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Root System Size Influences Water-Nutrient Uptake and Nitrate Leaching Potential in Wheat

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Abstract

Environmental and economic considerations require the effective use of water and nutrients to elevate grain production in bread wheat (*Triticum aestivum* L.) with concomitant reduction in nitrate leaching to minimize contamination of underground water. We determined the effect of the root system on leaching fraction, leachate N concentration, and N, P and K uptake using bread wheat 'Pavon 76' and its three near-isogenic translocation lines: Pavon 1RS.1AL, Pavon 1RS.1BL and Pavon 1RS.1DL. These genotypes were grown in sand-tube experiments under optimum and low level of nutrients for 2 years. Root, stem and leaves, and grain N, P, and K content, and agronomic characters were measured. Leaching fraction and leachate nitrate concentration were measured at early tillering, booting and early grain filling. Significant main effects for year, nutrient level and genotype were found for the characters. Genotype × N interaction was significant only for root P content. Genotype × year interaction was significant only for plant N content, root P content and plant P content. Genotype × year × N interaction was significant only for root N uptake efficiency. Thus, genotypic means averaged across years and nutrient levels are reported. Low levels of nutrients (1330, 235 and 793 mg vs. 1915, 375 and 1268 mg N, P and K, respectively) reduced mean root biomass, plant biomass and grain yield by 27 %, 25 %, and 19 %, respectively. The translocation lines produced 31–46 % more root biomass, 11–14 % heavier grains and 6–8 % greater grain yield than Pavon 76. Leaching fraction was higher under low level of nutrient at booting and grain filling. Leaching fraction at tillering, booting, and grain filling was 67%, 42% and 25%, respectively. Leaching fraction at early tillering was lower for Pavon 1RS.1AL (39 %) and Pavon 1RS.1DL (40.5 %) than for Pavon 76 (45.3 %). Leachate nitrate concentration was lower for two translocation lines at all three stages of plant growth compared to Pavon 76. The correlation coefficient between plant N content and root biomass, between plant N content and plant biomass, and between grain yield and root biomass was positive and significant. Significant positive correlation was found between root biomass and P and K uptake. Multiple small applications of N fertilizer during early plant growth with adequate irrigation water are recommended. Wheat genotypes with superior root characteristics for efficient nutrient uptake, especially during tillering and booting, should be developed in breeding programmes to increase grain yield and to minimize the nitrate leaching.

Introduction

Environmental and economic considerations require the effective use of fertilizer nitrogen (N), phosphorus (P) and potassium (K) in crop production systems. Among the fertilizer chemicals, N has the greatest risk for contaminating the environment. This is caused by higher usage of N in agricultural production compared with

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other chemicals and to high mobility of nitrate (NO_3–N) in the soil and its potential to leach below the root zone and into ground water; especially if the root zone is small and shallow. Once nitrate has leached to ground water, there is little chance of upward movement back to the root zone.

Nitrate leaching has become a concern of bread wheat (*Triticum aestivum* L.) and durum wheat (*T. turgidum* L. ssp. *durum* Desf.) crop managers in Southwest USA because a high yielding and high protein wheat crop with 6600 kg ha^{-1} grain yield and 13 % grain protein requires about 225 kg ha^{-1} applied N in a season. It is recommended that at least one-half, but not more than two-thirds, of the seasonal N fertilizer requirement be applied pre-plant to establish a vigorous irrigated crop with a high grain yield potential (Munier et al. 2008). The remainder of the N requirement should be supplied as supplemental N applications, one during tillering before stem elongation and another one between booting and flowering to ensure high grain protein. The N-use efficiency (the ratio of grain N yield to supplied N) of irrigated spring wheats grown in California was estimated between 51% (Dhugga and Waines 1989) and 60 % (Ehdaie and Waines 2001). The loss of supplied N fertilizer results from surface runoff, leaching, soil denitrification, volatilization and gaseous plant emission.

Nitrate leaching is a complex process affected by plant N uptake, soil type, irrigation, N source, N application rates, time of N application and activities of soil organisms (Petrovic 1990). Root morphological characteristics affect N uptake in crop plants and therefore the amount of nitrate leached below the root zone. The fraction of supplied N leached is larger in plants with small and shallow root systems than those with a large and deep root system. Also, a plant with a dense root system with many lateral branches and root hairs is better adapted to take up nutrients due to its greater root surface area than a plant with a sparse root system (Gahoonia et al. 2007). In a corn field, depletion of subsoil nitrate was closely related to root length density (Wiesler and Horst 1994), whereas root length density of bread wheat was shown to be of minor importance for nitrate uptake from the soil (Robinson et al. 1994). Genotypic differences in uptake of N during early growth have been shown in wheat genotypes differing in vigour and were associated with differences in root biomass (Liao et al. 2004). In another study by Liao et al. (2006), the vigorous lines produced 50–70 % more root biomass than the control by stem elongation. The greater root biomass was associated with 42–60 % higher N uptake in the vigorous lines. In a study comparing nitrate leaching losses from seeded vs. sodded Kentucky bluegrass (*Poa pratensis* L.), Geron et al. (1993) suggested that greater root biomass contributed to less nitrate leaching under the seeded turf due to increased nitrate uptake. Bowman et al. (1998) examined the effect of root architecture on nitrate leaching and found that nitrate leaching from a shallow-rooted genotype of creeping bentgrass (*Agrostis palustris* Huds.) was greater than from a deep-rooted genotype.

Raun and Johnson (1999) described and discussed production practices that might result in increased nitrogen-use efficiency (NUE) in cereals, but they did not consider plant root characteristics that might improve NUE through greater absorption of soil N. Two measures of NUE have been considered in the literature (Van Sanford and MacKown 1986): NUE for grain yield and NUE for grain protein. The two primary components of NUE for grain are N-uptake efficiency (plant N/N supplied) and N-utilization efficiency (grain yield/plant N). Also, two primary components are involved in determination of NUE for protein; N-uptake efficiency and N-partitioning efficiency (grain N yield/plant N). Therefore, nitrogen uptake by the plant is a primary component in determination of both types of NUE.

Field experiments with spring bread and durum wheat cultivars have shown that N-uptake efficiency was more important than N-utilization efficiency in determining NUE for grain as N supply increased (Dhugga and Waines 1989, Ehdaie et al. 2001) and also across different sowing dates (Ehdaie et al. 2001). Also, N-uptake efficiency was more important than N-partitioning efficiency in determining NUE for protein across different sowing dates (Ehdaie et al. 2001). Le Gouis et al. (2000) also found that N-uptake efficiency was more important than other components of N-use efficiency for grain and protein when 20 winter wheat genotypes were evaluated in the field under no and optimum rate of N fertilizer. These observations indicated that under low and optimum rates of N, the ability of spring and winter wheat to absorb N becomes the most important component in determination of NUE and absorption of N is related to root biomass and root characteristics as mentioned above.

Genotypic differences in N uptake have been reported in wheat (Van Sanford and MacKown 1986, Dhugga and Waines 1989, Ehdaie et al. 2001). The reasons for these genotypic differences are still not fully understood. However, differences in plant N uptake were attributed largely to availability of N (Rao and Rains 1976) or mainly to plant growth rate (Rodgers and Barneix 1988). Recent studies indicated that plant N uptake is more likely controlled by both the plant growth rate and N availability (Gastal and Lemaire 2002). In these studies, the role of roots in N uptake was ignored. Genotypic differences in P uptake in wheat (Manske et al. 2000; Manske and Vlek 2002) and in P and K uptake in chickpea (Gahoonia et al. 2007) also have been reported.

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Genetic variation for root characteristics has been reported in wheat (Ehdaie and Waines 2006) and for other crops (Zobel 2005). Mian et al. (1993) found significant differences in root fresh weight, number of roots greater than 40 cm, longest root length and total root length among 40 winter wheat genotypes grown in hydroponic culture for four weeks. Significant differences among spring bread wheat genotypes have been reported for root biomass at maturity under well-watered and droughted pot conditions (Ehdaie et al. 1991, Ehdaie and Waines 1994, Ehdaie 1995). Greater root biomass has been considered an important criterion for drought tolerance in wheat (Bangal et al. 1988) and for yield stability across variable moisture regimes (Blum et al. 1983); which might be due to more efficient capture of water and nutrients.

Wheat-rye translocation lines involving the short arm of rye chromosome 1R (1RS) have been widely used in wheat breeding programs (Lukaszewski 1990, Rajaram et al. 1990). We evaluated a CIMMYT spring bread wheat Pavon 76 and its three 1RS translocation lines; namely Pavon 1RS.1AL, Pavon 1RS.1BL and Pavon 1RS.1DL, in sand-pot and field experiments under well-watered and droughted treatments for two years (Ehdaie et al. 2003). The detailed development of these translocation lines was reported elsewhere (Lukaszewski 1993, Ehdaie et al. 2003). Root biomass per plant, averaged across irrigation treatments and years, was greater in Pavon 1RS.1AL by 30 %, in Pavon 1RS.1BL by 11 % and in Pavon 1RS.1DL by 26 % compared with Pavon 76. We hypothesized that a larger root biomass would enhance water and nutrient uptake, which may have contributed to the greater grain yield observed in the translocation lines under field conditions (Ehdaie et al. 2003).

Very little is known about the effect of root biomass on uptake of water and nutrients and on genotypic variation on leaching potential of nitrate in bread wheat. In a few studies conducted to determine the genotypic variation in wheat for the ability of roots to uptake N, only N content of different plant parts was measured. In this study, in addition to plant N content, we also quantified leaching fraction and leachate N concentration, which are important parameters in determination of nitrate degradation of underground water as they are influenced by the plant root system.

The primary objective of this study was to determine the effect of root biomass on nitrate leaching and uptake of water-nutrient in wheat: (i) to quantify the leaching fraction and leachate N concentration during early, mid and late growth stages in Pavon 76 and its 1RS translocation lines; (ii) to measure N, P and K content in plant parts at maturity and (iii) to determine the relationship between plant root biomass and plant nutrient uptake and grain yield at maturity.

Materials and Methods

Genotypes and growth conditions

The selection of wheat genotypes for this study was based on results from pot and field studies conducted by Ehdaie et al. (2003) in 1997 and 1998, where root biomass in spring bread wheat Pavon 76 and its 1RS translocation lines, namely Pavon 1RS.1AL, Pavon 1RS.1BL and Pavon 1RS.1DL, were measured under well-watered and droughted pot conditions. Root biomass, averaged across the irrigation treatments and years, was 2.7 g plant^{-1} for Pavon 76, 3.5 g plant^{-1} for Pavon 1RS.1AL, 3.0 g plant^{-1} for Pavon 1RS.1BL and 3.4 g plant^{-1} for Pavon 1RS.1DL translocation lines. We hypothesized that a larger root biomass will enhance water and nutrient uptake, which may contribute to increased grain yield and decreased leaching fraction and leachate N concentration. Based on these hypotheses, the genotypes were grown in sand-tube experiments in 2006 and 2008 under optimal level and low level of N–P–K in an unheated glasshouse at the University of California, Riverside, using factorial treatments in a randomized complete block design with four replicates (blocks) to test our hypotheses (Waines et al. 2007). Grains of similar size from each genotype were treated in 3.5 % Clorox for 5 min then washed by tap water for 10 min before being soaked in water for 24 h. Grains were then germinated in Petri dishes on 10 March 2006 and on 17 January 2008. Six days later, seedlings with similar growth were transplanted in polyethylene tubing bags sleeved into polyvinyl chloride (PVC) tubes, 80 cm long and 10 cm in diameter. Two drainage holes made at the bottom of each bag were covered with a filter paper before being filled with 8.5 kg of dry silica sand #30 with 24 % field capacity (w/w). Each bag was brought to water-holding capacity using half-strength Hoagland solution provided in the glasshouse before transplanting a seedling into it. This nutrient solution was used during the experiment to irrigate tubes under the optimum level of nutrients including N, P and K. This nutrient solution was diluted with tap water in a ratio of 1 : 1 to provide nutrient solution to irrigate tubes under low level of nutrients. The low level treatment was initiated after seedlings were grown under optimum level treatment for 25 days. The amount of irrigation solution used was recorded and samples of irrigation solution and tap water were taken regularly during experiment to determine nitrate content.

Sample collection and measurements

During early tillering, 35 days after grain germination (Zadok's decimal code = DC 23–24, Zadok et al. 1974), leachate was collected for five consecutive days from each tube by placing each tube in a plastic bucket on a ring of PVC. The ring of PVC in the collection bucket allowed the tube to be elevated above the level of the leachate. Leachate was collected from buckets each day, the volume was measured and then kept in a cold room (4 °C). Leachate collected from each tube after 5 days was combined so there was one leachate sample per tube for analysis of NO_3–N and NH_4–N concentration in the leachate. Ammonium N concentration in leachate was typically very low (<0.5 mg l^{-1}). Also, nitrate and ammonium N concentration in tap water were very low. Total amount of NO_3–N in each leachate sample was calculated by multiplying NO_3–N concentration by the total volume of leachate. Leachate collection was repeated during mid-booting, about 55 days after grain germination (DC = 45–47) and also during early grain filling period, about 10 days after anthesis, 67 and 83 days after grain germination (DC = 70) in 2006 and 2008, respectively.

Irrigation was terminated 90 and 119 days after grain germination in 2006 and 2008, respectively. Average monthly maximum, minimum and average air temperature during the growing season in 2006 ranged from 16.9 °C to 35.6 °C, from 6.1 °C to 20.2 °C, and from 11.0 °C to 27.5 °C, respectively. In the same season, average air relative humidity varied from 49 to 61 %. In the 2008 season, these averages ranged from 16.6 °C to 32.4 °C, from 5.6 °C to 15.5 °C, and from 10.9 °C to 23.2 °C, respectively, and with air relative humidity ranging from 41 to 52 %. Maximum photonflux density during the day was 900 mol m^{-2} s^{-1} in 2006 and 2008.

Total irrigation solution supplied to each plant was 25 and 43 l in 2006 and 2008, respectively. In 2006, total N supplied to each plant was 1330 and 1915 mg under low and optimum level of nutrient solution, respectively. In the same year, 235 and 375 mg of P and 793 and 1268 mg of K was supplied to each plant under the low and optimum level of nutrient solution, respectively. In 2008, 1653 and 2643 mg of N, 311 and 547 mg of P, and 1242 and 2185 mg of K were supplied to each plant under low and optimum level of nutrient solution, respectively.

The phenological traits such as number of days from grain germination to booting, to heading, and to anthesis were recorded. At maturity, plant height, number of tillers and number of spikes per plant was measured. Then, shoots were excised at the shoot/root interface. Shoot materials including stems, leaves, and spikes were dried in a forced-air drier for 24 h at 80 °C and weighed. Number of grains and grain yield per plant was measured.

To retrieve intact root systems, each polyethylene bag was pulled from the PVC tube and was laid on a screen frame in a tub half-filled with water and cut length wise without damaging the roots; then the plastic sheet was pulled out leaving the sand core with root system on the screen frame. The frame was moved gently in the tub to separate sand from the roots. Intact roots were floated to the water surface and washed carefully by hand to remove attached sand without damaging the root system. The washed roots were laid out on a plastic surface; the maximum root length was measured and then the whole root system was cut into two parts, the roots developed between 0 and 30 cm (shallow roots) and those below 30 cm (deep roots). Roots were dried on a paper towel for a week in the glasshouse before being put in a forced-air drier for 24 h at 80 °C. Shallow and deep root weight and total root weight (sum of shallow and deep roots) were determined. The ratio of root dry weight to plant dry weight (sum of root and shoot dry weight) was calculated.

Stem, leaves and chaff of each plant were chopped into small pieces together and were ground in a Wiley mill using a 0.4 mm screen for determination of N, P and K content. Similarly, grains and roots were ground for N, P and K determination. Nutrient uptake was calculated by multiplying the dry weight of plant parts to their respective nutrient concentrations. Nitrate content in leachate and tap water was analysed with a Technicon TRAAC 800 Autoanalyzer (Technicon Instruments Corp., Tarrytown, NY, USA). Total N in plant samples was determined by LECO-FP528 nitrogen Gas Analyzer (Sweeny 1989). Total P and K in plant samples were analysed using microwave acid digestion/dissolution and quantitative determination by AAS and ICP-AES (Meyer and Keliher 1992). Plant nutrient content and leachate N concentration were determined at Agriculture and Natural Resources Analytical Laboratory, University of California, Davis. From these analyses, nutrient content in roots, shoots (excluding grains) and grains; and nitrate content in leachates were determined. Nutrient uptake efficiency was calculated as the plant nutrient content to the amount of nutrient supplied. Nitrogen harvest index was calculated as grain N content to plant N content. Similarly, P and K harvest index was calculated. Root N uptake efficiency was calculated as plant N content to root biomass.

Statistical analysis

Analysis of variance (ANOVA) was performed for each character measured or calculated for each year (Steel et al. 1997). The combined ANOVA was also performed across years, treating nutrient level and genotype as fixed effects and year and replication, and their interactions with nutrient level and genotype as random effects. Test of significance of fixed effects were accomplished by using appropriate mean squares (Steel et al. 1997). Associations between characters were examined by correlation and regression analysis. Mean values were compared using the F-protected LSD test (Steel et al. 1997).

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Results

General

The combined ANOVA (not shown) indicated significant main effects for year, nutrient level and genotype for most of the characters examined. The first-degree interactions involving genotype such as genotype × year and genotype × nutrient level were significant only for a few characters. The genotype × year × nutrient level was significant only for one character. On the basis of these observations, means averaged across years and nutrient levels will be reported for the genotypes.

The number of days from grain germination to booting, to heading and to anthesis showed a narrow range among the genotypes; ranging within 4, 5 and 6 days in 2006 and within 4, 5 and 5 days, in 2008, respectively. Also, a small range was observed for plant height varying from 88 (Pavon 1RS.1AL and Pavon 1RS.1BL) to 92 cm (Pavon 76) and for number of tillers and spikes per plant ranging from 11 (Pavon 76 and Pavon 1RS.1BL) to 13 (Pavon 1RS.1AL and Pavon 1RS.1DL) and from 10 (Pavon 1RS.1BL) to 12 (Pavon 1RS. 1DL), respectively. Therefore, shoot biomass also showed a narrow range varying from 36.4 (Pavon 76) to 39.1 g plant^{-1} (Pavon 1RS.1DL). The genotypic differences in plant biomass; thus were mainly caused by differences in root biomass. These observations indicated that the effect of root system on water-nutrient uptake and on leachate fraction and N concentration measured in this study were not confounded by the phenological period nor by plant height or by number of tillers per plant.

Root and shoot characters

Mean values for root and shoot characters, including grain yield, measured in the second year were significantly greater than those in the first year (Table 1). Maximum root length was 12 % longer, the ratio of root biomass to plant biomass was 16 % higher, grain weight was 28% heavier, and number of grains per plant was 96 % more in the second than in the first year. Similarly, shallow and deep root weight, root biomass, grain number and grain yield were more than twofold greater in the second year (Table 1).

Mean values for root and shoot traits were reduced under low nutrient level, except for maximum root length, grain weight and the ratio of root biomass to plant biomass (Table 1). Low level of nutrient reduced mean root biomass, plant biomass and grain yield by 27, 25 and 19 %, respectively.

The translocation lines produced 31–46 % more root biomass at maturity, 11–14 % heavier grains and 6–8 % greater grain yield than Pavon 76 (Table 1). The 1RS translocation lines and Pavon 76 had similar maximum root length. Number of grains per plant in Pavon 76 was significantly greater than that of Pavon 1RS.1DL. The proportion of root biomass to total plant biomass was similar in the translocation lines, but significantly greater than that in Pavon 76 (Table 1).

Leachate fraction and N concentration

Leachate fraction at early tillering was significantly greater in the second year but lower at early grain filling than in the first year. About 40 % of water-nutrient supplied to the plants was leached during booting in both years (Table 2). Leaching fraction at early tillering was similar for low and optimum nutrient levels, but lower for optimum level at booting and early grain filling than for low nutrient level. Pavon 76 and its 1RS translocation lines showed similar leaching fraction at early tillering and grain filling, but had different leaching fraction at

Table 1 Mean values of root and shoot characteristics per plant for different years, nutrient levels, and spring bread wheat genotypes

	Max. root Length (cm)	Shallow root weight (g)	Deep root weight (g)	Root biomass (g)	Grains (n)	Grain weight (mg)	Grain yield (g)	Plant biomass (g)	Root/plant biomass (%)
Year									
2006	98 a	1.75 a	0.73 a	2.44 a	307 a	42 a	12.7 a	26.4 a	9.1 a
2008	110 b	4.44 b	1.74 b	6.19 b	602 b	54 b	32.1 b	57.8 b	10.6 b
Nutrient level									
Low	104 a	2.60 a	1.10 a	3.66 a	394 a	48 a	20.0 a	36.2 a	9.8 a
Optimum	104 a	3.59 b	1.38 b	5.00 b	514 b	48 a	24.8 b	48.2 b	10.0 a
Genotype									
Pavon 76	104 a	2.41 a	0.99 a	3.37 a	472 a	44 a	21.2 a	39.8 a	8.1 a
Pavon 1RS.1AL	105 a	3.22 b	1.26 ab	4.48 b	470 ab	49 b	23.1 b	42.2 ab	10.0 b
Pavon 1RS.1BL	104 a	3.19 b	1.34 b	4.54 b	446 ab	49 b	22.8 b	42.8 b	10.4 b
Pavon 1RS.1DL	103 a	3.56 b	1.35 b	4.92 b	430 b	50 b	22.4 ab	44.0 b	11.0 b

In each section, mean values followed by the same letter within columns are not significantly different ($P < 0.05$) according to LSD test.

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Table 2 Mean values of leaching fraction, leachate N concentration and the amount of N in leachate collected during five consecutive days at early tillering, booting, and early grain filling for different years, nutrient levels, and spring bread wheat genotypes

	Leaching fraction			Leachate N concentration			Leachate N content		
	Tillering (%)	Booting (%)	Grain filling (%)	Tillering (mg l^{-1})	Booting (mg l^{-1})	Grain filling (mg l^{-1})	Tillering (mg)	Booting (mg)	Grain filling (mg)
Year									
2006	57.6 a	43.7 a	34.6 a	74.2 a	35.1 a	50.6 a	50.7 a	23.2 a	36.0 a
2008	76.8 b	41.1 a	16.1 b	86.9 a	92.7 b	74.5 b	69.6 b	61.0 b	29.9 a
Nutrient level									
Low	68.3 a	45.5 a	29.2 a	77.9 a	51.1 a	60.4 a	60.0 a	35.2 a	33.3 a
Optimum	66.1 a	39.4 b	21.5 b	83.2 a	76.6 b	64.8 a	60.0 a	49.0 b	32.6 a
Genotype									
Pavon 76	67.4 a	45.3 a	26.9 a	89.6 a	72.7 a	71.9 a	67.3 a	51.4 a	40.7 a
Pavon 1RS.1AL	67.3 a	39.6 c	25.1 a	83.4 ab	58.0 b	53.2 b	62.3 ab	35.5 bc	29.4 bc
Pavon 1RS.1BL	65.9 a	44.4 ab	25.3 a	75.0 b	69.6 ab	69.3 a	55.7 b	46.7 ab	36.0 ab
Pavon 1RS.1DL	68.2 a	40.5 bc	24.1 a	74.2 b	55.2 b	55.7 b	55.2 b	34.8 c	25.7 c

In each section, mean values followed by the same letter within columns are not significantly different ($P < 0.05$) according to LSD test.

booting. Mean genotypic leaching fraction was about 67 % at early tillering, 42 % at booting and 25 % at early grain filling period.

Nitrate concentration in leachate was similar at tillering in both years, but greater in the second year at booting and early grain filling (Table 2). Leachate nitrate concentration at low and optimum levels of nutrient were similar at early tillering and grain filling, but lower for the low level at booting. Significant differences were found among the genotypes for nitrate concentration in leachate at early tillering, booting and early grain filling period (Table 2). Pavon 1RS.1DL and Pavon 1RS.1BL had significantly lower leachate N concentration, 74.2 and 75.0 mg l^{-1}, respectively, than Pavon 76 (89.6 mg l^{-1}) at early tillering. At booting, leachate N concentration for Pavon 1RS.1DL (55.2 mg l^{-1}) and for Pavon 1RS.1AL (58.0 mg l^{-1}) was significantly lower than for Pavon 76 (72.7 mg l^{-1}). At early grain filling period, Pavon 1RS.1AL (53.2 mg l^{-1}) and Pavon 1RS.1DL (55.7 mg l^{-1}) had lower leachate N concentration than Pavon 76 (71.9 mg l^{-1}) (Table 2).

The amount of N leached during five consecutive days at early tillering was significantly greater in the second than in the first year (69.6 vs. 50.7 mg 5 day^{-1} $plant^{-1}$), was similar for the two nutrient levels (60.0 mg 5 day^{-1} $plant^{-1}$), and was significantly lower for Pavon 1RS.1DL (55.2 mg 5 day^{-1} $plant^{-1}$) and Pavon 1RS.1BL (55.7 mg 5 day^{-1} $plant^{-1}$) than for Pavon 76 (67.3 mg 5 day^{-1} $plant^{-1}$) (Table 2). At booting, leachate N content in the second year and in optimum level of nutrient was greater than in the first year and the low level of nutrient, respectively, and Pavon 1RS.1DL (34.8 mg 5 day^{-1} $plant^{-1}$) and Pavon 1RS.1AL (35.5 mg 5 day^{-1} $plant^{-1}$) had significantly lower leachate N content than Pavon 76 (51.4 5 day^{-1} $plant^{-1}$) (Table 2). At early grain filling, similar leachate N content was observed for both years and nutrient levels, but again Pavon 1RS.1DL and Pavon 1RS.1AL had significantly lower leachate N content, 25.7 and 29.4 mg 5 day^{-1} $plant^{-1}$, respectively, than Pavon 76 (40.7 mg 5 day^{-1} $plant^{-1}$) (Table 2).

Plant P, K and N uptake

Uptake of P and K in different plant parts were significantly greater in the second than first year (Table 3). Similar trends were found for optimum level compared with low level of nutrient. Root, grain and plant P content were greater in 1RS translocation lines than in Pavon 76. Stem P content was similar among the genotypes. Grain K content was lower in Pavon 76 compared with those in 1RS translocation lines (Table 3).

Uptake of N in different plant parts was significantly greater in the second year than first year (Table 4). Similar trends were observed for optimum compared to low level of nutrient. Root, grain and plant N content were greater in the 1RS translocation lines than in Pavon 76. Plant N-use efficiency, grain N-use efficiency and NHI were greater in the second year compared with the first year. However, root N-uptake efficiency was similar in both years. Greater plant N-use efficiency (NUEP) and grain N-use efficiency (NUEG) was observed under low level than optimum level of nutrient. In contrast NHI was greater in optimum than in low level of nutrient. Root N-uptake efficiency was similar for both levels of nutrient (Table 4). Plant N-use efficiency and grain N-use efficiency in 1RS translocation lines was, on average, greater than Pavon 76 by 10 % and 9 %, respectively. In contrast, Pavon 76 had significantly greater root N-uptake efficiency than 1RS translocation lines (Table 4).

Table 3 Fertilizer P and K uptake per plant in different plant parts for years, nutrient levels, and spring bread wheat genotypes

	P content				K content			
	Root (mg)	Stem (mg)	Grain (mg)	Plant (mg)	Root (mg)	Stem (mg)	Grain (mg)	Plant (mg)
Year								
2006	1.18 a	6.3 a	68.7 a	76 a	8.58 a	440.6 a	88.7 a	539 a
2008	3.97 b	21.1 b	158.0 b	183 b	16.58 b	678.8 b	180.0 b	875 b
Nutrient level								
Low	1.87 a	8.2 a	91.1 a	101 a	9.67 a	440.4 a	113.8 a	564 a
Optimum	3.28 b	19.2 b	135.7 b	158 b	15.50 b	679.0 b	154.8 b	849 b
Genotype								
Pavon 76	1.99 a	12.8 a	104.4 a	119 a	8.60 a	563.8 ab	120.9 a	693 a
Pavon 1RS.1AL	2.88 b	13.7 a	118.1 b	135 b	11.67 ab	526.8 a	150.2 c	689 a
Pavon 1RS.1BL	2.63 b	13.5 a	116.3 b	132 b	14.41 bc	558.9 ab	132.0 b	705 a
Pavon 1RS.1DL	2.79 b	14.9 a	114.8 b	133 b	15.66 c	589.4 b	134.2 b	739 a

In each section, mean values followed by the same letter within columns are not significantly different ($P < 0.05$) according to LSD test.

Table 4 Fertilizer N uptake in different plant parts, plant N-use efficiency (plant N/N supplied, NUEP), grain N-use efficiency (grain N/N supplied, NUEG), root N-uptake efficiency (plant N/root biomass, N-uptake E), and N harvest index (grain N/plant N, NHI) for years, nutrient levels, and spring bread wheat genotypes

	N content							
	Root (mg)	Stem (mg)	Grain (mg)	Plant (mg)	NUEP (%)	NUEG (%)	Root N-uptake E (%)	NHI (%)
Year								
2006	24 a	139 a	415 a	578 a	36 a	26 a	25 a	72 a
2008	57 b	275 b	1021 b	1353 b	64 b	49 b	23 a	76 b
Nutrient level								
Low	33 a	144 a	647 a	824 a	54 a	42 a	24 a	71 a
Optimum	49 b	270 b	789 b	1108 b	47 b	33 b	24 a	77 b
Genotype								
Pavon 76	32 a	195 a	666 a	893 a	47 a	35 a	27 a	74 a
Pavon 1RS.1AL	42 b	203 a	729 b	974 b	51 b	38 b	22 b	75 a
Pavon 1RS.1BL	42 b	200 a	744 b	986 b	51 b	39 b	22 b	75 a
Pavon 1RS.1DL	46 b	230 b	733 b	1009 b	52 b	38 b	21 b	72 b

In each section, mean values followed by the same letter within columns are not significantly different ($P < 0.05$) according to LSD test.

Total plant N uptake and root biomass were closely and positively correlated ($r = 0.81$; Fig. 1a) and plant biomass was highly and positively correlated with plant N uptake ($r = 0.83$; Fig. 1b). Similarly, grain yield was highly and positively correlated with root biomass ($r = 0.73$; Fig. 1c).

Discussion

In this study, plants were grown under glasshouse conditions; therefore, plant size reported might not reflect the plant size grown under field conditions. The greater root biomass and shoot biomass, including grains, in the second year compared with the first year (Table 1) was because of earlier and normal planting time (January vs. March planting). Consequently, the second year was characterized with longer growth period accompanied with relatively lower temperatures. As a result, the genotypes used 72 % more water-nutrient solution and the plant biomass produced was more than twice as much in the second year (Table 1). Similarly, mean root biomass and grain yield in the second year were 2.5-fold greater than those in the first year. The lack of significant genotype × year interactions for most of the traits associated with root biomass and shoot biomass indicated that the genotypes responded positively and similarly to the longer growth period in the second year.

Lowering the optimum rate of nutrients by 40 % reduced root biomass by 27 %, plant biomass by 25 %, and grain yield by 19 % (Table 1). More reduction was observed in shallow root weight (−27 %) than in deep root weight (−20 %). Wheat roots are more abundant in the upper soil layers, which are better aerated and richer in nutrients than deeper horizons. Usually, 70 % of total

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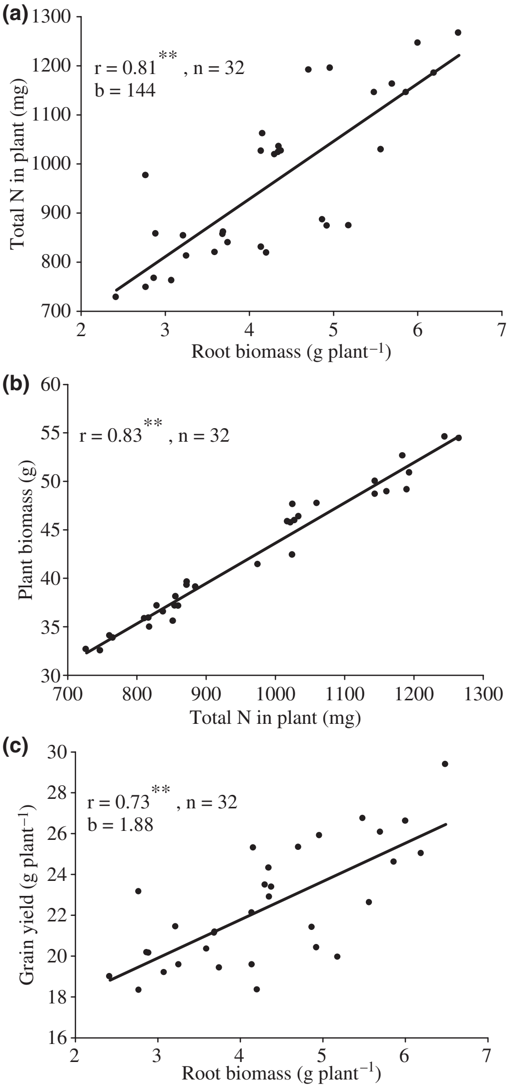

Fig. 1 Relationship between (a) total N in plant and plant root biomass, (b) plant biomass and total N in plant, and (c) grain yield per plant and plant root biomass for spring bread wheat Pavon 76 and its 1RS translocation lines; Pavon 1RS.1AL, Pavon 1RS.1BL and Pavon 1RS.1DL, grown under optimum and low levels of N, P and K in sand-tube experiments in glasshouse across 2 years.

root length is found in the top 30 cm of soil layer, where nutrients are concentrated (Manske and Vlek 2002). Our results indicated that application of low level of nutrients resulted in more reduction in shallow than in deep root production; consequently plants recovered a smaller fraction of applied nutrients, which resulted in smaller plant size (Table 1). It appears that the genotypes responded positively to the optimum level of nutrients by producing greater shallow roots to absorb a larger fraction of the applied nutrients and produced larger plant size. Bloom et al. (1988) concluded that wheat genotypes with large plant size recovered more fertilizer N than those with small plant size. This brings up the question of whether large plant size/greater growth rate is the result of efficient recovery of fertilizer N or whether large plants are able to capture a greater amount of soil N. Our earlier study (Ehdaie et al. 2001) indicated that both plant size and an efficient root system were involved in recovery of fertilizer N. Our results from this study indicated that root biomass and its partitioning to shallow and deep roots also influence plant N and P uptake (Tables 1 and 3). The genotypes responded negatively and similarly to the lower rate of nutrients with respect to production of root biomass and shoot biomass, including grain yield as indicated by the lack of genotype × nutrient level interactions for these traits.

Both shallow and deep root weight contributed to greater root biomass observed in the 1RS translocation lines compared with root biomass in Pavon 76 (Table 1). The greater deep root weight in the 1RS translocations could be due to more root branching and/or more roots reaching deep soil. In our previous study (Ehdaie and Waines 2006), the number of roots longer than 30 cm at tillering (45 days after grain germination) was significantly greater in Pavon 1RS.1BL (6.7) than that in Pavon 76 (5.3). Also, total root length in Pavon 1RS.1BL (476 cm) and deep root weight per plant (69 mg) was greater than those in Pavon 76 at the same growth stage, 370 cm and 43 mg, respectively. Early and abundant root branching is likely to improve early N uptake in wheat crops (Fillery and McInnes 1992, Liao et al. 2004). King et al. (2003), using modelling techniques, concluded that a larger investment by a wheat crop in fine roots at depth in the soil and less proliferation of roots in surface layers, would improve yields by accessing extra resources such as water and nitrogen. In the present study, Pavon 76 allocated 2.5 % of its total dry matter to production of deep roots compared with 3.0 % by Pavon 1RS.1AL and to 3.1 % by Pavon 1RS.1BL and Pavon 1RS.1DL. Shallow roots, on average, contributed about 70–72 % to total root dry matter whereas deep roots contributed about 27–30 % (Table 1) which concurs with the results reported by Manske and Vlek (2002). The ratio of root biomass to plant biomass was similar under low and optimum levels of nutrients (Table 1). Usually, this ratio in spring bread wheats is higher under water-nutrient stress (Ehdaie et al. 1991). The lack of a significant difference in this study could be due to the possibility of the rye genes carried by 1RS overriding the nutrient sensing system as it relates to altered root biomass to shoot biomass ratio.

Correlation and regression analysis indicated that as plant root biomass increased by 1 g, total N in the plant increased by 144 mg. Plant root biomass explained 65 % of the variation observed for total plant N. The correlation

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coefficient between plant biomass and plant N content was positive and significant (r = 0.83**) (Fig. 1b). Paré et al. (2006) reported a similar relationship between total plant N uptake and plant biomass for several grass species used for golf greens. Strong correlations between root biomass and root length and nitrate uptake have been reported in wheat (Brady et al. 1993). Similarly, as root biomass per plant increased by 1 g grain yield per plant increased by 1.88 g. Plant root biomass explained 53 % of the variation observed for plant grain yield. Strong positive correlation between root biomass and grain yield was reported for the same genotypes when grown under well-watered ($r = 0.89$; $P < 0.01$) and droughted ($r = 0.66$, $P < 0.07$) pot experiments (Ehdaie et al. 2003). There was positive and significant correlation between uptake of P and K with root biomass (r = 0.82 and 0.79, respectively). Also, plant biomass was positively and closely correlated with plant P and K uptake (r = 0.98).

The greater grain yield per plant observed in Pavon 1RS.1AL and Pavon 1RS.1BL compared with Pavon 76 was caused by larger grain size rather than to number of grains per plant (Table 1). There was a negative correlation between number of grains per plant and grain size. The 6–8 % greater grain yield observed for the 1RS translocation lines compared to Pavon 76 in this study was in agreement with the results reported earlier by Carver and Rayburn (1994) and Moreno-Sevilla et al. (1995). Genotypic differences for harvest index, calculated as the ratio of grain yield to plant biomass including roots, ranged from 50 % for Pavon 1RS.1DL to 54 % for Pavon 1RS.1AL with 52 % for Pavon 76 and Pavon 1RS.1BL. Therefore, despite greater allocation of dry matter for root production by Pavon 1RS.1AL and Pavon 1RS.1BL (Table 1) these two genotypes had either significantly greater or similar HI compared with Pavon 76.

The percentage of leaching significantly decreased as plants grew from early tillering to booting and to early grain filling period presumably due to development of an enlarged root system (Table 2). In the longer growth period of the second season, leaching fraction was greater at early tillering, but less at early grain filling compared with shorter growing season in the first year. Interestingly, percentage of leaching at optimum level of nutrients was significantly less at booting and early grain filling compared with low level of nutrients (Table 2). This could be due to less vigorous plants and root system developed under low level of nutrients that allowed more water-nutrients to be leached. Liao et al. (2006) reported superior uptake of N by wheat lines with vigorous early growth. The leaching fraction was the highest at early tillering and the lowest at early grain filling (Table 2). These results suggest management strategies for N fertilizer for a wheat crop. For example, further improvement in the recovery and uptake of the applied N by the plant might result by splitting the N fertilizer application at planting and at the onset of tillering. Also, as it is the excess water that transports nitrate to the deep layers of soil that eventually results in nitrate leaching, the amount of irrigation water should be carefully monitored to match plant water requirement and leave minimum excess water.

Nitrate concentration in leachate decreased as plants grew from early tillering (81 %) to booting (64 %), but did not change from booting to early grain filling period (63 %). This decline in nitrate concentration in leachate might be due to greater plant demand for C and N during rapid growth and development around boot stage prior to heading and anthesis and also during early linear grain growth (Ehdaie et al. 2008). The amount of N in leachate at early tillering, booting and grain filling was consistently and significantly lower for Pavon 1RS.1DL than for Pavon 76 (Table 2). Also, Pavon 1RS.1AL had significantly less N in leachate at booting and early grain filling. The genotypic mean for the amount of N in leachate was the highest at early tillering and progressively decreased at booting and at early grain filling (Table 2). These results indicated that early uptake of N is critical to reduce leaching loss of N as leaching fraction, nitrate concentration and N content in the leachate was highest during early plant growth. Therefore, wheat genotypes with early vigour and a bigger root system should be selected or developed to take up a large fraction of N fertilizer applied during early plant growth.

The greater plant P and K content at maturity in the second year and under the optimum level of nutrients (Table 3) was caused by a longer growing season along with more demand for water-nutrient application and more vigorous plants developed in this year compared with the first year (Table 1). The 1RS translocation plants accumulated significantly more P than Pavon 76 (Table 3). Most of P absorbed by the plant was transported to the grains (87 %) whereas most of K absorbed remained in the stems and leaves (79 %) (Table 3). Therefore, P harvest index, on average, was 87 %, which was greater than that reported by Manske et al. (2002) for wheat cultivars (66–80 %), and K harvest index was, on average, 19 % (Table 3). The differences between P harvest indices reported by Manske et al. (2002) and that observed in this study could be due to different wheat genotypes used and/or be due to growing conditions. The concentration of P and K in grains was significantly higher in 1RS translocation lines than in Pavon 76.

The trend for partitioning of N to different plant parts was different from those observed for P and K. Of the total amount of plant N uptake, on average, 4 and 21 % remained in roots and stems and leaves, respectively, and 74 % was transported to the grains (Table 4). Thus, NHI defined as the ratio of grain N content to plant N content was, on average, 74 % (Table 4) which concurs with the values reported for several spring wheat cultivars examined under field conditions (Ehdaie and Waines 2001) and for a different set of spring bread wheat genotypes grown in solution culture (Andersson and Johansson 2006). However, the percentage of root N and stem and leaf N at maturity reported for spring wheats grown under solution culture, 10–20 % and 7–17 %, respectively (Andersson and Johansson 2006), was different form our observations. The amount of N uptake per unit root biomass (root N-uptake efficiency) was greater in Pavon 76 (Table 4) because the average increase in plant N content in 1RS translocation lines (11 %) compared to Pavon 76 was not proportional to increase in root biomass observed in the former genotypes (37.8 %) (Table 1). However, plant N content at maturity was significantly greater for 1RS translocation lines than in Pavon 76 because of greater root biomass which might reflect their higher combinations of root number, root length and root branching (Table 4). As a result, NUEP and NUEG were greater in 1RS translocation lines.

There is a possibility of other genes carried on 1RS in the translocation lines examined that might influence biomass production independent of root biomass. Foulkes et al. (2007), using two doubled-haploid populations of wheat, associated higher biomass production with the 1RS arm in a translocated chromosome which might be due to greater capacity of the 1RS translocated lines to accumulate water-soluble carbohydrates in the stem (Snape et al. 2007).

The results obtained in this study support our hypothesis that greater root biomass would enhance water and nutrient uptake that may result in higher grain yield in bread wheat. Therefore, the greater grain yield observed in Pavon 1RS.1AL, Pavon 1RS.1BL and Pavon 1RS.1DL when evaluated under field conditions for two years (Ehdaie et al. 2003) might be attributed to their relatively greater root biomass.

Conclusions

Wheat genotypes that take up a high percentage of the recommended N application provide a lower hazard for N leaching than those which absorb a lower percentage, thus leaving much N in the soil. The 1RS translocation lines used in this study allocated more dry matter for production of the root system and consequently absorbed more N, produced larger plants and higher grain yield and left less residual N for nitrate leaching than Pavon 76 that produced less root biomass. Also, P and K uptake was positively and significantly correlated with plant root biomass at maturity. The 1RS translocation lines had either greater or similar harvest index than Pavon 76, despite investing greater dry matter for root production. Hence a wheat plant that develops a larger root system does not necessarily decrease grain yield. As a larger percentage of applied N fertilizer was leached during early plant growth, wheat genotypes with early shoot vigour and a large root system should be developed to increase uptake of plant N and other nutrients during tillering and booting. Although reduction in N fertilizer application appears to be an obvious remedy to reduce leachate N concentration and the amount of N in leachate, this study with Pavon 76 near isogenic lines indicated that reduction of N from optimum level would result in a smaller plant size and root system which would result in lower grain yield but greater leaching fraction. Lower leachate N concentration was associated with lower N application. Multiple smaller applications of N fertilizer, especially during early plant growth, that more closely matches plant N uptake and with adequate irrigation water, seems better than a single or a few applications, but with relatively larger rate of N fertilizer.

Significant genetic variation exists for root system characters in bread wheat. It may be worthwhile to identify wheat genotypes with superior root properties for efficient nutrient uptake, especially during tillering and booting, and then combine them through crossing to develop progenies/germplasm for breeding of nutrient-efficient wheats. For example, the Pavon 1RS translocation lines have 31–46 % more root biomass than near-isogenic Pavon 76, which resulted in 6–8 % greater grain yield. Pavon 76 and many other CIMMYT green-revolution wheats such as ‘Anza’ and ‘Yecora Rojo’ have small root systems (2–3 g per plant) relative to landraces that have two- to threefold larger root systems (Waines and Ehdaie 2007). Crop physiologists may need to determine what will be the nitrate leaching and grain yield of a plant with two or three times the root biomass of Pavon 76, and with optimum stem height for a particular growing region (80–100 cm) (Ehdaie and Waines 1994, Flintham et al. 1997).

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