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MAPPING POPULATION

Registration of the Louise/Alpowa Wheat Recombinant Inbred Line Mapping Population

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Abstract

A mapping population was developed from the cross of soft white spring wheat (*Triticum aestivum* L.) cultivars 'Louise' and 'Alpowa' for use in investigating the genetic architecture of drought tolerance in the US Pacific Northwest. The Louise/Alpowa (Reg. No. MP-8, NSL 520824 MAP) recombinant inbred line mapping population was developed through single seed descent from the F_2 generation to the F_5 generation. The population consists of 141 $F_{5:6}$ recombinant inbred lines, of which 132 were used to construct the genetic linkage map. The 32 linkages groups included 882 single nucleotide polymorphism markers and one simple sequence repeat marker spanning 18 of 21 chromosomes. The Louise/Alpowa population was characterized for variation in agronomic traits, phenology, and end-use quality traits. This population will be used for identification and introgression of multiple loci providing resistance to environmental stress such as drought, stripe rust, and high temperatures.

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The inland northwest of the United States is a major wheat (*Triticum aestivum* L.)–producing region comprising eastern Washington, eastern Oregon, Idaho, and parts of western Montana. Three-quarters of the water-limited dryland farmland in the western United States is located in the inland northwest (Schillinger and Young, 2004). The value of the 2016 wheat crop of Washington, Idaho, and Oregon was $1.27 billion (USDA–NASS, 2017). This environment is unique in that it has the precipitation pattern of a mediterranean climate (winter snow and rain and dry summers) combined with high latitude. The soils in this region retain as much as 70% of annual precipitation, allowing the production of wheat on stored soil moisture. Nevertheless, wheat yield and grain filling remain particularly vulnerable to periodic and severe drought, causing an average yield loss of 10 to 20%, with a value of $90 million per year (USDA–NASS, 2017). Climate models for the next 30 yr predict increasing incidence of drought in this region (Rehfeldt et al., 2006; Klos et al., 2014).

The inland northwest is an excellent source of drought-tolerant wheat germplasm. Historically, plant breeding programs have capitalized on stress-tolerant genes without knowing the genetic mechanisms contributing to environmental resilience. While "weighing the bag" provides an adequate target for selection, faster progress and greater efficiency could be gained through knowledge of the genetic architecture of stress tolerance and by mapping the contributing quantitative trait loci (QTL) for production characteristics. The soft white spring cultivar Alpowa (PI 566596; Konzak et al., 1994) was widely grown for over 14 yr from 1994 to 2008 in the dryland areas of eastern Washington in part because of its stripe rust (causal agent *Puccinia striiformis* Westend f. sp. *tritici* Erikss.) resistance, due to *Yr39* and other minor genes, and high grain yield potential (Chen, 2005; Lin and Chen, 2007). Although Alpowa was criticized at the time

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Abbreviations: HTAP, high-temperature adult-plant; QTL, quantitative trait loci; RIL, recombinant inbred line; SNP, single nucleotide polymorphism; SSR, simple sequence repeat.

it was widely grown for slow early growth, it was one of few cultivars capable of yielding well under drought-stress conditions (Santra et al., 2009). The widely grown soft white spring cultivar Louise (PI 634865, PVP 200500311; Kidwell et al., 2006) has been one of the highest yielding cultivars in eastern Washington since 2006. It is known for its superior end-use quality, high-temperature adult-plant (HTAP) resistance to local races of stripe rust, and high grain yield potential in both high and low rainfall zones (Kidwell et al., 2006; Carter et al., 2009). The Louise/Alpowa (Reg. No. MP-8, NSL 520824 MAP) recombinant inbred line (RIL) population was developed to examine the genetic components contributing to the superior environmental stress resilience of both cultivars and to provide progeny for breeder selection.

Louise and Alpowa are both well adapted to the inland northwest, but they differ in the loci controlling flowering time in response to vernalization (requirement for exposure to cold to flower) and photoperiod response (requirement for long days to flower) genes. This allows examination of the effect of phenology and flowering time on stress response. The photoperiod genes are major determining factors of climate adaptability in barley (*Hordeum vulgare* L.) and wheat (Worland et al., 1998; Cockram et al., 2007). The major locus controlling wheat photoperiod response is *Photoperiod-D1* (*Ppd-D1*) (Beales et al., 2007). Alpowa has the dominant *Ppd-D1a* allele, resulting in complete photoperiod insensitivity, early flowering, and lack of response to the circadian rhythm (Table 1). Louise has the recessive *Ppd-D1b* photoperiod sensitive allele. Winter wheat requires 4 to 8 wk of vernalization, or cold treatment, to induce flowering. The major loci that are segregating for vernalization response in cultivated wheat are the *Vrn-1* homeologous genes, *Vrn-A1*, *Vrn-B1,* and *Vrn-D1,* on the long arms of chromosomes 5A, 5B, and 5D, respectively (Cockram et al., 2007). The winter growth habit (vernalization required) requires recessive *vrn-1* alleles at all three loci, whereas the spring growth habit (no vernalization required) results from a dominant allele at any one of the three *Vrn-1* loci. Louise has two strong spring alleles, *Vrn-A1a* and *Vrn-B1a*, either of which eliminates the requirement for a cold period before initiation of flowering, whereas Alpowa has a single weaker spring *Vrn-B1b* allele, which still has a short (1–2 wk) requirement for a cold period.

This study describes the initial characterization of the Louise/Alpowa RIL population. The effect of varying photoperiod and vernalization loci on the timing of plant developmental events was examined. The population was also examined for variation in agronomic traits under irrigated and nonirrigated conditions, for variation in resistance to stripe rust, and for end-use quality. Finally, we describe the genetic map of the Louise/Alpowa RIL population based on single nucleotide polymorphism (SNP) and simple sequence repeat (SSR) markers examined in 132 $F_{5:6}$ generation RILs.

Table 1. Alleles for major genes in the Louise and Alpowa wheat cultivars.

Gene	Chromosome	Parent	Allele†	Phenotype
Ppd-D1	2D	Louise	*Ppd-D1*b	sensitive
		Alpowa	*Ppd-D1*a	insensitive
Vrn-A1	5A	Louise	*Vrn-A1*a	spring
exon4		Alpowa	*vrn-A1b*	longer vrn
Vrn-B1	5B	Louise	*Vrn-B1*a	spring
		Alpowa	*Vrn-B1*b	weak spring
HTAP‡	2B	Louise	155	HTAP
(wmc474)		Alpowa	150	non-HTAP

† We analyzed the *Glu-D1* (5+10), *Rht-B1b* (wild-type), *Rht-D1b* (dwarf), *Pina-D1* (soft), and *Pinb-D1* (soft) and found no polymorphism between the two parents.

‡ HTAP, high-temperature adult-plant.

Methods

Parents

Louise was selected from the cross Wakanz (PI 506352)/Wawawai (PI 574538) (Kidwell et al., 2006). Wakanz has a pedigree of K-78504//K-7400195/Arthur-71/5/Henry/Karrn-90//Onas-52/4/Lemhi-66/3/Yaktana-54-A//Norin-10/Brevor, whereas Wawawai has a pedigree of ID-000190//Potam-70/Fielder/5/Tifton-3725/Walladay//Fielder/Potam-70/3/N-700315/ID-00065/4/ID-00065/Potam-70. Alpowa (PI 566596) is derived from the cross Fielder/Potam-70//Walladay/3/Walladay/Potam-70 (Konzak et al., 1994) and is closely related to Louise.

Population Development

The F_1 between Louise and Alpowa was made at the Washington State University Plant Growth Facility in 2004, with Louise as the female parent and Alpowa as the male. The hybrid (F_1) seed from one cross was harvested for population development. The F_2 seed was harvested from two to five F_1 plants. The exact number of F_1 plants was not recorded. The population was developed without selection through single seed descent of 141 RILs from the F_2 generation to the F_5 generation. During each generation, plants were grown in a controlled greenhouse environment under a 16-h photoperiod and 22°C day/15°C night cycle. The F_5 plants were grown in 3-L pots in the Plant Growth Facility at Pullman, WA, to increase seed. $F_{5:6}$ seeds were harvested, bulked, and planted at the Washington State University Spillman Research Farm, Pullman in 2010. The $F_{5:7}$ increase was planted in single replicate (2.44 m length × 1.68 m width) 4.1-m^2 plots. Subsequent generations were derived from this bulk plot harvested from the Pullman field location.

Population Phenotyping

The Louise/Alpowa mapping population was characterized in the field over 5 yr, 2010 to 2014. Three climates were studied including "rainfed," "irrigated," and "drought" conditions. The rainfed treatment was planted in Pullman, a higher rainfall area receiving an average of 53-cm annual precipitation (AgWeatherNet, weather.wsu.edu). Irrigated and nonirrigated (drought) plots were grown side-by-side in Prosser (about 20 cm of annual precipitation) and Lind, WA, (<30 cm of annual precipitation). Plant development was compared at 60 d after planting by rating Zadoks growth stage in Prosser, 2011 (Fig. 1; Zadoks et al., 1974). Stripe rust ratings of intensity and percentage severity were collected in Pullman in 2012 without any fungicide protection (unprotected) and in Pullman in 2014 under a single early (Zadoks stages 30–33) fungicide application of propiconazole at the labeled rate (Fig. 2; Line and Qayoum, 1992). Plant height was determined after senescence

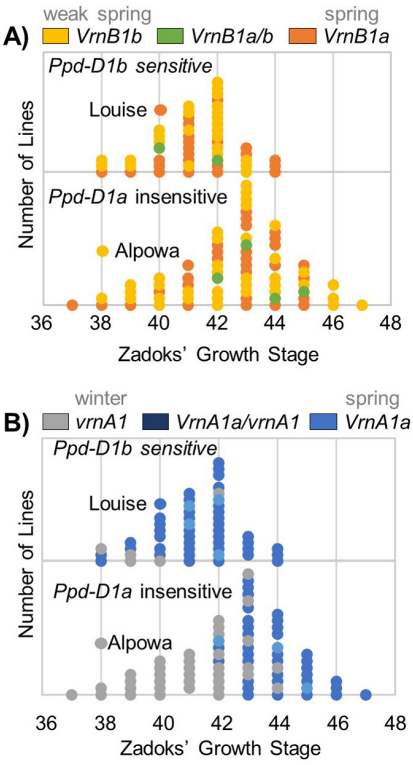

Fig. 1. Comparison of Louise/Alpowa recombinant inbred line (RIL) *Ppd-D1*, (A) *Vrn-B1*, (B) *Vrn-A1*, and the Zadoks growth stage rating during the booting stage in an irrigated trial at Prosser, WA., 2011. Each dot represents one RIL. The *y* axis represents the number of lines measured for growth stage 60 d after planting.

based on the average distance from the soil surface to the top of the canopy on a plot basis in Lind in 2012. Grain yield was measured during harvest with a Wintersteiger Classic Plot Combine equipped with the Harvest Master Grain Gage mobile harvesting system (Wintersteiger Inc.). Fertilizer and herbicide treatments were applied according to Washington State University Extension guidelines for eastern Washington in all years unless otherwise stated (Koenig, 2005).

Population Genotyping

Genomic DNA was prepared from leaf tissue harvested from the F_6 generation from each of the 132 RILs advanced by single seed descent from individual F_2 plants. Tissue was immediately frozen in liquid nitrogen, stored at −80°C, and then lyophilized. Genomic DNA was extracted using a Sarkosyl lysis buffer protocol, as in Thompson et al. (2015). After extraction, DNA concentration was determined with the NanoDrop 2000c (Thermo Scientific). Single nucleotide polymorphic markers were genotyped using the Illumina Infinium iSelect 9k SNP assay for wheat (Cavanagh et al., 2013). Marker data were manually curated in GenomeStudio (Illumina), and 1031 polymorphic markers identified. The Louise/Alpowa population was assessed for known alleles at major wheat loci, including *vernalization-A1* (*Vrn-A1*, *Vrn-B1*) (Yan et al., 2003; Zhu et al., 2014), the puroindolines (*PinA-D1* and *PinB-D1*) (Morris, 2002), reduced height (*Rht-B1b* and *Rht-D1b*) (Ellis et al., 2002), photoperiod (*Ppd-D1*) (Beales et al., 2007), high molecular weight glutenins (*Glu-D1*) (Liu et al., 2008), and the Louise HTAP stripe rust resistance QTL, *QYrlo.wpg-2BS* (Tables 2 and 3, Supplemental Table S2; Carter et al., 2009). All genes except for *QYrlo.wpg-2BS* were assayed using Kompetative Allele Specific polymerase chain reaction (KASP) markers (LGC Genomics; MASWheat, 2017). We did not examine alleles at the *Vrn-2* (Yan et al., 2004) and *Vrn-3* (Yan et al., 2006) vernalization genes because our population is not polymorphic at these loci. The QTL at *QYrlo.wpg-2BS* was examined using the wmc474 SSR marker as described in Carter et al. (2009).

Genetic Linkage Map

Linkage maps were created using JoinMap4 (Van Ooijen, 2006). Linkage groups were determined using the grouping parameter of the test for independence with a minimum logarithm of odds score of 3.0. The Kosambi mapping function was applied to calculate the distances in centimorgans between markers. The maximum likelihood mapping algorithm was used to build the map. Linkage groups were assigned to specific

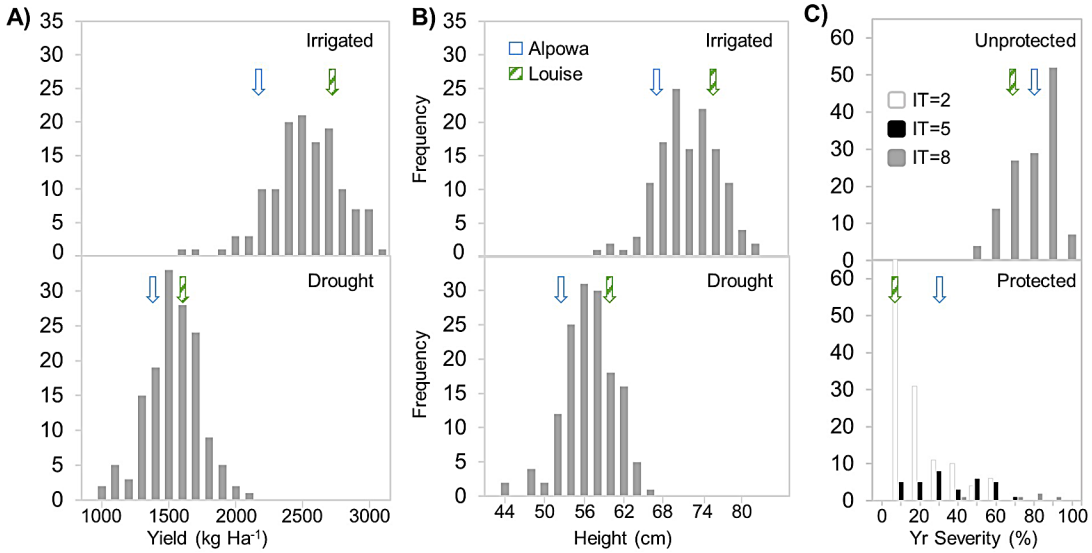

Fig. 2. Distribution of (A) yield and (B) height across the Louise/Alpowa recombinant inbred line (solid gray bars), Louise (green stripe arrow), and Alpowa (blue hollow arrow) parents under irrigated and drought conditions at Lind, WA, 2012. (C) Stripe rust ratings of intensity and percent severity in Pullman, WA, 2012, without any fungicide protection (unprotected) and in Pullman, WA, 2014, under fungicide protection (protected).

Table 2. Description of the 32 linkage groups mapped in the Louise/Alpowa wheat mapping population.

Linkage group†	Assigned chromosome‡	Map distance§	Number of markers per group	Total number of markers
		cM	no.	
LGML1	1AS	9.3	9	9
LGML2,3	1BL, 1BS	73.7, 26.4	32, 9	41
LGML4	1DL	8.1	12	12
LGML5,6	2A, 2AL	105.22, 188.9	66, 60	126
LGML14,15,16	2B, 2BL, 2BL	51.8, 62.2, 21.0	36, 41, 11	88
LGML17	2DSL	145.7	36	36
LGML19,20,21	3AS, 3AL, 3AL	44.3, 11.5, 37.6	14, 17, 28	59
LGML22,23,24	3B, 3BS, 3BL	18.6, 83.2, 22.6	9, 46, 48	103
–	3D	–	–	–
LGML25	4AS	61.0	14	14
LGML26	4BL	27.6	15	15
–	4D	–	–	–
LGML27,28,30	5AS, 5A, 5A	40.6, 37.3, 158.7	15, 18, 75	108
LGML31,32	5B	110.1, 221.4	71, 41	112
–	5D	–	–	–
LGML33,34	6AS, 6AL	27.3, 5.2	15, 9	24
LGML35,36	6BS, 6BL	11.5, 42.7	18, 21	39
LGML37	6DL	29.6	23	23
LGML38,39	7AS	23.4, 11.5	12, 8	20
LGML40	7BL	114.2	47	47
LGML41	7D	70.3	7	7
Total	18/21			883 SNP, 1 SSR

† Linkage using the maximum likelihood (LGML) mapping function were selected using the following criteria: a minimum logarithm of odds (LOD) of 3.0 and a minimum of seven markers per linkage group.

‡ The 32 linkage groups were assigned to chromosomes (S, short arm; L, long arm) based on previously published consensus map of the iSelect 9k single nucleotide polymorphism Assay (Cavanagh et al., 2013).

§ Map distance indicates the total length on a linkage group.

chromosomes based on the previously published consensus map of the iSelect 9k SNP Assay (Cavanagh et al., 2013). The visual of the linkage map in Supplemental Fig. S1 was created using the rQTL package in R (Broman et al., 2003).

Characteristics

The genetic map for the Louise/Alpowa population consists of 32 linkage groups, covering 18 of the 21 (1*n*) wheat chromosomes (Table 2). Of the 1031 polymorphic SNP markers, 882 markers were assigned to a linkage group. The haplotype data and genetic map are found in Supplemental Table S1 and are formatted for rQTL.

Several known genes were added to the linkage map, including the *Ppd-D1* alleles on chromosome 2D (LGML17) at 55.3 cM; the *Vrn-A1* Exon4 SNP on chromosome 5A (LGML30) at 0.0 cM; and the *Vrn-B1a* and *Vrn-B1b* alleles on chromosome 5B(LGML32) at 204.9 cM and 211.3 cM, respectively (Supplemental Fig. S1, Supplemental Table S1). The Wmc474 SSR marker that was linked to the QTL for HTAP resistance to stripe rust in Louise on chromosome 2BS was expected to link to the 2BS linkage group in our map (Carter et al., 2009). Its failure to fall into a linkage group suggests that there are gaps in the genetic map.

Table 3. Number of recombinant inbred lines (RILs) containing parental and heterozygous genotypes for six genes assayed across 132 individuals in the Louise/Alpowa wheat RIL population.

	Louise genotype	Heterozygous	Alpowa genotype	NA†
Vrn-A1 exon4‡	50	10	70	2
Vrn-B1‡	61	3	67	1
Ppd-D1‡	62	13	49	8
HTAP‡	66	4	58	4

† NA, markers could not be amplified for *n* RILs after multiple attempts.

‡ Louise and Alpowa alleles for each gene are, respectively, *Vrn-A1a* and *vrn-A1b*; *Vrn-B1a* and *Vrn-B1b*; *Ppd-D1b* and *Ppd-D1a*; high-temperature adult-plant (HTAP) resistant and HTAP susceptible.

Effect of *Ppd-D1* and *Vrn* Alleles on Phenology

The population was segregating for two alleles for vernalization requirement at the *Vrn-A1* gene. The *Vrn-A1a* allele removes the requirement for vernalization and results in a strong spring growth habit, while the recessive *vrn-A1* allele results in a winter growth habit requiring vernalization to flower. At the homeologous, *Vrn-B1* gene, the population was segregating for two alleles, the strong spring *Vrn-B1a* and the weak spring *Vrn-B1b,* but not for the recessive allele. The two alleles at the *Ppd-D1* gene were the photoperiod insensitive *Ppd-D1a* and the photoperiod sensitive *Ppd-D1b*.

We characterized the impact of the segregating photoperiod and vernalization alleles on the timing of RIL developmental events based on Zadoks growth stages (Fig 1). Lines with the photoperiod insensitive *Ppd-D1a* allele showed faster development (higher growth stage values) at 60 d after planting than sensitive (*Ppd-D1b*) lines, regardless of whether they were

associated with the stronger *Vrn-B1a* or the weaker *Vrn-B1b* alleles ($p < 0.001$; difference of 1.4 Zadoks stage; Fig. 1A). Photoperiod insensitive lines (*Ppd-D1a*) also showed faster development when associated with the strong spring vernalization allele, *Vrn-A1a* ($p < 0.001$; difference of 3.1 Zadoks stage; Fig. 1B, light blue dots).

The *Ppd-D1a* insensitive lines with the winter-type recessive *vrn-A1* allele (Fig. 1B, gray dots) were all slower growing (lower growth stage; $p < 0.001$; difference of 3.1 Zadoks stage) than those containing the spring *Vrn-A1a* allele (Fig. 1B, light blue dots). This same pattern was observed for lines with the *Ppd-D1b* photoperiod sensitive allele, but there were not many lines with both the *Ppd-D1b* and *vrn-A1* alleles.

In contrast, the *Ppd-D1a* insensitive lines with the weaker *Vrn-B1b* allele (Fig. 1A, yellow dots) did not differ in the average growth stage ($p < 0.44$) compared with *Ppd-D1a* insensitive lines containing the stronger *Vrn-B1a* allele (Fig. 1A, orange dots). This suggests while the *Ppd-D1a* insensitive allele had an effect in the absence of the strong *Vrn-A1a* allele, the interaction with specific spring habit alleles at *Vrn-B1* was weak. When the *Ppd-D1a* insensitive lines with the *Vrn-B1a* allele (Fig 1A, orange dots) were compared with those with the *Vrn-A1a* allele (Fig. 1B, light blue dots), the lines with the *Vrn-B1a* allele showed greater variation of growth stages (Zadoks growth stages 37–45) compared with lines with the *Vrn-A1a* allele (Zadoks growth stages 42–47). Thus, it appears that the presence of *Vrn-A1a* and *Ppd-D1* is associated with increased rate of development in this population. If a RIL had both *Vrn-A1a* and *Ppd-D1a* insensitive alleles, the development was accelerated, which may be too rapid for optimal grain filling and further downstream developmental processes.

In the greenhouse, the lines with carrying the recessive *vrn-A1* and the weak spring *Vrn-B1b* alleles need 2 wk of vernalization to flower synchronously. This minimum vernalization requirement is also needed in the field and is usually met by reduced night temperatures.

Agronomic Characteristics

The agronomic characteristics of the RILs were examined under irrigated and nonirrigated (drought) field conditions. Under the drought conditions, grain yield was much lower (an average of 1485 kg ha^{-1} compared with 2480 kg ha^{-1} irrigated), and the population variance for grain yield was reduced (Fig. 2A). Since there are RILs that have a higher yield compared with either parent, there is a potential to increase yield under stress through selection (irrigated: $p < 0.03$; drought: $p < 0.1$). Plant height also varied less under dry conditions (Fig. 2B). The Louise/Alpowa population varied in plant height from 52.8 to 77.8 cm even though the RILs were not segregating for alleles at the major *Rht* (*Reduced height*) loci *Rht-B1* and *Rht-D1*. Both Louise and Alpowa carry both the *Rht-D1b* allele (Table 1), suggesting that other loci likely control the observed variation in plant height.

Genes for stripe rust resistance that have been mapped in Alpowa include one all-stage resistance gene, *Yr-Alp*, which was mapped to chromosome 1B but is no longer effective in the Pacific Northwest, and one named gene for HTAP resistance, *Yr39*, on chromosome 7BL (Lin and Chen, 2007; Rosewarne et al., 2013). The main stripe rust resistance locus in Louise is the QTL *QYrlo.wpg-2BS* for HTAP resistance (Table 2; Carter et al., 2009). Although the population segregated for resistance, there were no strongly resistant RILs, indicating that the all-stage resistance gene was ineffective and the RILs contain one, both, or no adult plant resistance genes. These breeding lines may provide sources of multigenic adult-plant resistance to stripe rust that can be combined with seedling resistance to increase durability to that disease (Fig. 2C).

Conclusions

Genes affecting developmental rate and flowering time can have a profound effect on drought tolerance. For example, the weak spring vernalization allele (*Vrn-B1b*) of Alpowa slows spring growth, allowing initial water conservation (Santra et al., 2009). Once the mild vernalization requirement of Alpowa is met, its photoperiod insensitivity (*Ppd-D1a*) results in rapid growth and possibly escape of drought-stress conditions. Louise, in contrast, has no vernalization requirement due to two strong spring *Vrn-A1a* and *Vrn-B1a* alleles and is photoperiod sensitive (*Ppd-D1b*). Thus, Louise must use different strategies to acclimate to drought. Preliminary results suggest that Alpowa and Louise differ for both root architecture and water use efficiency traits (K. Sanguinet, B. Ghimire, L. Murphy, unpublished data).

The Louise/Alpowa RIL population provides a resource for mapping and as breeding lines segregating for differences in stress tolerance and for genes governing flowering time and development. Because this population was derived from cultivars well adapted in the inland Northwest, it is an excellent resource for plant breeding in that region. It is also an interesting population to examine the impact of phenology on stress tolerance and for investigating the genetic control of plant height when alleles at the *Rht* loci are fixed.

Availability

Seed of the Louise/Alpowa population and the Louise and Alpowa parents used to generate the population 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 from the corresponding author for research purposes. Five hundred seeds from each RIL (F_8) have been deposited in the USDA–ARS National Laboratory for Genetic Resources Preservation, where they will become available 5 yr from date of publication. It is requested that appropriate recognition of the source be given when the population contributes to the research or development of new genetic stocks, molecular tools, germplasm, and improved cultivars.

Supplemental Material

Three supplemental files are available with this article:

- Supplemental Fig. S1: Visualization of the genetic linkage map with the known genes.
- Supplemental Table S1: The haplotype and genetic map info formatted for rQTL.
- Supplemental Table S2: KASP marker primer information and sequences.

Acknowledgments

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