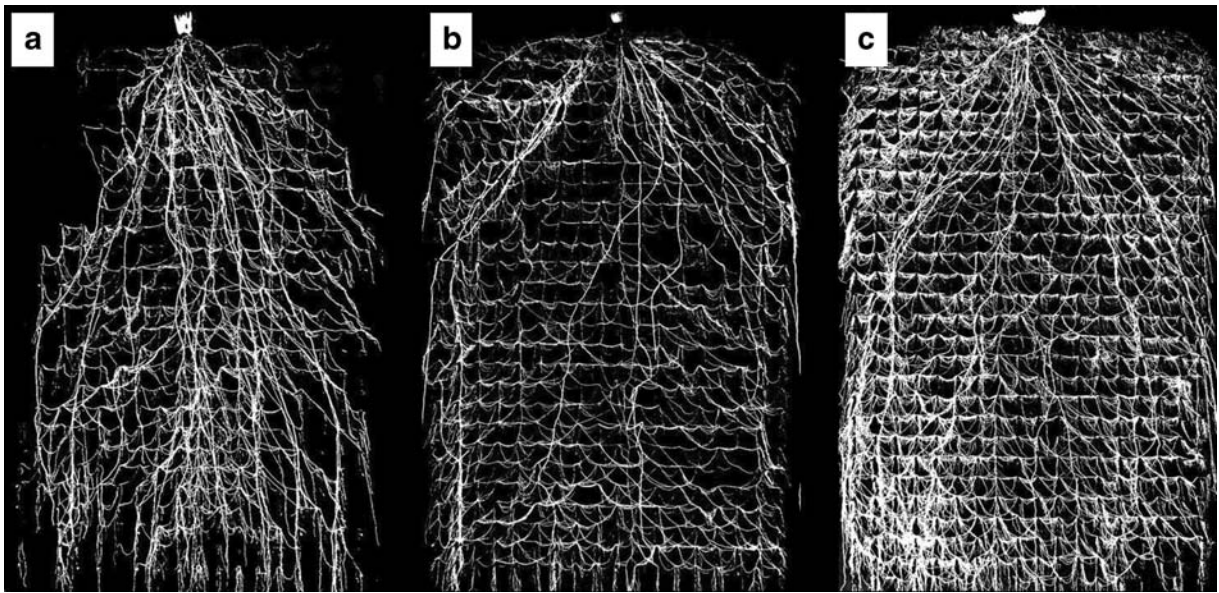
the greater  $D$  values found for the top-centre (TC), middle-centre (MC) and bottom-centre (BC) sections of the SeriM82 root system compared to those for the lateral sections. A similar pattern of spatial root deployment was also observed for the wheat cv. Dharwar Dry and Baxter with the difference that the  $D$  values for Dharwar Dry were generally greater than those calculated for SeriM82 and Baxter.

The data on biomass production and partitioning indicated that barley cv. Mackay accumulated about 50 and 62% more above-ground and root dry mass, respectively, than the wheat plants (Table 3). Among the wheat genotypes, SeriM82 was the least vigorous



**Fig. 4** Mean seminal root growth angle (degrees) and number (plant<sup>-1</sup>) for each group of wheat genotypes as represented in Fig. 3. The bars indicate standard error of the mean





**Fig. 5** Representative root system images at 33 days after emergence for wheat genotypes Serim82 (a) and Hartog (b), and barley cv. Mackay (c) grown in soil-filled root observation chambers

plant, with its shoot and root dry mass being 46 and 31%, respectively, of that measured for Hartog. The growth attributes of Rees, Baxter and Dharwar did not differ significantly from those of Hartog.

All genotypes had less dry matter in the roots than in the shoots. The ratio of root to shoot dry mass (R:S) ranged from 0.31 ( $\pm 0.016$ ) for Hartog to 0.45 ( $\pm 0.047$ ) for the barley cv. Mackay (Table 3). The wheat cultivars Baxter and Rees had a similar pattern of root to shoot biomass partitioning to Hartog. Serim82 and Dharwar Dry, however, exhibited significantly greater R:S ratios, with the values being about 30% higher than that for Hartog.

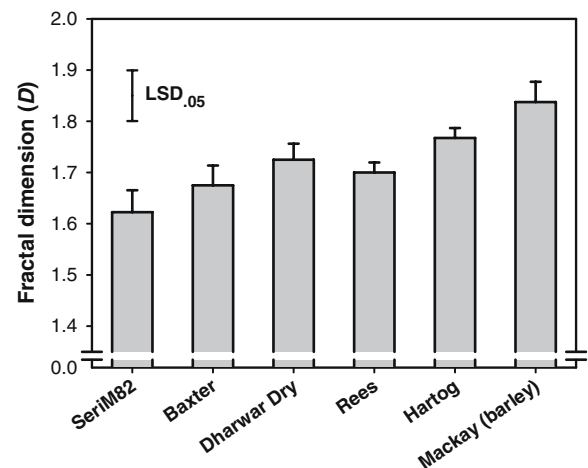
## Discussion

### Growth angle and number of seminal roots

In this study, we adopted the method of gel-filled chambers combined with digital imaging, described by Bengough et al. (2004), to investigate genotypic variation in seminal root characteristics among a set of wheat genotypes. This technique allowed for simple, rapid, and cost-effective screening of seminal root traits in an unimpeded environment and therefore appears to be suitable for large-scale screening of

seedling root characteristics in crop improvement programs.

Our results demonstrated that significant genetic variation exists in the growth angle and number of seminal roots among the wheat cultivars tested. The range of values for the growth angle of the first pair of seminal roots measured in our study (36.2–56.3



**Fig. 6** Fractal dimension calculated at 33 days after emergence for the whole root system of wheat and barley (cv. Mackay) genotypes grown in soil-filled root observation chambers. The bars indicate standard error of the mean; vertical bar represents LSD ( $p=0.05$ ) for comparing the mean values

**Table 2** Fractal dimension ( $D$ ) for the individual 110×180 mm sections of wheat and barley root systems grown in soil-filled root chambers

Genotype	$D$ of section								
	TL	TC	TR	ML	MC	MR	BL	BC	BR
SeriM82	1.53	1.72	1.60	1.52	1.57	1.51	1.55	1.58	1.50
Baxter	1.64	1.73	1.62	1.62	1.60	1.61	1.70	1.61	1.68
Dharwar Dry	1.58	1.75	1.60	1.65	1.70	1.71	1.70	1.75	1.69
Rees	1.68	1.76	1.68	1.69	1.60	1.63	1.64	1.62	1.69
Hartog	1.71	1.77	1.72	1.71	1.67	1.70	1.77	1.74	1.76
Mackay (barley)	1.80	1.80	1.80	1.75	1.74	1.83	1.84	1.81	1.83
LSD ( $P=0.05$ )	0.141	0.094	0.097	0.183	0.117	0.101	0.138	0.150	0.130

$T$ ,  $M$ , and  $B$  indicate top, middle, and bottom layers;  $L$ ,  $C$ ,  $R$  represent left, centre, and right segments within each layer.

degrees) is similar to that reported by Nakamoto and Oyanagi (1994) for winter wheat Japanese germplasm. This range may not necessarily encompass the full extent of genetic variation for the angle of seminal axes in wheat germplasm, as we tested only a set of genotypes with limited variation in pedigree and genetic background. The wheat genotypes also exhibited substantial variation in the number of seminal roots ranging from three to five axes. Similar to our results, O'Brien (1979) observed on average three to four seminal roots in a study involving Australian spring wheat cultivars. However, for winter wheat varieties grown in temperate environments, Gregory et al. (1978) reported that on average six seminal axes were produced. Furthermore, the lack of correlation between the growth angle and number of seminal root axes observed in this study is consistent with the results of a previous report (O'Brien 1979). We found no evidence of a correlation between seed size and either seminal root number or growth angle in the tested wheat genotypes. This appears to contrast the results of previous studies

(Fritsch 1977; Mac Key 1979) suggesting a strong correlation between the number of seminal roots and seed size. However, in those studies a large number of wheat species from *Aegilops* and *Triticum* genera were compared, while we investigated various cultivars of the same species (*Triticum aestivum* L.). Similar to our findings, Fritsch (1977) also noted that the relationship between seminal root number and seed size is less strong when comparison is made between cultivars within wheat species.

Cluster analysis of wheat genotypes based on similarity in their seminal root characteristics resulted in four groups each comprising of genotypes with a combination of wide/narrow growth angle and low/high number of axes. The group composition reflected to some extent the genetic background and environment adaptation of genotypes. For instance, all Pavon-type cultivars, including Hartog, were clustered together in Group 3 and the CIMMYT/Cook-derived cultivars Baxter and EGA Wylie were clustered in Group 2 (Fig. 3). Wheat cultivars grown widely in the southern and western regions generally

**Table 3** Total above-ground dry mass, dry weights of plant organs, and root to shoot ratio (R:S) of wheat and barley (cv. Mackay) genotypes grown in soil-filled root observation chambers at 33 days after emergence

Genotype	Above-ground	Leaf	Stem	Root	R:S ratio
	g plant <sup>-1</sup>				
SeriM82	0.85	0.62	0.23	0.34	0.40
Baxter	1.41	1.06	0.36	0.47	0.33
Dharwar Dry	1.34	0.94	0.39	0.55	0.41
Rees	1.75	1.26	0.49	0.59	0.34
Hartog	1.58	1.08	0.50	0.49	0.31
Mackay (barley)	2.82	1.90	0.92	1.27	0.45
LSD ( $P=0.05$ )	0.330	0.205	0.136	0.160	0.085

had wider growth angle and lower number of seminal axes (Group 1). In contrast, cultivars with superior performance on deep clay soils in the northern region, such as SeriM82, Baxter, Babax, and Dharwar Dry exhibited narrower angle of seminal axes (Groups 2 and 4). The only southern cultivar that expressed a narrow growth angle was Yitpi which is known to rank well in low-rainfall areas. The other varieties, which are widely grown in the northern region, expressed contrasting combinations of seminal root angle and number and were clustered separately in Groups 2 and 3. This may be due to the fact that possessing drought-adaptive root system architecture is not the only criterion affecting the selection, release and adoption of wheat cultivars in a particular production environment. Other factors such as resistance to biotic stresses and improved grain quality may also be equally important and play a decisive part in selection and adoption of cultivars by breeders and growers.

#### Fractal analysis of whole root system architecture

The fractal analysis of seedling root systems indicated, for the first time, that wheat genotypes differ significantly in root architecture and branching pattern as shown by variations in fractal dimension (Fig. 6). The  $D$  values obtained in this study (1.6–1.8) are similar to those reported by Masi and Maranville (1998), but generally greater than those measured in some other studies (Tatsumi et al. 1989; Fitter and Stickland 1992; Eghball et al. 1993; Berntson 1994; Eshel 1998; Nielsen et al. 1999). The variation among various studies in the fractal dimension values may be due to differences in plant age, growth conditions, and techniques used to determine  $D$ , as well as interspecific differences in root architecture.

The value of  $D$  is an index of the “space filling” properties of the root system and encompasses both topological and geometric root characteristics. Compared to wheat genotypes, the greater value of  $D$  calculated for the barley cv. Mackay can be attributed to the relatively more vigorous and highly-branched root system of barley. This is consistent with our previous observations (Manschadi et al. 2006) as well as other reports (Gregory et al. 1992; López-Castañeda and Richards 1994) demonstrating that the mature root system of barley tends to explore the topsoil more efficiently by producing greater root

length and mass compared to wheat. Among the wheat genotypes, Hartog exhibited the greatest value of  $D$ , while the root system of SeriM82 was characterised by the lowest  $D$  value suggesting significant differences in root development and branching structure between these two genotypes.

Fractal analysis of the individual root segments yielded some interesting results. The spatial distribution of roots in drought-tolerant genotypes SeriM82, Baxter, and Dharwar Dry differed markedly from those in Hartog and Rees. As indicated by the values of  $D$  (Table 2), the drought-tolerant genotypes tended to produce greater root distribution in the top, middle, and bottom central segments, while the root systems of Hartog and Rees appeared to spread more laterally. This distinct pattern of spatial root distribution was particularly expressed by the root system of SeriM82. The observed concentration of roots in the soil volume directly underneath the plant can be attributed to the growth angle of seminal root axes. In fact, SeriM82, Baxter, and Dharwar Dry were among the wheat genotypes exhibiting a narrower seminal root growth angle compared to Hartog and Rees (Fig. 1). These results confirm the previous reports on the close relationship between the growth angle of root axes and vertical patterns of root distribution in wheat. In a detailed study of root growth and water extraction pattern of single plants grown in large root observation chambers, we demonstrated that, compared to Hartog, the mature root system of SeriM82 was less laterally-spread and more compact. This resulted in significantly greater root length production at depth and hence higher water extraction from deeper soil layers (Manschadi et al. 2006). While little is known about the mature root system architecture of other wheat genotypes tested in this study, our findings and the observations of Oyanagi (1994) suggest that wheat root system architecture is closely linked to the angle of seminal root axes at the seedling stage, and that the early rooting characteristics determine the architecture and functioning of the mature root system later in the season. That means wheat genotypes exhibiting a narrow seminal root angle are likely to develop a compact and deep root system, whereas those with wider angle of seminal axes tend to form a broad, shallow root system. Similar relationships between gravitropic growth of the root axes and spatial deployment of root systems have also been reported in other crops such as rice

(Kato et al. 2006) and common bean (Lynch and van Beem 1993; Nielsen et al. 1999; Liao et al. 2001). Given the existence of genetic variability, expression at a very early stage of crop development, and availability of a relatively simple, rapid, and inexpensive screening technique, the growth angle of seminal roots appears to represent a promising trait that can potentially be exploited in wheat improvement programs. However, it must be noted that root characteristics commonly exhibit a high degree of phenotypic plasticity in response to temporal and spatial variation in rooting environment (Poorter and Nagel 2000; Fitter 2002) and this may complicate the identification of genotypic variation in root traits (Price et al. 2002). The results presented here and our previous observations on the architecture of mature root systems (Manschadi et al. 2006) provide strong evidence that the angular spread of seminal roots is a major determinant of post-anthesis root architecture in SeriM82 and Hartog under controlled conditions. However, further root architectural studies are required to determine how widely such a correlation occurs in the field.

#### Implications of seedling root architectural traits for drought adaptation

Root traits can moderate the effects of drought either by increasing the rate of water uptake through increased root-length density or by allowing a greater amount of water extraction through increased root length distribution at depth (Passioura 1983; Gregory 1989; Manschadi et al. 2006). By determining the form or geometric configuration of the root system, architectural traits such as growth angle of seminal axes may play a significant role in adaptation of wheat to water-deficit environments. The overall advantage of the architectural root traits, however, must be interpreted in the context of the type of environment in which the wheat crops are grown. For instance, the environments across the Australian wheat cropping belt differ markedly in the temporal pattern of rainfall distribution and hence the timing and severity of drought stress during the crop life cycle. In the northern production environments, which are characterised by a summer-dominant rainfall pattern, wheat crops are grown largely on water stored in the subsoil with a substantial risk that water may run out before the completion of grain

filling. In contrast, genotypes adapted to the winter-rainfall-dominant Mediterranean environments of the southern and western zones rely heavily on in-season rainfall (Nix 1975).

Root architecture is likely to be associated with genotypic adaptation to these contrasting environments. Forgoing some lateral root development in favour of a deeper root system to increase access to water from the deeper soil layers during the critical grain filling phase appears to be desirable in the northern environments. Possessing a large and shallow root system with greater potential for water extraction early in the season in order to reduce unproductive soil evaporation is more suitable for Mediterranean environments. Considering that the growth angle of seminal axes is one of the principal determinants of root system architecture, this study has shown that wheat cultivars grown in the Mediterranean environments of southern and western Australia tended to have a wide root angle, whereas drought-tolerant genotypes with higher yield in the northern cropping region exhibited narrower angular spread of seminal axes. Our observations are consistent with those reported by Oyanagi (1994) suggesting that Japanese winter wheat cultivars adapted to drier environments possess a narrow seminal root angle and consequently a deeper root system, whereas genotypes developed for more favourable, wetter environments express a more horizontal seminal root growth and superficial root system.

In addition to growth angle, the number of seminal roots may also affect the degree of adaptation to drought stress. Seminal roots tend to grow in deeper soil horizons and can therefore make a significant contribution to water uptake from subsoil. It has been reported that nodal roots, particularly those from early rooting nodes, can penetrate down to 1.3m in wheat plants grown in root boxes that were rewatered each week (Araki and Iijima 2001). However, detailed anatomical studies of xylem vessels of wheat roots indicated that under field conditions all roots occurring in subsoil were seminal axes and their branches, and no nodal roots were present at depth greater than 60 cm (M. Watt, personal communication). Thus, a greater number of seminal root axes may result in more intensive root branching and root length density at depth, which substantially enhances the capacity of root systems to explore the deep soil layers more effectively. Genotypes expressing high number of

seminal roots combined with a narrow growth angle, such as SeriM82, may be ideally suited to environments where plants rely largely on subsoil water.

The architecture of a mature wheat root system is not only determined by the number and growth angle of seminal roots that develop from the embryonic primordia present in the seed, but is also affected by the development of nodal or adventitious roots that arise from the basal nodes of the main shoot and tillers. The development of nodal roots in wheat is linearly related to the number of leaves on the culm (Gregory et al. 1978; Klepper et al. 1984), so that genotypes with faster leaf appearance rate and higher tillering capacity are expected to produce more nodal roots. Published information on the genotypic variation in gravitropic response of nodal axes in wheat is limited. Klepper (1992) reported that nodal roots are much less sensitive to gravitropism than seminal roots. Hence under field condition, nodal roots are likely to occur mainly in the top soil layers. Therefore, in environments where wheat crops rely largely on stored water in subsoil, the contribution of nodal roots to plant water uptake from subsoil, particularly during the generative phase, appear to be limited. In contrast, nodal axes may play a major role in water extraction from the shallow soil layers in Mediterranean-type environments where, due to substantial in-season rainfall, rewetting of the topsoil occurs more frequently. Furthermore, it has been demonstrated that the density of roots in the upper soil layers is the most important trait associated with improved acquisition of relatively immobile nutrients such as phosphorus (Manske et al. 2000).

It is important to note that drought tolerance is a complex character resulting from the interaction of a host of root and shoot traits (Ludlow and Muchow 1990; Richards et al. 2002). Root and shoot growth are inextricably linked because root system growth and maintenance depend on the assimilate supply by shoot. Concurrently, the size and activity of the root system determines the rate at which the shoot system can produce photosynthates. Therefore, in evaluating the implications of root architectural traits for drought adaptation, it is important to consider the attributes governing leaf canopy growth and development, timing of anthesis, and biomass allocation to the root system. In this study, we found significant genotypic variation in above-ground dry mass, root biomass, and R:S dry matter ratio among the wheat seedlings

(Table 3). Compared to Hartog, SeriM82 appeared to be less vigorous as indicated by significantly lower shoot and root dry weights, but exhibited substantially higher R:S ratio. Allocating relatively more biomass into the root system early in the life cycle combined with lower early shoot vigour may be an adaptive advantage of SeriM82 as this will reduce pre-anthesis water use and, hence, improve post-anthesis water availability. It has been shown in wheat (Manschadi et al. 2006; Kirkegaard et al. 2007) and sorghum (Hammer 2006) that small amounts of water “shifted” from pre- to post-anthesis in this way can have major effects on grain yield in water-limited situations. It seems that by linking this strategy with drought-adaptive root traits such as narrower growth angle and higher number of seminal axes, which result in greater distribution of roots at depth, SeriM82 possesses an optimal combination of attributes for adaptation to summer-dominant rainfall environments where effective utilisation of stored soil moisture is critical for improved yields under drought stress. In contrast, wheat genotypes with increased early shoot vigour and greater root growth and branching intensity have been shown to be better adapted to Mediterranean-type environments. The yield advantage of vigorous wheat genotypes has been attributed to greater water use and above-ground biomass production early in the season when vapour pressure deficit is low, reduced soil evaporative loss of water, and greater water-use efficiency (Rebetzke and Richards 1999; Liao et al. 2004, 2006).

The results presented here suggest that selection for growth angle and number of seminal roots may help to identify genotypes with a root system architecture that is better adapted to drought conditions. However, considering the complex interactions between plant attributes such as leaf canopy development, timing of anthesis, and R:S biomass partitioning with root growth and development, it is evident that improving wheat yield under drought conditions will require a whole plant growth and functioning approach. Further, drought adaptation must be evaluated in relation to the timing and severity of drought stress, which may vary according to soil water-holding capacity, moisture availability at crop sowing, and timing and quantity of in-season rainfall. Nonetheless, the findings of this study on root architectural traits identify it as one of the key attributes necessary for improved adaptation to drought in wheat.

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