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REVIEW

Domestication and Crop Physiology: Roots of Green-Revolution Wheat

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- **Background and Aims** Most plant scientists, in contrast to animal scientists, study only half the organism, namely above-ground stems, leaves, flowers and fruits, and neglect below-ground roots. Yet all acknowledge roots are important for anchorage, water and nutrient uptake, and presumably components of yield. This paper investigates the relationship between domestication, and the root systems of landraces, and the parents of early, mid- and late green-revolution bread wheat cultivars. It compares the root system of bread wheat and ‘Veery’-type wheat containing the IRS translocation from rye.
- **Methods** Wheat germplasm was grown in large pots in sand culture in replicated experiments. This allowed roots to be washed free to study root characters.
- **Key Results** The three bread wheat parents of early green-revolution wheats have root biomass less than two-thirds the mean of some landrace wheats. Crossing early green-revolution wheat to an F_2 of ‘Norin 10’ and ‘Brevor’, further reduced root biomass in mid-generation semi-dwarf and dwarf wheats. Later-generation semi-dwarf wheats show genetic variation for root biomass, but some exhibit further reduction in root size. This is so for some California and UK wheats. The wheat–rye translocation in ‘Kavkaz’ for the short arm of chromosome 1 (IRS) increased root biomass and branching in cultivars that contained it.
- **Conclusions** Root size of modern cultivars is small compared with that of landraces. Their root system may be too small for optimum uptake of water and nutrients and maximum grain yield. Optimum root size for grain yield has not been investigated in wheat or most crop plants. Use of IRS and similar alien translocations may increase root biomass and grain yield significantly in irrigated and rain-fed conditions. Root characters may be integrated into components of yield analysis in wheat. Plant breeders may need to select directly for root characters.

Key words: Root biomass, root branching, unconscious selection, *Triticum*, Mexican wheat, breeding, ‘Veery’ wheat, wheat–rye translocation, IRS translocation, components of grain yield.

INTRODUCTION

Domestication of plant species by humans in the last 10 000 years proceeded with observation and direct selection of mostly above-ground organs, namely stems, leaves, flowers and fruits. Below-ground organs, such as roots, were little observed, unless the root comprised a food-storage organ that was selected for directly. This general lack of interest in plant root systems, where up to half the plant was neglected, contrasts strongly with animals where the whole organism was observed and selected during domestication. Most plant scientists acknowledge roots are important for anchorage, and water and nutrient uptake from the soil solution. A small number consider the root system important for components of yield analysis (Bazzaz *et al.*, 2000).

Bread wheat (*Triticum aestivum* L.) is an allohexaploid ($2n = 6x = 42$) with the genome formula BBAADD. It was formed from hybridization of domesticated tetraploid wheat [*T. turgidum* L. ssp. *dicoccum* (Schrank) Thell. genome formula BBAA] with diploid weedy goat grass (*Aegilops tauschii* Coss. DD) in north-west Iran or Armenia (Dvorak *et al.*, 1998). *Triticum turgidum* ssp. *dicoccum* is a domesticated race of wild emmer *T. turgidum* L. ssp. *dicoccoides* (Korn. ex Asch. & Graebn.)

Thell. native to the fertile crescent of the Near East, and itself an allotetraploid formed from an ancestor of *Aegilops speltoides* Tausch as female parent (BB) and *T. urartu* Tum. ex Gandil. as male parent (AA) (Waines and Barnhart, 1992).

The history of the green revolution in wheat in the mid-20th century was outlined by Dr Norman Borlaug (Borlaug, 1968). This internationally important plant breeding programme was conducted largely by selection of above-ground organs. Wheat roots were rarely studied by breeders in the CIMMYT or national programmes. This paper investigates the relationship between domestication and the root system of bread wheat. It looks at root biomass of landraces and of the parent lines hybridized to select early-, mid- and late-generation green-revolution cultivars of bread wheat in Mexico, California and the UK.

This paper also compares root biomass of pure bread wheat and of ‘Veery’-type wheat that contains the IRS translocation from rye (*Secale cereale* L.). ‘Veery’ wheats are popular under drought or heat-stressed conditions for, on average, they may produce a 7% grain yield advantage (Rajaram *et al.*, 1983). They are favoured where grain yield is more important than bread-making quality. Up to 50% of all wheat cultivars in China may now carry the ‘Veery’ IRS translocation (Zhou *et al.*, 2003). ‘Veery’ wheats may have the IRS arm from two sources: the more common IRS_(K) is

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from 'Kavkaz' winter wheat, and the original translocation was selected in Germany from crosses of wheat with a 'Petkus' rye for resistance to fungal diseases (Schlegel and Korzun, 1997), while the more recent $1RS_{(A)}$ arm is from 'Amigo' winter wheat and the translocation was selected in Oklahoma from crosses with Brazilian 'Insave' rye for aphid resistance (Sebesta and Wood, 1978).

One of the first scientists to excavate and illustrate the root system of bread wheat and rye was Weaver (1926) who noted differences in length of seminal roots and lateral roots between the two species, but did not investigate cultivar differences within a species. Root growth differences among seven cultivars of Canadian spring bread wheat were reported by Hurd (1968) who hybridized parents with large, deep root systems and other desirable characters to select new cultivars with larger root systems and higher grain yield. Mac Key (1973) was the first to observe roots and shoots of F_1 hybrid plants of spring tall cultivar 'Prins' and tall winter cultivar 'Starke' with 'Norin 10' and 'Tom Thumb' the source of the *Rht1*, *Rht2* and *Rht3* alleles used by Borlaug (1968) in his Mexican semi-dwarf wheat breeding programme. Mac Key (1973) noted 'Prins' and 'Starke' had larger root dry weights than the F_1 hybrids with 'Norin 10' or 'Tom Thumb'. He concluded that 'a tall wheat plant tends to have a deep, and a short wheat plant a shallow, root system'. This raised the possibility that breeding for semi-dwarf stems, controlled by the *Rht1* and *Rht2* alleles on homoeologous group 4 chromosomes, might condition semi-dwarf root systems that might affect adversely the amount of water and nutrients absorbed by the plant, and hence grain yield. This was investigated in isogenic lines of UK winter wheat by Lupton *et al.* (1974) and found not to be so. Ehdaie and Waines (1994) in California, and Mirrales *et al.* (1997) in Argentina, used isogenic lines of the Brazilian spring cultivar 'Maringa'. The semi-dwarf *Rht1* and *Rht 2* isolines had larger root biomass than the tall *rht* line. The dwarf *Rht3* isolate with the shortest stems also had the smallest root system. In the semi-dwarf *Rht1* and *Rht2* isolines, assimilates not used to develop a large shoot system might be diverted to the roots to develop a larger root system. Secondly, Mac Key (1973, table 5) observed large differences in root biomass among old and modern wheats. Old varieties such as German 'Brown Schlanstedt' had three times larger root biomass than dwarf Mexican 'Mayo 64' or dwarf Japanese 'Kohnosu 25' while Brazilian 'Frontana' and Mexican 'Pictic 62' were intermediate. Troughton and Whittington (1968) using cultivar chromosome substitution lines, observed that differences in root size between tall landrace 'Chinese Spring' with large root biomass, and cultivar 'Hope', with small root biomass, were largely governed by genetic factor(s) on chromosome 1A, which is a different genetic system from that controlling the *Rht* stem dwarfing genes on chromosome 4, which have a smaller effect on root size. (See Appendix for a full list of cultivars mentioned in the text, together with brief descriptions.)

Similarly, three old tall landraces from China and Iran had 2- to 4-fold larger root biomass than four semi-dwarf Mexican, Iraqi, Pakistani and California cultivars, all of

which were descended from CIMMYT breeding material (Ehdaie *et al.*, 1991; Ehdaie and Waines, 1993, 1997; Ehdaie, 1995). The root biomass differences between the landraces and the CIMMYT-derived modern cultivars were always significantly different. The root size of other CIMMYT-derived bread wheats have since been determined and they are always significantly smaller than drought-tolerant landraces (J. G. Waines and B. Ehdaie, unpubl. res.), though admittedly only a few accessions have been observed. This tends to support the view that direct selection for only above-ground organs might also indirectly select for a small root system, especially under well-irrigated and well-fertilized growing conditions, as at CIMMYT breeding stations, where there would be no selection advantage for a larger root system.

What is lacking in this review of the few published observations on bread wheat root systems is knowledge of what happened, in a historic sense, in the progression from tall landraces to semi-dwarf and dwarf cultivars in the last 100 years. In barley (*Hordeum vulgare* L.) seedlings, Grando and Cecarelli (1995) noted an initial increase in root size from ten wild barleys to ten landrace barleys, then a marked decrease in root size from landraces to ten modern barley cultivars. Wild collections of bread wheat do not exist, only landraces. As far as we are aware, there is no report in the literature of the root systems of the three spring wheat parents which Borlaug (1968) hybridized to select the first-generation, tall Mexican wheats such as 'Nainari 60' or 'Lerma Rojo', or the root system of the Japanese two-gene-dwarfed wheat 'Norin 10' that contributed the *Rht1* and *Rht2* stem-dwarfing genes to mid-generation semi-dwarf and dwarf cultivars released by CIMMYT. This research was undertaken to fill this void.

MATERIALS AND METHODS

Kernels of the three spring wheat parental cultivars, namely 'Gabo' from Australia, and 'Marroqui' and 'Mentana' from the Mediterranean region, hybridized by Borlaug (1968) to form early green-revolution bread wheats, and of Japanese, tall 'Aka Komugi' were obtained from Dr Harold Bockelman, USDA Small Grains Collection, Aberdeen, ID, USA. Kernels of early Mexican tall 'Nainari 60' were obtained from Dr M. D. Gale, John Innes Centre, Norwich, UK, and mid-generation Mexican semi-dwarf 'Anza', 'Pavon 76' and 'Yecora Rojo' cultivars were obtained from Dr C. O. Qualset, Department of Plant Sciences, University of California, Davis. Kernels of late-generation Mexican wheats 'Bacanora', 'Pastor' and 'Rayon' were obtained from CIMMYT. Grains of the Pavon 1RS near isogenic lines, namely 'Pavon 76', 'Pavon $1RS_{(K)}.1AL$ ', 'Pavon $1RS_{(K)}.1BL$ ' and 'Pavon $1RS_{(K)}.1DL$ ' (Lukaszewski, 1993, 2000) and other Pavon translocation stocks were donated by Dr A. J. Lukaszewski, University of California, Riverside. Wheat kernels of similar weight were surface sterilized in a 10% solution of commercial sodium hypochlorite, washed in distilled water, and allowed to germinate in Petri dishes. Seedling plants of similar primary leaf length and seedling root number were transplanted to black plastic pots containing a polyethylene bag with 5 kg washed sand #30

TABLE 1. Root biomass of landrace bread wheats from Iran and China, an old Californian cultivar and mid-green revolution cultivars from California, Iraq and Pakistan (data from Ehdaie, 1995, table 2)

Genotype	Dwarfing gene	Group	Root biomass (g)	% Anza	Height (cm)
Iran 49	<i>rht</i>	Landrace	6.43 ^{a*}	273	115
Chinese Spring	<i>rht</i>	Landrace	4.38 ^b	186	112
Iran 14	<i>rht</i>	Landrace	3.35 ^c	138	111
Ramona 50	?	CA cultivar	2.70 ^{cd}	114	108
Anza	<i>Rht1</i>	mid-gr [†]	2.35 ^d	100	88
Chenab 70	<i>Rht1</i>	mid-gr	2.43 ^{cd}	103	92
Sholeh	<i>Rht1</i>	mid-gr	2.30 ^d	97	100
Yecora Rojo	<i>Rht1/Rht2</i>	mid-gr	2.00 ^d	85	76

* Means followed by the same letters within a column are not significantly different at $P \leq 0.05$, using an LSD test.

[†] mid-gr = mid-green revolution cultivar.

(Ehdaie *et al.*, 2003). A small hole in the bag allowed excess water to drain without sand being lost.

In an early experiment (Table 1; Ehdaie, 1995) plants were watered every 2–3 d and returned to field capacity in a closed sand culture system. CIMMYT semi-dwarf and dwarf wheats had root biomass values between 2.0 g and 2.5 g per plant in the sand-culture experiments, and ‘Anza’ with 2.35 g per plant was intermediate. Root biomass was expressed as a percentage of mid-generation CIMMYT wheat ‘Anza’.

A second experiment was started in mid-January 2006, with ‘Pavon 76’ as the standard cultivar. UK winter cultivar ‘Zion 19’ requiring vernalization was given cold temperatures of 5°C and 8 h light, for 6 weeks beginning 1 December 2005. Two ancestors of CIMMYT wheats, namely ‘Norin 10’ and ‘Brevor’ were initially included in the experiment, but their data were later removed because plants were extremely long-day photoperiodic and did not head, in the case of ‘Brevor’ at Riverside, until the end of July 2005, and even then poorly. Both wheats, which contributed the *Rht1* and *Rht2* stem dwarfing genes, were bred to be grown in northern Japan or in Washington State where summer day lengths may exceed 16 h. The genotypes grown in pots and for which data are reported are listed in Table 2. At physiological maturity, irrigation ceased and plants were allowed to dry. Shoots were separated from roots at the soil surface. Roots were gently washed free of sand and allowed to dry in a forced air oven at 60°C for 7 d, then weighed.

In the second experiment (Table 2) plants were watered generally each day as needed and allowed to drain. All root biomass values were expressed as a percentage of ‘Pavon 76’, also a mid-green-revolution wheat similar to ‘Anza’. Further, ‘Pavon 76’ was chosen as the standard CIMMYT cultivar by Dr A. J. Lukaszewski and has replaced landrace ‘Chinese Spring’ as the cytogenetic-stock wheat. Wheat breeders do not like the morphological or quality characters of ‘Chinese Spring’, whereas they do

TABLE 2. Root biomass of a Japanese bread wheat landrace, parents of early, mid- and late green revolution cultivars and two modern cultivars from California and Europe

Genotype	Dwarfing gene	Group	Root biomass (g)	% Pavon 76	Height (cm)
Aka	<i>rht</i>	Landrace	9.33 ^{a*}	186	130
Komugi					
Marroqui	<i>rht?</i>	Tunisia	6.38 ^{bcd}	127	91
Mentana	<i>rht?</i>	Italy	6.19 ^{bcd}	123	122
Gabo	<i>rht?</i>	Australia	4.00 ^{cd}	80	90
Nainari 60	<i>rht</i>	early-gr [†]	7.15 ^{ab}	142	100
Pavon 76	<i>Rht1</i>	mid-gr	5.00 ^{bcd}	100	76
Bacanora	<i>Rht1</i>	late-gr	6.22 ^{bc}	124	87
Rayon	<i>Rht1</i>	late-gr	4.17 ^{cd}	83	76
Pastor	<i>Rht1</i>	late-gr	3.69 ^d	74	70
Summit	<i>Rht1</i>	late CA	4.49 ^{cd}	90	68
Zion 19	<i>Rht8</i>	late UK	4.61 ^{cd}	92	72

* Means followed by the same letters within a column are not significantly different at $P \leq 0.05$, using an LSD test.

[†] early-gr = early-green revolution cultivar; mid-gr = mid-green revolution cultivar; late-gr = late-green revolution cultivar.

like ‘Pavon 76’, which is a semi-dwarf CIMMYT wheat, of high grain quality that is also cytogenetically tractable. The rye 1RS translocations are in the background of ‘Pavon 76’ wheat.

Root biomass and grain yield of the ‘Pavon 76’ near-isogenic line series that compared bread wheat with 1RS_(K) ‘Veery’ wheats, in glasshouse and field experiments, were reported by Ehdaie *et al.* (2003). Experiments that investigated the effect of the 1RS_(K) arm in tetraploid wheat and compared root biomass of ‘Aconchi’ durum and ‘Aconchi 1RS_(K).1BL’, and that investigated the effect of different sources of the 1RS arm on root biomass in ‘Pavon 1RS_(A).1AL’ and ‘Pavon 1RS_(K).1AL’ were reported earlier (Waines *et al.*, 2004; Waines and Ehdaie, 2005).

RESULTS

Mexican wheats

In the first experiment conducted in 1993, the three tall bread wheat landraces, presumed to carry a *rht* allele, though not necessarily the same one, had root biomass ranging from 3.25 g (Iran 14) to 6.43 g (Iran 49) with a mean root biomass of 4.68 g (Table 1). Plant height for the same genotypes ranged from 111 cm to 115 cm. ‘Ramona 50’, a popular California wheat released before the introduction of Mexican wheats, had root biomass smaller than the landraces, but larger than four mid-generation, green-revolution wheats released in California, Iraq and Pakistan. The cultivar with the smallest root biomass was the two-gene (*Rht1/Rht2*) dwarf ‘Yecora Rojo’, which also had the shortest stem height at 76 cm.

In the second experiment conducted in 2006 (Table 2) root biomass values were larger than those reported in Table 1, presumably because the plants received twice as much water (25 kg vs. 12.74 kg). However, the same

trend was observed. The tall (137 cm) Japanese landrace ‘Aka Komugi’ also had the largest root biomass (9.33 g). The parents of early-generation Mexican wheats had root biomass that ranged from 4.01 g (‘Gabo’) to 6.38 g (‘Marroqui’) with a mean of 5.52 g. Plant height of these lines was similar (119–122 cm). The tall (100 cm) (*rht*) early-generation Mexican wheat ‘Nainari 60’, with root biomass of 7.15 g was selected from segregating hybrid populations of the three parents, which root biomass, but not plant height, it exceeded. Early-generation Mexican wheats were crossed to segregating F_2 lines of ‘Norin 10’ × ‘Brevor’, whose root biomass it was not possible to measure because both cultivars were day-length sensitive for flowering at Riverside. The mid-generation green-revolution wheat, ‘Pavon 76’, that carried the semi-dwarf *Rht1* allele had root biomass of 5.01 g and plant height of 87 cm. Late-generation semi-dwarf green-revolution wheats that carried the *Rht1* allele had variable root biomass that ranged from ‘Bacanora’ with 6.22 g and 86 cm, to ‘Pastor’ with 3.69 g and 70 cm and a mean root biomass of 4.69 g. A recent California semi-dwarf (*Rht1*) wheat ‘Summit’ had root biomass of 4.49 g and height of 68 cm, and a recent semi-dwarf UK winter wheat ‘Zion 19’ had root biomass of 4.60 g and height of 72 cm.

‘Veery’ wheats

Earlier, experiments were undertaken to elucidate the morphological and/or physiological basis of ‘wide adaptation’ in ‘Veery’-type wheats carrying the IRS arm translocated for wheat chromosome arm 1BS or 1AS. That this might involve differences in root biomass was supported by use of near-isogenic lines where plants with the IRS translocation always had larger root biomass and branching in pot cultures (Fig. 1). In this experiment, where pots were weighed every 2–3 d and returned to field capacity, CIMMYT bread wheat ‘Pavon 76’ had root biomass of

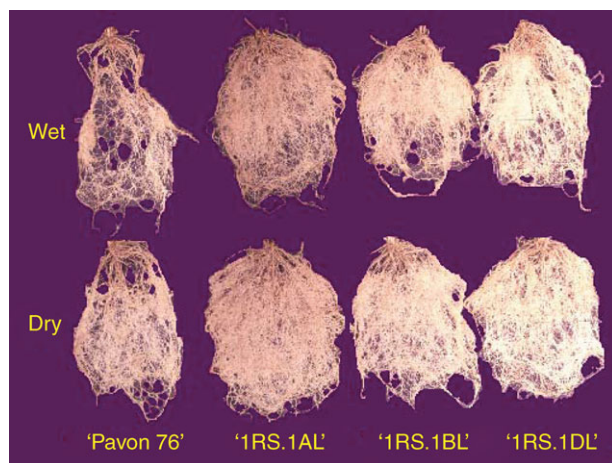


FIG. 1. Root biomass of green-revolution bread wheat ‘Pavon 76’ and its near isogenic rye IRS translocation lines ‘Pavon 1RS.1AL’, ‘Pavon 1RS.1BL’ and ‘Pavon 1RS.1DL’ grown under well-watered (wet) and drought-stressed (dry) pot sand-culture conditions in a cooled glasshouse.

2.5 g, while near-isogenic lines for the $1RS_K$ arm had in ‘Pavon 1RS.1AL’ 3.4 g, ‘Pavon 1RS.1BL’ 3.0 g and ‘Pavon 1RS.1DL’ 3.4 g root biomass, respectively, in well-watered pot cultures. Root biomass was similar to results obtained in Table 1. In drought stressed pot cultures root biomass showed a similar trend. In field experiments, grain yield under irrigation was positively associated with root biomass in glasshouse sand cultures (Ehdai *et al.*, 2003).

In another experiment, the root biomass of ‘Aconchi’ durum was 3.17 g per plant whereas that of ‘Aconchi 1RS_(K).1BL’ was 4.41 g per plant and showed a 39 % increase (Waines *et al.*, 2004). In a separate experiment, root biomass of ‘Pavon 1RS_(A).1AL_(A)’ showed a 9 % increase over that of ‘Pavon 76’, while ‘Pavon 1RS_(K).1AL_(P)’ showed a 31 % increase over the ‘Pavon 76’ control (Waines *et al.*, 2004; Waines and Ehdai, 2005).

DISCUSSION

In these pot, sand culture studies, tall landrace bread wheats had larger root biomass than mid-green revolution wheats (Tables 1 and 2). These results were confirmed independently using field soil and sand cultures in Indiana by Crowley *et al.* (2005, 2006) who found ‘Iran 49’ always had more root biomass than ‘Iran 14’, and some local bread wheat cultivars. In contrast, the three parents of Mexican wheat listed by Borlaug (1968) have a mean root biomass of 5.52 g well below landrace ‘Aka Komugi’. ‘Gabo’ from Australia had an especially small root system, relative to the other parents ‘Mentana’ and ‘Marroqui’. CIMMYT’s early-generation ‘Nainari 60’ had root biomass (7.15 g) that exceeded its parents.

Crossing the early-generation Mexican wheats with F_2 segregants of ‘Norin 10’ and ‘Brevor’ to introduce the stem-dwarfing *Rht1* and *Rht2* alleles did not increase the root biomass of the mid-generation green-revolution wheat such as ‘Pavon 76’ (Table 2), which has root biomass below the mean of the parents (5.52 g). The results are, by implication, similar in Table 1. Further hybridization and selection of late green-revolution wheats from the CIMMYT programme did introduce some variability in the case of ‘Bacanora’, but ‘Rayon’ and ‘Pastor’ show a continued decrease in root biomass. A similar trend of unconsciously selecting wheats with small root biomass, as a consequence of selection under optimum growing conditions, is evident in two randomly chosen cultivars, modern Californian ‘Summit’ and United Kingdom ‘Zion 19’ bread wheat. As ‘Zion 19’ is a winter wheat, there may have been similar unconscious selection of small root biomass in winter wheat as well as spring wheat.

‘Ramona 50’ bread wheat was released in California in 1950 before the introduction of CIMMYT germplasm. It has a root biomass of 2.70 g per plant. Thus the selection of one cultivar with a small root system occurred in the USA before the introduction of germplasm from the CIMMYT programme in Mexico. Gabo bread wheat from Australia is another example of a cultivar released around

1945 that has a small root system and is adapted to Australia's summer rainfall regime.

One of the first reports of genetic control of cultivar differences for root biomass in bread wheat was by Troughton and Whittington (1968), and Monyo and Whittington (1970) who observed landrace 'Chinese Spring' had root biomass twice that of 1930 cultivar 'Hope'. The difference, discerned by use of cultivar whole-chromosome substitution lines, was controlled by gene(s) on chromosome 1A. The controlling factor(s) were not mapped to chromosome arms, nor does this information appear to have been much used in wheat breeding programmes with the possible exception of that of Hurd (1971) in Canada.

No evidence was found that Borlaug (1968) and the CIMMYT wheat breeding team considered root size or other root characters in the parents or offspring of their breeding programmes in the 1940s through 1970s. In this respect, plant breeding is different from animal breeding where healthy feet and strong legs were observed and selected for in breeding programs throughout animal domestication. Most wheat breeding programmes involve only above-ground plant organs that are readily observed and selected. With a few exceptions (Hurd *et al.*, 1972; Hurd, 1974; Richards and Passioura, 1989) root characters were not observed or selected for. The need to breed for root characters was advocated by Mac Key (1973, 1978) who reported a positive relationship between use of *Rht* stem dwarfing alleles and small root size. Even though later workers did not confirm this relationship (Lupton *et al.*, 1974; Mirrales *et al.*, 1997), investigation of a possible grain yield advantage by selecting for a larger root system has been slow. Part of the problem was that there are few near-isogenic line series in bread wheat with known differences in root size that might be used to demonstrate the advantage of a larger root size. Another reason may be that many plant scientists do not like to work with roots because root measurements are time consuming and it is difficult to measure root traits for a large number of breeding lines.

One near-isogenic set is material developed at CIMMYT which differs for presence and absence of the 'Veery $1RS_{(K)}.1BL$ ' translocation in the same genetic background. This translocation from winter wheat 'Kavkaz', involves the short arm of chromosome 1 of rye translocated for the short arm of chromosome 1B or 1A of bread wheat, and hence may involve the same genetic system identified by Troughton and Whittington (1968). Field research by Manske and Vlek (2002) at CIMMYT in Mexico was the first to report that wheat genotypes containing IRS had thinner roots and higher root-length density compared with their 1BS checks. In glasshouse pot studies involving IRS isolines of 'Pavon 76', the lines containing $1RS_{(K)}.1AL$, $1RS_{(K)}.1BL$ and $1RS_{(K)}.1DL$ always had more root biomass and root branching than 'Pavon 76' (Fig. 1; Ehdaie *et al.*, 2003). Root biomass and grain yield were positively correlated under well-watered and droughted pot conditions. In companion field studies, lines containing IRS also yielded more grain in a well-irrigated treatment, but not in a drought-stressed treatment.

The stress tolerance index, calculated from field grain yield and kernel weight, indicated 'Pavon 76' isolines for $1RS_{(K)}$ had greater tolerance to stressful environments than 'Pavon 76' (Ehdaie *et al.*, 2003). Based on these pot and field studies those authors concluded the greater adaptability of certain $1RS.1BL$ translocation lines reported in the literature may be due to their greater root biomass and higher transpiration rate. Root biomass was not investigated in the field experiments. However, grain yield measured in the field experiments was positively correlated with root biomass measured in the pot experiments (Ehdaie and Waines, 2003). If root biomass is increased in the field, these results might be in agreement with the model developed for winter wheat in the UK by King *et al.* (2003), who predicted more grain yield from a wheat plant with a deep root system that was able to mine a larger soil profile for more water and nutrients than a shallow root system mining a smaller soil profile.

Comparing CIMMYT semi-dwarf durum 'Aconchi $1BS.1BL$ ' with the near isogenic durum 'Aconchi $1RS_{(K)}.1BL$ ' indicated IRS increased root biomass by 39% in tetraploid wheat. Hence, the IRS effect has similar root biomass results in tetraploid and hexaploid wheat. However, the IRS arm, in 'Aconchi' durum background, carries a gene that also conditions partial floret sterility (Waines *et al.*, 2004).

Comparing different sources of the IRS arm from 'Kavkaz' or from 'Amigo' in 'Pavon 76' bread wheat background, root biomass of 'Pavon $1RS_{(A)}.1AL_{(A)}$ ' was 9% more than 'Pavon 76', whereas 'Pavon $1RS_{(K)}.1AL_{(P)}$ ' was 31% more than 'Pavon 76' (Waines *et al.*, 2004). Therefore in 'Pavon 76' background, the 'Kavkaz' IRS arm has a 3-4 times larger effect on root biomass than the 'Amigo' IRS arm, which suggests there may be genetic variation for root size within rye.

It was assumed that genotypes containing IRS that increase root biomass in sand cultures will also increase root biomass in field soils, though not necessarily to the same extent. This is supported by the field results of Manske and Vlek (2002) and the sand pot and field results of Ehdaie *et al.* (2003). The general increase in grain yield reported in 'Veery' wheats containing IRS may not be attributed solely to increase in root biomass. Research in the UK reports isogenic lines with the IRS arm may also store more water-soluble carbohydrates in the stems before anthesis and mobilize more water-soluble carbohydrates to grains during grain filling (Shearman *et al.*, 2005). The increased production of water-soluble carbohydrates may be due to increased uptake of water and nutrients, as the model of King *et al.* (2003) suggests, and/or to increased photosynthesis, with carbohydrates produced before flowering stored in the stem before being re-mobilized after flowering to fill the grains.

This research demonstrated the parental genotypes used to breed early-generation green-revolution wheats have small root biomass in sand cultures, especially 'Gabo' from Australia. This may be controlled by genes on homoeologous chromosome group 1, rather than by the *Rht* dwarfing genes on homoeologous group 4. This interpretation is supported by the F_2 segregation data from a cross

of tall 'Chinese Spring' with large root biomass and dwarf 'Yecora Rojo' with small root biomass where plants with small root biomass and tall stems or large roots and dwarf stems were obtained (Ehdaie and Waines, 1993).

Some semi-dwarf mid- and later-generation green-revolution cultivars selected in Mexico, California and the UK also have small root systems in sand cultures. The root systems of some modern bread wheat cultivars appear to be getting smaller or at least not increasing. The reduction in root size began before introduction of green-revolution wheats and may be a general result of domestication and breeding (Mac Key, 1978). In the case of Mexican wheats, this may also be the result of unconscious selection for increased grain yield in irrigated and well-fertilized conditions. Small root systems may account for why some green-revolution wheats perform well in optimum conditions, but poorly in drought and heat-stressed conditions. Alternatively, the parents presently used in crossing blocks may all have similar small root size, and with little available genetic variation, there is no ability to select for a larger root system. There may be reluctance on the part of crop physiologists and breeders to experiment with near-isogenic variation in root size and to investigate its effect on water and fertilizer uptake and grain yield. The lack of root studies contrasts with the many experiments on the effect of near-isogenic variation for shoot height on grain yield in bread wheat.

There has been little characterization of differences in the root systems of wild diploid and tetraploid wheats and their relatives, or of landraces of diploid, tetraploid or hexaploid wheats by germplasm curators. However, this germplasm is recognized as a source of potential drought-adaptive traits for wheat breeding programmes (Reynolds *et al.*, 2007). Also, the possibility of using plant-adaptive mechanism, including genetic variation in wheat root systems, to breed crops for drought and salinity-prone environments has been considered (Reynolds *et al.*, 2005).

In conclusion, presence of IRS_K , from 'Petkus' rye, and IRS_A from 'Insave' rye, associates with larger root biomass and branching than 'Pavon 76' hexaploid wheat. Similarly, presence of the $IRS_K.1BL$ translocation in 'Aconchi' increased root biomass over that of 'Aconchi' tetraploid wheat. The IRS arm may increase root biomass in other tetraploid and hexaploid wheats. Grain yield was associated with increased root biomass in the 'Pavon 76' near-isogenic lines with or without the IRS arm. This may open a way to improve root characters, grain yield and ultimately grain quality in bread wheat. If a larger root biomass increases water and nitrogen absorption, this may also suggest a way to reduce nitrate pollution. These results raise the question is the root size of modern wheat large enough for maximum yield? Would more root biomass and branching increase grain yield of pure wheats with semi-dwarf stems in irrigated and rain-fed conditions? Has unconscious selection for small root characters been taken too far in wheat domestication and breeding? The shallow soils reported in Australia, with high boron in the subsoil and largely spring–summer rainfall, suggests not all environments might benefit from a larger root system. However, wheat grown in deeper soils and in other areas such as

California and Western Europe, may benefit from a larger root system. To optimize grain yield, it may be necessary to tailor the root system to the soil. At present, root characters are not considered important for components of grain yield analysis in wheat (Donald, 1968), even though a general model for all plants that includes both shoot and root biomass has been published (Bazzaz *et al.*, 2000). Crop physiologists and plant breeders may need to design the complete wheat plant, including roots and shoots, not only the organs observed above ground.

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APPENDIX

List of species and/or of bread wheat cultivars mentioned in the text, their origin and pertinent comments.

‘**Aconchi**’: semi-dwarf (*Rht1*), spring, CIMMYT, durum released in Mexico.

‘**Aconchi 1RS_K.1BL**’: durum ‘Veery’ near-isogenic line.

‘**Akakomugi Tall**’: very tall (*rht*) plants in seed of dwarf Japanese ‘Akakomugi’ received from USDA Small-Grains Germplasm Collection, Aberdeen, ID.

‘**Amigo**’: Oklahoma winter wheat contains 1RS.1AL ‘Veery’ translocation from ‘Insave’ rye.

‘**Anza**’: semi-dwarf (*Rht1*) CIMMYT-derived bread wheat released in California and Australia.

‘**Bacanora**’: semi-dwarf (*Rht1*), spring, late-generation CIMMYT bread wheat, Mexico.

‘**Brevor 51**’: Vogel’s semi-dwarf, winter long-day responsive cultivar with stiff straw that allowed increased nitrogen rates and higher grain yields in Pacific Northwest, USA.

‘**Brown Schlanstedt**’: selected from landrace, end of 19th century, Germany.

‘**Chenab 70**’: semi-dwarf (*Rht1*) CIMMYT-derived bread wheat released in Pakistan.

‘**Chinese Spring**’: 1940 selected from Chinese wheat landrace by E. R. Sears.

‘**Frontana**’: 1945, Brazilian bread wheat cultivar tolerant of soil acidity.

‘**Gabo**’: 1945, tall bread wheat, Australia.

‘**Hope**’: 1935, winter wheat cultivar, USA, with small root system relative to ‘Chinese Spring’.

‘**Insave**’: rye (*Secale cereale*) cultivar released in Brazil.

‘**Iran 14**’: tall (*rht*) selection out of Iranian Khuzistan bread wheat landrace by Ehdai.

‘**Iran 49**’: tall (*rht*) selection out of Iranian Baluchistan bread wheat landrace by Ehdai.

‘**Kavkaz**’: Siberian winter bread wheat contains 1RS.1BL ‘Veery’ translocation from ‘Petkus’ rye.

‘**Kohnosu 25**’: bread wheat cultivar released by the Kohnosu station near Tokyo, Japan.

‘**Lerma Rojo 64**’: early tall (*rht*) Mexican spring bread wheat cultivar released by CIMMYT.

‘**Maringa**’ (IAC-5): 1970, tall Brazilian bread wheat cultivar

‘**Marroqui**’ (‘Florence Aurore’): Tunisia, spring bread wheat grown in North Africa.

‘**Mayo 64**’: CIMMYT semi-dwarf bread wheat.

‘**Mentana**’: 1930, tall, disease-resistant, Italian bread wheat.

‘**Nainari 60**’: early tall (*rht*) Mexican spring bread wheat cultivar released by CIMMYT.

‘**Norin 10**’: dwarf Japanese cultivar, used as source of *Rht1* and *Rht2* genes in USA after 1946 and Mexican wheat breeding programmes after 1950.

‘**Pavon 76**’: semi-dwarf (*Rht1*) spring CIMMYT bread wheat released in Mexico.

‘**Pavon 1RS_K.1AL**’: Veery (Kavkaz) near-isogenic line of ‘Pavon 76’.

‘**Pavon 1RS_K.1BL**’: Veery (Kavkaz) near-isogenic line of ‘Pavon 76’.

‘**Pavon 1RS_K.1DL**’: Veery (Kavkaz) near-isogenic line of ‘Pavon 76’.

‘**Pavon 1RS_A.1AL**’: Veery (Amigo) near-isogenic line of ‘Pavon 76’.

‘**Pastor**’: semi-dwarf (*Rht1*) spring, late-generation CIMMYT bread wheat, Mexico.

‘**Petkus**’: rye (*Secale cereale*) one of several cultivars released commercially in Germany.

‘**Pitic 62**’: CIMMYT semi-dwarf bread wheat cultivar.

‘**Prins**’: tall Swedish spring bread wheat.

‘**Ramona 50**’: tall (*rht*) spring bread wheat from California.

‘**Rayon**’: semi-dwarf (*Rht1*) spring, late-generation CIMMYT bread wheat, Mexico.

‘**Sholeh**’: semi-dwarf, CIMMYT-derived bread wheat introduced to Khuzistan from Iraq.

‘**Starke**’: tall Swedish winter bread wheat.

‘**Summit**’: modern commercial semi-dwarf spring bread wheat released in California.

‘**Tom Thumb**’: very dwarf cultivar, source of *Rht3* gene. Not used commercially.

‘**Yecora Rojo 70**’: two-gene dwarf (*Rht1*, *Rht2*) CIMMYT spring bread wheat released in Mexico, still grown in southern California/Arizona, with small root biomass.

‘**Zion 19**’: modern UK commercial semi-dwarf (*Rht8*) winter bread wheat.