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Citation	Thompson, A. L., Smiley, R. W., & Garland-Campbell, K. (2015). Registration of the LouAu (Louise/IWA8608077) wheat recombinant inbred line mapping population. Journal of Plant Registrations, 9(3), 424-429. doi:10.3198/jpr2015.01.0002crmp
DOI	10.3198/jpr2015.01.0002crmp
Publisher	Crop Science Society of America
Version	Version of Record
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

Published August 21, 2015
JOURNAL OF PLANT REGISTRATIONS

MAPPING POPULATION

Registration of the LouAu (Louise/IWA8608077) Wheat Recombinant Inbred Line Mapping Population

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Abstract

LouAu (Louise/IWA8608077) (MP-7, NSL 511036) is a wheat (*Triticum aestivum* L.) recombinant inbred line population developed by the USDA-ARS, with Oregon State and Washington State Universities, from a cross between the soft white spring cultivar Louise and the white facultative Iranian landrace IWA8608077. The population was developed by single seed descent from the F_2 generation to the F_5 generation. The population has 150 $F_{2:5}$ recombinant inbred lines and has been used to study the genetics of resistance to root-lesion nematodes (*Pratylenchus neglectus* and *P. thornei*), and root architecture. The 26 linkage groups identified include 30 codominant simple sequence repeat markers and 2008 single nucleotide polymorphic markers from the Illumina 9K wheat single nucleotide polymorphism chip. Chi-square analysis shows 21 to 95% of identified polymorphic markers within individual linkage groups were in segregation distortion. The population frequency distributions have a normal distribution for the measured traits *P. neglectus* resistance, root length, root weight, root lignin content, and plant height. The population frequency distribution has a bimodal distribution for *P. thornei* resistance, left skewed for lateral root number and right skewed for growth stage. This population has shown potential for mapping resistance to other soilborne pathogens as well as abiotic stresses and will be useful in that endeavor.

Journal of Plant Registrations 9:424–429 (2015).
doi:10.3198/jpr2015.01.0002crmp
Received 26 Jan. 2015. Accepted 18 Apr. 2015.
Registration by CSSA.
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Root-lesion nematodes (RLN)—primarily *Pratylenchus neglectus* (Rensch, 1924) Filipjev Schuurmans & Stekhoven, 1941 and *P. thornei* Sher & Allen, 1953—are serious pathogens of wheat (*Triticum aestivum* L.) production in the Pacific Northwest (Smiley et al., 2005a,b). The wheat landrace accession IWA8608077 from the East Azerbaijan province of Iran, was identified as having resistance to *P. neglectus* and *P. thornei* (Sheedy and Thompson, 2009; Thompson et al., 2007), identified as AUS28451 in these papers. The landrace IWA8608077 is part of the 1935 Iranian landrace collection curated at the USDA National Small Grains Collection (NSGC) (NSGC accession PI 621458), the International Maize and Wheat Improvement Center (CIMMYT) (CIMMYT accession CWI57134), and the Australian Winter Cereals Collection (AWCC) (AWCC accession AUS28451). A recombinant inbred line (RIL) population was developed from a cross between the Pacific Northwest-adapted soft white spring wheat cultivar Louise (PI 634865; PVP 200500311) and IWA8608077 to study the inheritance of RLN resistance. The population is composed of 150 $F_{2:5}$ RILs and was developed by the USDA-ARS in collaboration with Oregon State University and Washington State University. The adapted parent cultivar, Louise, was developed and jointly released by Washington State University, the University of Idaho, and Oregon State University in August 2005 (Kidwell et al., 2006). The population, later named LouAu (MP-7, NSL 511036), segregates for resistance to RLN, stripe rust (caused by *Puccinia striiformis* Westend. f. sp. *tritici*), root architecture traits, and agronomic traits.

Methods

Parents

Louise was derived from the cross 'Wakanz' (PI 506352)/'Wawawai' (PI 574538). Louise is a soft white, spring

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Abbreviations: AWCC, Australian Winter Cereals Collection; CIMMYT, International Maize and Wheat Improvement Center; HTAP, high-temperature adult-plant; NSGC, National Small Grains Collection; QTL, quantitative trait loci; RIL, recombinant inbred line; RLN, root-lesion nematodes; SNP, single nucleotide polymorphism; SSR, simple sequence repeat.

wheat possessing the semidwarf allele, *Rht-D1b*, with midseason maturity. Louise has good milling and baking characteristics and has the high molecular weight glutenin subunits 5+10 coded by *Glu-D1d* on chromosome 1D (Kidwell et al., 2006). Louise has high-temperature adult-plant (HTAP) resistance to stripe rust races PST-78 and PST-100 with associated quantitative trait loci (QTL) identified on chromosome 2B (Carter et al., 2009), and partial resistance to Hessian fly [*Mayetiola destructor* (Say)] (Kidwell et al., 2006). Greenhouse trials have found Louise to be susceptible to both RLN species (*P. neglectus* and *P. thornei*) (Sheedy et al., 2007a,b; Thompson et al., 2007).

The landrace accession IWA8608077 was originally collected in 1935 and held at the University of Tehran, Iran, as part of an 11,000 accession collection. The collection was transferred to the University of California at Davis between 1980 and 1988 and then later distributed to NSGC, CIMMYT, and the AWCC for curation. IWA8608077 is a tall accession possessing the wild-type alleles for height (*Rht-B1a* and *Rht-D1a*). IWA8608077 is a facultative (late-maturing) spring (*Vrn-D1*) hexaploid with white seed color. IWA8608077 is resistant to both RLN species (Sheedy et al., 2007a,b; Thompson et al., 2007), has a large, fibrous rooting system, but is susceptible to stripe rust races prevalent in the Pacific Northwest.

Population Development

The cross between Louise and IWA8608077 was made at the Oregon State University Columbia Basin Agricultural Research Center in 2006, with Louise seed provided by Kim Kidwell (Washington State University) as the female parent and IWA8608077 received from the NSGC (PI 621458) as the male. The hybrid (F_1) seed from a single cross was harvested and transferred to Washington State University for population development. The F_2 seed from seven F_1 plants, derived from that single cross, was bulk harvested. A total of 358 $F_{2:5}$ derived RILs were generated by single seed decent using the following conditions. Plants were grown in a controlled greenhouse set at 25°C with a 14-h day length after a 6-wk vernalization period in a 4°C Conviron GR48 growth chamber. Heads were bagged at the onset of anthesis (Zadoks growth stage 60 [Zadoks et al., 1974]) to prevent outcrossing and then removed for grain fill. The F_5 seed was grown in 2-L pots for leaf tissue harvest and seed increase. The F_6 and subsequent generations were bulk harvested by RIL. The population is currently in the F_8 generation.

Genotyping of the Population

Leaf tissue from each of the 358 $F_{5:6}$ lines and the population parents was harvested at Zadoks growth stage 29 (no nodes detected) and stored at −80°C. Whole leaf tissue was ground in liquid nitrogen to a fine powder and DNA was extracted using a Sarkosyl lysis buffer protocol (5 M Tris-Cl [pH 7.5], 1 M ethylenediaminetetraacetic acid [pH 8.5], 0.25 M NaCl, 20% sodium dodecyl sulfate). Extracted DNA was diluted in a 1:10 ratio with double-distilled water (ddH_2O), and concentrations were determined with a NanoDrop 2000c (Thermo Scientific) and then stored at −20°C before use.

The 358 lines were genotyped with 72 simple sequence repeat (SSR) markers previously identified as polymorphic between the population parents and representing each chromosome. The marker data were used to reduce the population to 150 lines with a greater frequency of crossovers as identified with an in-house program written using the R software package (version 2.14.2) (R Core Team, 2012). The 150 lines were collectively named the LouAu population, a truncation and combination of the parent names; the AUS28451 name was used because it is the name by which the RLN resistance was originally published. The LouAu population was further genotyped using the Illumina 9K wheat single nucleotide polymorphism (SNP) chip pilot assay (Cavanagh et al., 2013). The LouAu population has also been assessed for markers associated with the known wheat genes for vernalization (*Vrn-A1, Vrn-B1,* and *Vrn-D1*) (Yan et al., 2004), puroindolines (*PinA-D1* and *PinB-D1*) (Morris, 2002), height (*Rht-B1* and *Rht-D1*) (Ellis et al., 2002), photoperiod (*Ppd-D1*) (Beales et al., 2007), and the Louise HTAP resistance to stripe rust, designated *QYrlo.wpg-2BS* from Carter et al. (2009). The *Pin* and *Rht* were assayed using kompetative allele specific markers (LGC Genomics) with sequences provided by Gina Brown-Guedira (USDA-ARS).

Whole genome linkage maps were constructed for the population based on the 72 SSR markers discussed above, the markers associated with known genes (Table 1), and 2691 SNP markers from the Illumina wheat 9K chip that were scored as polymorphic within the population. The polymorphic SNP markers were further screened to identify those with highly skewed segregation ratios ($\chi^2 \geq 10.5$). Significant ($P \leq 0.005$) segregation distortion was detected for 672 markers, and these were removed from the dataset for linkage group development (Fig. 1). Linkage groups were generated using Kosambi's mapping function with a minimum LOD score of 2.0 and the maximum likelihood mapping algorithm using JoinMap software (Kyazma). Linkage groups were assigned to chromosomes by comparison to the wheat 9K SNP consensus map (Cavanagh et al., 2013).

Phenotyping the Population

The RLN phenotype data were collected on the LouAu population in 2012 for *P. neglectus* and for *P. thornei* from the $F_{5:6}$ generation. The two replicates for each species were assayed in separate experiments. Nematodes were collected from Palouse silt loam (fine-silty, mixed, superactive, mesic pachic Ultic Haploxerolls) samples collected in Pullman, WA, then increased and maintained on monoxenic carrot cultures. The carrot disks were prepared using a modified protocol described by Castillo et al. (1995). Cultures were kept in a growth cabinet (Percival Scientific) in the dark at 22°C. Before plant inoculation, nematodes were extracted from carrots and species determined following Yan et al. (2008) with species-specific primers. The population was evaluated for RLN resistance following a modified protocol described by Thompson et al. (2007). Plants were grown in containers (Stuewe and Sons) containing 150 g of soil. The soil was mixed as a 3:1 ratio of pasteurized Palouse silt loam soil to fine sand. Four granules of Osmocote 14–14–14 (N–P–K) (Scotts Co. LLC) slow-release fertilizer were added to each conetainer at planting. At the completion of each trial, before nematode extraction for enumeration, the roots from each plant were evaluated for damage using a 1-to-5 rating system where 1 = little to no damage, 2 = 1/4 of the root system has browning, 3 = 1/2 of the root system has browning, 4 = 1/2

Table 1. The trait investigated with known associated genes and class type of the marker on the parent lines 'Louise' and IWA8608077 and the ratio for the 150 recombinant inbred line population (LouAu) of the cross 'Louise'/IWA8608077. The chi-square for best-fit analysis and associated *P* values are given for the LouAu population.

Trait	Gene/QTL†	Class‡	IWA8608077	Louise	RIL ratio§	Fit ratio¶	χ^{2}#	*P* value††
Height	*Rht-B1*	a:b	a	a	142:0	1:0		
	Rht-D1	a:b	a	b	69:72	1:1	0.57	0.7519
Growth	*Vrn-A1*	a:h:b	b	a	94:49	2:1	13.54	0.0002
	Vrn-B1	a:h:b	b	a	69:20:60	3:1:3	363.99	0.0001
Habit	*Vrn-D1*	a:h:b	a	b	69:14:66	3:1:3	170.20	0.0001
	Ppd-D1	a:b	b	b	0:147	0:1		
Kernel	*PinA-D1*	a:b	a	a	143:0	1:0		
Texture	*PinB-D1*	a:b	a	a	141:0	1:0		
Stripe rust	*QYrlo.wpg-2BS*	–:h: +	HTAP–	HTAP+	121:2:24	5:1	65.45	0.0001

† QTL, quantitative trait locus.

‡ Class = classification of the marker as either dominant (a:b alleles) or codominant (a:h:b genes)

§ RIL ratio = ratio of called alleles for the given marker within the LouAu population.

¶ Fit ratio = ratio that best fits observed data.

χ^{2} = chi-square value.

†† *P* value = two tailed probability for fit to the expected 1:1 ratio.

of the root system has browning, and 5 = complete browning of the root system.

Plant height and maturity were first collected on the F_6 generation grown in the field in 2012 at the Columbia Basin Agricultural Research Center (Adams, OR) and then on subsequent generations in 2013 (F_7) and 2014 (F_8). The population was planted into single head rows in a randomized block design with two replicates for each RIL, except in 2014 where only a single replicate was planted. The head rows were 0.76 m long, four RILs across spaced 0.36 m apart, and planted on 10 Apr. 2012, 25 Mar. 2013, and 3 Apr. 2014. Growth stage was recorded using the Zadoks scale for the entire population on 24 June 2012, 22 June 2013, and 28 June 2014. Plant height was measured with a meter stick from the ground to the base of the tallest inflorescence for each row post-heading on 10 July 2012, 6 Aug. 2013, and 10 July 2014.

The seedling root architecture data were collected on the population from the F_7 generation. The population was evaluated for root length, number of lateral roots, root weight, and root lignin content. Plants were grown in Magenta GA-7 culture boxes (Bio-World) with 7 mL of 50% Murashige and Skoog growth media with 1% agar. Each RIL in the population was planted in two magenta boxes with five plants each, totaling 10 plants per RIL within two replicates for evaluation. At the end of a 2-wk growing period (Zadoks growth stage 12), each plant was measured to determine the number of lateral roots and root length of the primary root. Root dry weights were determined from a 2-cm section of the primary root sampled nearest the crown from each plant. These parameters were chosen because infection by soilborne pathogens, including nematodes, often occurs within the first few weeks of growth. Sampled roots were dried at ambient temperature (22°C) for 24 h before weighing. The remaining root tissue was collected in 2-mL tubes, flash frozen in liquid nitrogen, ground using a micropestle, and stored at −80°C for root lignin extraction. Total root lignin was assayed using a thioglycolic acid precipitation method as described by Brinkmann et al. (2002).

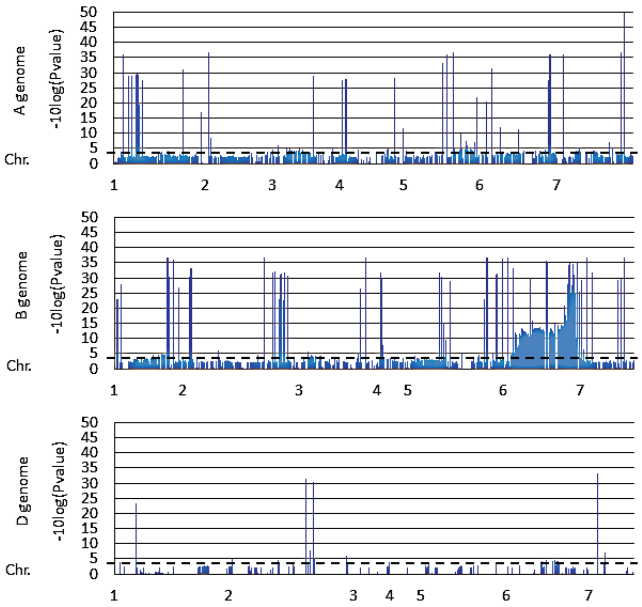

Fig. 1. Segregation distortion of polymorphic single nucleotide polymorphism (SNP) markers from the Illumina 9K SNP chip in the LouAu population aligned with the wheat 9K SNP consensus map. The dashed line indicates the significance threshold ($P \leq 0.005$). The chromosome number is at the beginning of each chromosome.

Characteristics

Population Genotyping

The genetic linkage map contains 2038 markers mapped on 26 linkage groups. Chromosomes that had more than one associated linkage group were 2D, 3A, 5A, 6A, and 6D. All 21 of the wheat chromosomes were represented by the linkage groups. The total map distance is 2426.8 cM, with an average intermarker spacing at 1.33 cM. Markers within linkage groups associated with chromosomes 6A, 2D, and 6B had the largest amounts of marker segregation distortion at 58, 63, and 95%, respectively. The markers within the remaining linkage groups showed segregation distortion ranging from 21 to 55% (Fig. 1).

The marker data for known wheat genes showed that the population was not segregating for the height gene *Rht-B1*

but was segregating for *Rht-D1* in a 1:1 ratio (Table 1). The population was also segregating at all three *Vrn-1* genes, *Vrn-A1, Vrn-B1,* and *Vrn-D1* located on each of the homeoelogous group 5 chromosomes. The segregation for *Vrn-A1* fit a 2:1 ratio, *Vrn-B1* fit a 3:1:3 ratio, and *Vrn-D1* fit a 3:1:3 ratio. The population was not segregating for photoperiod sensitivity (*Ppd-D1*) or either of the puroindoline (*PinA-D1* and *PinB-D1*) genes. The segregation ratio for the HTAP resistance fits a 5:1 ratio (Table 1).

Population Phenotyping

The LouAu population segregated for resistance to *P. neglectus* and *P. thornei* (Table 2). The nematode counts ranged from 1 to 21,600 for *P. neglectus* and 1 to 2760 for *P. thornei* among the RILs. In both experiments for both species, the resistant parent, IWA8608077, had decreased counts of nematodes compared with Louise (Table 2). The root ratings for damage ranged from 1 to 5 for both species over the whole population, with lower values for IWA8608077 compared with Louise (Table 2). The frequency distribution for *P. neglectus* counts, averaged from both experiments, closely followed a normal distribution skewed slightly toward susceptibility. The distribution for *P. thornei* was skewed toward resistance with a bimodal distribution, which is not unexpected given the lower counts for both parents (Fig. 2).

The population segregated for height and days to heading, which followed a normal distribution, and growth habit, which was skewed toward higher Zadoks scores at the time of the evaluation (Fig. 3). The plant height average in the LouAu population was similar in 2012 and 2013 but lower in 2014. The IWA8608077 parent had average heights from 71.7 to 88.3 cm over the 3 yr and Louise from 65.3 to 85.0 cm (Table 3). Four lines in the population, LouAu-102, LouAu-203, LouAu-326, and LouAu-359, had a winter growth habit and were not included in the 2013 and 2014 growing years. Therefore the Zadoks growth stage average for the LouAu population in 2012 was lower than in 2013 and 2014. The IWA8608077 parent had average Zadoks scores from 47.7 to 66.3 over the 3 yr and Louise from 63.3 to 70.0 (Table 3).

The population also segregated for the root architecture traits root length, root weight, number of lateral roots, and root lignin content (Table 4). From the 10 plants evaluated, IWA8608077 had increased lateral roots, root weight, and root lignin content compared with Louise. Louise had increased root length compared with IWA8608077. The distributions in the LouAu population for root length, root weight, and root lignin content all followed a normal distribution curve, while the distribution for the lateral root number was skewed slightly toward fewer lateral roots (Fig. 4).

Conclusions

The LouAu population was developed to identify useful molecular markers associated with resistance to root-lesion nematodes and root architecture traits. The distribution frequencies for both *Pratylenchus* spp. assessed confirm the polygenic control of resistance to *Pratylenchus* but suggest fewer QTL are involved in resistance to *P. thornei*. The bimodal distribution for the *P. thornei* counts could be influenced by escapes or lines that are susceptible but did not have nematode increase due to an unknown environmental interaction. However, the controls in the experiments performed as expected, so the escapes are thought to be minimal in the population (data not shown). Compared with the *Pratylenchus*-susceptible parent Louise, the resistant parent IWA8608077 was recently shown to significantly reduce population densities of *Pratylenchus* spp. under field conditions (Smiley et al., 2014).

Table 2. The mean data for the parental lines 'Louise' and IWA8608077 for the root-lesion nematode experiments for each *Pratylenchus* species, with the confidence limits (lower and upper) and associated *P* value. The mean data of these same traits for the 150 recombinant inbred line (RIL) population (LouAu) of the cross 'Louise'/IWA8608077 with the confidence limits are given.

Measurement†	IWA8608077						Louise						LouAu RIL population			
	P. neglectus			P. thornei			P. neglectus			P. thornei			P. neglectus		P. thornei	
	Mean	Conf. limit‡	*P* value	Mean	Conf. limit	*P* value	Mean	Conf. limit	*P* value	Mean	Conf. limit	*P* value	Mean	Conf. limit	Mean	Conf. limit
Count (*x*)	121	114–127	0.0026	61	54–67	0.0053	810	383–5003	0.2460	91	84–97	0.0035	1202	976–1428	79	54–104
ln(*x*)+1	5.8	5.8–5.9	0.0010	5.1	5.0–5.1	0.0004	7.6	2.1–13.1	0.0362	5.5	5.4–5.6	0.0006	6.8	6.6–7.1	3.7	3.4–4.0
Root rate	2.0	2.0–2.0	–	2.0	2.0–2.0	–	4.0	4.0–4.0	–	4.0	4.0–4.0	–	2.9	2.8–3.0	2.9	2.8–3.1

† Count = number of nematodes counted after extraction; root rate = assigned value determined on root damage.

‡ Conf. limit = the 95% confidence limit around the given mean.

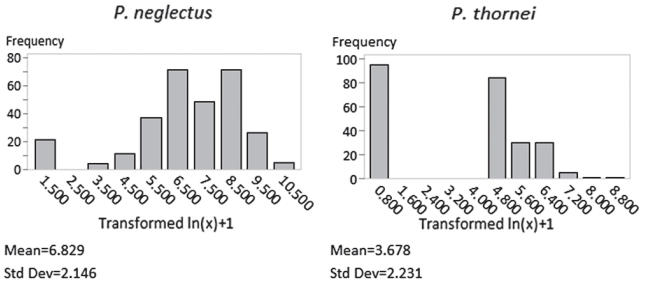

Fig. 2. Frequency distribution of the LouAu recombinant inbred line population to *Pratylenchus neglectus* and *P. thornei* averaged over two experiments for each species. The count data was transformed using a natural log function plus 1 (ln*x*+1).

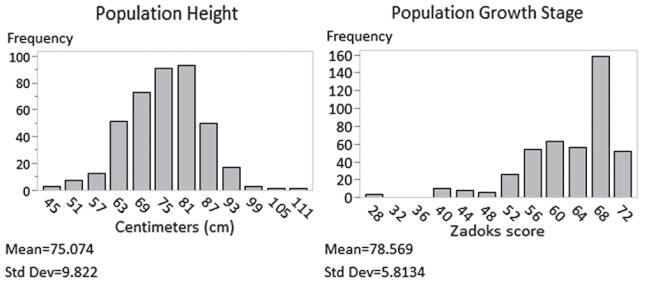

Fig. 3. Frequency distribution of the LouAu recombinant inbred line population of plant height and Zadoks growth stage on a given date. The distribution represents the data collected over the 3 yr from the field locations.

Table 3. The mean data for the parental lines 'Louise' and IWA8608077 for the 3-yr field assessment of height and growth development with the confidence limits (lower and upper) and associated *P* value. The mean data of these same traits for the 150 recombinant inbred line population (RIL) (LouAu) of the cross 'Louise'/IWA8608077 with the confidence limits are given.

Measurement	IWA8608077						Louise						LouAu RIL population			
	Height			Zadoks			Height			Zadoks			Height		Zadoks	
	Mean	Conf. limit†	*P* value	Mean	Conf. limit	*P* value	Mean	Conf. limit	*P* value	Mean	Conf. limit	*P* value	Mean	Conf. limit	Mean	Conf. limit
	— cm —						— cm —						— cm —			
2012 $F_{5:6}$	71.7	64.5–78.8	0.0005	47.7	32.5–62.8	0.0054	85.0	85.0–85.0	–	64.7	53.5–75.9	0.0016	78.6	77.5–79.6	54.5	53.2–55.7
2013 $F_{6:7}$	88.3	81.2–95.5	0.0040	66.3	60.6–72.1	0.0004	71.0	71.0–71.0	–	63.3	56.2–70.5	0.0007	78.8	77.2–80.3	68.2	67.6–68.8
2014 $F_{7:8}$	85.3	77.7–92.9	0.0004	66.3	60.6–72.1	0.0004	65.3	55.3–75.4	0.0013	70.0	58.6–81.4	0.0014	68.6	67–70.2	66.6	65.8–67.3

† Conf. limit = the 95% confidence limit around the given mean.

Table 4. The mean data for the parental lines 'Louise' and IWA8608077 for the root architecture traits with the confidence limits (lower and upper) and associated *P* value. The mean data of these same traits for the 150 recombinant inbred line population (LouAu) of the cross Louise/IWA8608077 with the confidence limits are given.

Measurement	IWA8608077			Louise			LouAu RIL population	
	Root architecture							
	Mean	Conf. limit†	*P* value	Mean	Conf. Limit	*P* value	Mean	Conf. Limit
Length (cm)	9.3	7.4–11.1	0.0001	14.9	13.9–15.9	0.0001	20.2	19.7–20.6
Lateral (total)	7.2	4.6–9.7	0.0001	6.5	4.7–8.3	0.0001	21.9	20.2–23.7
Weight (mg)	3.37	3.09–3.65	0.0001	2.70	2.27–3.13	0.0001	2.70	2.64–2.78
Lignin $(nm/mg)^2$	0.211	0.19–0.223	0.0001	0.198	0.176–0.221	0.0001	0.181	0.173–0.189

† Conf. limit = the 95% confidence limit around the given mean.

The differences in root architecture traits, particularly the lignin content, indicate this population could also have resistance to other soilborne pathogens. Early greenhouse and field trials have shown the LouAu population segregates for resistance to crown rot caused by *Fusarium culmorum* (data not shown) and root rot caused by *Rhizoctonia* spp. (Aaron Mahoney, personal communication, 2013). The root traits also show promise for tolerance to abiotic drought stress, and the population is currently undergoing evaluation in field trials. Future studies regarding the mechanisms controlling root growth and development would be beneficial to understand

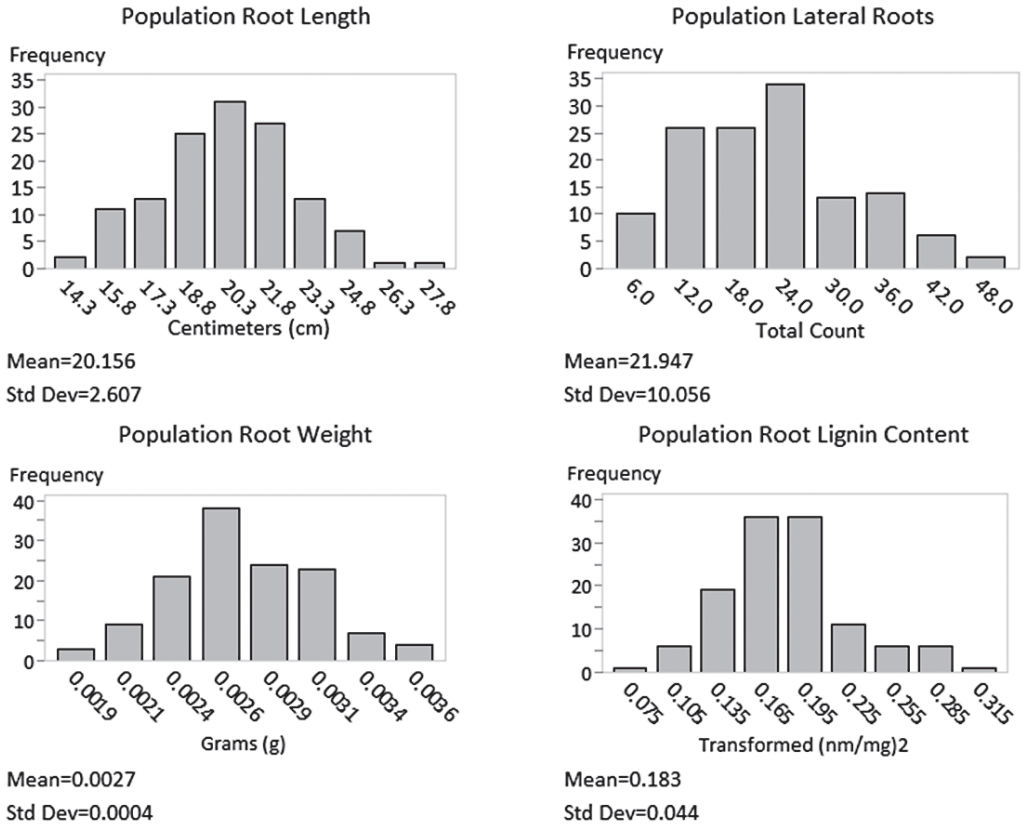

Fig. 4. Frequency distribution of the LouAu recombinant inbred line population of the root architecture traits, length (cm), weight (g), number of lateral roots, and root lignin content $(nm/mg)^2$ of 2-wk-old seedlings.

how root development may be affecting agronomic traits such as heading date, grain quality, and grain yield.

The segregation distortion of polymorphic markers in this population was not unexpected given the wide nature of the cross between a highly cultivated wheat cultivar and a landrace accession. According to Alheit et al. (2011), segregation distortion has been reported in many plant species and can be caused by both biological and nonbiological factors. In the instance of the LouAu population, gametic selection is a highly suspect cause for the segregation distortion as the Louise allele was often favored in loci deviating from the expected Mendelian segregation. The deviation from the expected 1:1 ratio for the *Vrn-A1* marker may be the result of unintentional selection. The $F_{2:3}$ grow-out was conducted in D40H deepots (Stuewe and Sons) that were not sufficiently spaced, causing competition for light. Spring lines with the *Vrn-A1* gene are known to progress more quickly, which gave them an advantage over lines with the *Vrn-B1* or *Vrn-D1* gene.

The wide nature of this cross provides opportunities to assess many agronomic traits that segregate in the population. The LouAu population has potential to be highly useful for identifying molecular markers associated with soilborne pathogen resistance, abiotic stresses, and root development, making it a useful tool for wheat breeders.

Availability

Seed of the LouAu mapping population and its parents Louise and IWA8608077 will be maintained by the USDA-ARS wheat breeding program at Washington State University, Pullman WA, 99164; small quantities of seed (5 g) may be requested for research purposes. Five hundred seeds from each RIL (F_8) have been deposited in the USDA-ARS National Small Grains Collection. Appropriate recognition of the source should be noted if the population contributes to research on soilborne pathogen resistance, root architecture traits, drought tolerance or to the development of new genetics stocks, molecular tools, germplasm, or cultivars.

Acknowledgments

Financial support from the Washington Grains Commission project no. 3949, USDA-ARS (in house) projects: 5348-21220-003-00D and 5348-22000-013-00, the Washington State University O.A. Vogel grant 8334, and the Washington State BIOAg research grant 10A30618915; Vickie Lutes for budget support; Jason Sheedy for help with the parental cross; Kim Kidwell for providing 'Louise' seed; members of the Garland-Campbell laboratory and Steber laboratories for help with the TGA assays; Deven See for providing the 9K SNP consensus map and guidance; Arron Carter for help with the linkage map development; and Scott Hulbert for contributions to the BIOAg research grant.

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