

Stocking the Breeder's Toolbox: An update on the status of resistance to stem rust in wheat

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Abstract

The number of designated stem rust resistance genes has increased by ~10 over the past four years. Translocations involving several broadly-effective alien resistance genes with limited or no previous agricultural deployment were engineered to reduce the likelihood of linkage drag, and the foundations of adult plant resistance were established. This progress resulted from international collaboration, increased global coordination, and critical financial support. By building on these initial accomplishments and improving genetic and genomic resources over the next four years we expect to achieve: 1. more than 10 additional formally designated stem rust resistance genes conferring resistance to Ug99-complex races, 2. robust/diagnostic DNA marker haplotypes identified for most sources of resistance, 3. multiple linkage blocks of two or more resistance genes to enhance gene pyramiding efforts, and 4. knowledge of numerous additional sources of resistance completely or partially identified. Never before have so many resources and supporting tools been available to combat the wheat rusts. It is an opportune time for the international community to strategically deploy and responsibly steward our genetic resources for durable control of wheat stem rust.

Introduction

A primary focus of pre-breeding research supported as part of the Durable Rust Resistance in Wheat (DRRW) project is to fundamentally change how host resistance to stem rust of wheat is selected and deployed. Simultaneous pursuit of effective sources of resistance from readily accessible gene pools, introgression and cytogenetic manipulation of new sources of resistance from alien gene pools, genetic mapping and development of diagnostic DNA markers for desirable sources of resistance, determination of optimal combinations of resistance genes, and germplasm development is expected to provide the materials and information to strategically confront stem rust in the coming years on a global scale in way never before possible.

Approximately 30 major genes (genes with noticeable seedling, all-stage resistance) conferring resistance to Ug99-complex races, plus at least five designated adult plant, or slow-rusting, resistance genes that contribute to stem rust resistance and ~10 additional consistent stem rust QTL have been identified to date. Several additional newly discovered resistance loci/sources are at various stages of development and validation. The following summaries provide updates for many of these genes, and most are part of ongoing DRRW research efforts. DRRW collaborators urge breeders and geneticists throughout the world to use these resources in a responsible and strategic manner, and to combine three or more major genes in future varieties relying on race-specific resistance. Development of varieties with high levels of adult plant resistance, lacking major genes, is also especially encouraged.

Major genes (seedling, race-specific)

Sr13: A number of Ug99-complex resistant durum and cultivated emmer varieties contain *Sr13* on the long arm of chromosome 6A. High-resolution genetic mapping and positional cloning of *Sr13* are underway for cloning and development of diagnostic DNA markers (Simons et al. 2011; Dubcovsky et al. unpublished).

Sr22: The region surrounding this *Triticum monococcum*-derived resistance gene introgressed to chromosome 7AL was modified to minimize the *T. monococcum* chromatin, and useful DNA markers were identified (Olson et al. 2010; Periyannan et al. 2011). High resolution mapping and positional cloning are also underway (Rouse and Lagudah unpublished). *Sr22* was deployed in one Australian cultivar (McIntosh et al. 1995); deployment is not documented in other wheat production areas, but many programs are currently using *Sr22* in resistance breeding efforts.

Sr25: Robust DNA markers for *Sr25* were identified (Liu et al. 2010), enabling selection of this *Thinopyrum ponticum*-derived alien resistance on chromosome 7DL. CIMMYT germplasm containing *Sr25*, and presumably *Lr19*, in combination with *Sr2* was recently released in Afghanistan (Muqawim 09), Egypt (Misr 1, Misr 2), and Pakistan (NR356) (<http://www.globalrust.org/traction/project/varieties>).

Sr26: New translocation stocks with reduced *Thinopyrum ponticum* chromatin containing *Sr26* on chromosome 6AL were identified (Dundas unpublished). PCR-based markers that allow for routine detection (Liu et al. 2010) can be used to identify these smaller translocations. Australian varieties with the original translocation developed by D.R. Knott have been grown for over 30 years (McIntosh et al. 1995); deployment of *Sr26* is not documented in the rest of the world presumably due to real or perceived evidence of linkage drag preventing realization of other traits, but many programs are currently using the new translocation derivatives in resistance breeding efforts.

Sr28: While widely ineffective against most isolates of *Puccinia graminis*, *Sr28* does confer resistance to races in the Ug99 complex. *Sr28* is of common wheat origin (Kota and Ceres) and recently reported DNA markers should aid in identification of germplasm with this gene (Rouse et al. 2012). A single nucleotide polymorphism (SNP) marker for *Sr28* has been tentatively identified, and appears diagnostic based on genotyping and phenotyping of ~1000 wheat lines from a world collection (Rouse and Pumphrey unpublished). An effort to recombine *Sr28* with other effective stem rust and stripe rust resistance genes in a single linkage block on chromosome 2B is also underway (Rouse and Xu unpublished). If linked to other effective genes, such as *SrGabo56* and *Sr47*, and used in combination, *Sr28* may be useful in wheat breeding for Ug99 resistance.

Sr32: Dundas and others (unpublished) recently developed several recombinant translocation stocks with reduced *Aegilops speltoides* chromatin harboring *Sr32* on chromosome 2DS. DNA markers have not been reported for these new lines, but several laboratories have identified markers that successfully identify the original translocation. Deployment of *Sr32* has not been reported, but several programs are actively using the new translocation derivatives in resistance breeding efforts.

Sr33: Documented deployment of *Sr33*, an *Aegilops tauschii*-derived gene on chromosome 1DS, is limited to Australia in the cultivar Lorikeet (Park and Bariana 2008). Single gene lines with *Sr33* show an intermediate level of resistance as adult plants in the screening nurseries in Kenya (Jin et al. 2007). The *Sr33* gene was genetically mapped (Sambasivam et al. 2008) and cloned by a map-based approach (Lagudah et al. unpublished).

Sr35: DNA markers for *Sr35* were developed (Zhang et al. 2010), and candidates were identified by map-based cloning (Dubcovsky et al. unpublished). Virulence to *Sr35* is relatively common throughout the world (McIntosh et al. 1995, and references cited therein; Rouse and Jin unpublished), and while it does confer near immunity to Ug99-complex races, resistance gene combinations using *Sr35* should be chosen carefully.

Sr37: The original translocation stock with *Sr37* present in a large translocated segment of chromosome 4G from *Triticum timopheevii* to wheat chromosome 4B was not deployed because of obvious linkage drag problems (McIntosh et al. 1995). Recently, secondary recombinants with smaller alien segments were produced using the

ph1b system, but inheritance of resistance in these recombinants has been unstable to date and the usefulness of these stocks is uncertain (Xu et al. unpublished). DNA markers were developed that track these smaller alien segments.

Sr39: Multiple stocks with reduced *Ae. speltooides* chromatin segments harboring *Sr39* on chromosome 2BS were recently developed (Mago et al. 2009; Niu et al. 2011); useful DNA markers for those alien segments are also available. *Sr39* has not been previously deployed and virulence has not been detected to date. Several programs around the world are currently using *Sr39* in breeding.

Sr40: Dundas et al. (unpublished) developed four recombinants with reduced *T. timopheevii* chromatin surrounding this gene located on chromosome 2BS. DNA markers linked to *Sr40* in these recombinants were also identified (Wu et al. 2009), but markers useful in using the recombinant lines have not been published.

Sr42: *Sr42* is derived from common wheat germplasm. Recent genetic mapping of *Sr42* resulted in identification of closely linked DNA markers on chromosome 6DS (Ghazvini et al. 2012). The similar map position of this gene and *SrCad* (Heibert et al. 2011) suggests that *Sr42* and *SrCad* may be the same gene. *SrCad* is deployed in Canadian spring wheat varieties containing the bunt resistance gene *Bt10*.

Sr43: Xu et al. (unpublished) recently produced two putative translocation lines on chromosome 7D with *Sr43* from *Thinopyrum elongatum* and reduced alien chromatin. Further characterization of these lines is underway, along with identification of markers.

Sr44: Liu et al. (2012) developed a compensating 7DL.7JS Robertsonian translocation with *Sr44* from *Th. intermedium*. Homoeologous recombination to reduce the size of this translocation is underway. A second stem rust resistance gene from the same source and effective against isolates in the Ug99-race complex was identified on chromosome 7JL from the original donor stock. According to information for *SrAgi* (a synonym for *Sr44*) described in McIntosh et al. (1995) this latter gene was apparently not effective in early Australian studies because races virulent for *Sr44* were virulent on addition line TAF2 which carried an entire 7JS chromosome pair.

Sr45: *Sr45* is an *Ae. tauschii*-derived stem rust resistance gene on chromosome 1DS (Sambasivam et al. 2008). Deployment of *Sr45* has not been documented to date, but is possible due to the use of *Ae. tauschii*-derived germplasm in many programs; this gene is effective against TTKSK, but does not confer resistance to many other races found throughout the world. Due to their similar, but not identical, chromosome positions, efforts to recombine *Sr33* and *Sr45* into a linkage block on chromosome 1DS are underway (Lagudah unpublished). This should improve the value of deploying these genes.

Sr46: Genetic mapping of *Sr46* placed this *Ae. tauschii*-derived stem rust resistance gene on chromosome 2DS (Lagudah unpublished). *Ae. tauschii* accessions with *Sr46* are resistant to TTKSK in seedling tests (Rouse et al. 2011), but other characteristics of this gene have not been extensively documented.

Sr47: Faris et al. (2008) described *Sr47* in a large translocation involving wheat chromosome 2B and *Ae. speltooides* 2S. Recombinants with reduced alien chromatin were recently produced by homoeologous recombination and *Sr47* was located on a small segment on chromosome 2BL along with supporting DNA markers (Klindworth et al. 2012). *Sr47* confers seedling resistance to all races tested to date. A second gene, possibly *Sr39*, was identified in the short arm of the original translocation line with *Sr47*.

Sr50: Originally temporarily designated *SrR* (Anugrahwati et al. 2008), this Imperial rye-derived resistance gene is located in an interstitial translocation on chromosome 1DS. Preliminary data suggest that recombination with *Sr33* on 1DS to form a linkage block is not feasible (Lagudah et al. unpublished), but coupling with *Sr45* or other recently identified resistance genes on 1DS may be possible. *Sr50* could be an allele of *Sr31*, but has different race specificity and is contained in a different rye translocation. A further specificity involves the *SrAmigo* gene present in a 1AL.1RS translocation present in some plants of Amigo and again, the allelic status of this gene is unknown.

Sr51: Chromosome engineering of this resistance gene in *Ae. searsii* chromosome 3SS resulted in transfer to the short arms of chromosomes 3A, 3B, and 3D as compensating Robertsonian translocations (Liu et al. 2011a). Further chromosome manipulation to isolate small translocations with *Sr51* is targeting 3D as the recipient chromosome.

Sr52: This alien-derived gene from *Dasyphyrum villosum* is present in a compensating 6AL.6VS Robertsonian translocation line (Qi et al. 2011). Seedling resistance conferred by *Sr52* is temperature sensitive, and the utility of this gene in wheat improvement has not been fully determined.

Sr53: An interstitial translocation line was identified with the *Ae. geniculata*-derived resistance gene *Sr53* from chromosome 5M⁹L recombined in wheat chromosome 5DL (Liu et al. 2011b). DNA markers closely linked to *Sr53* were also reported. Seedling and adult plant screening of *Sr53* stocks indicate this gene provides a moderate level of resistance.

SrWeb (Hiebert et al. 2010) and **SrGabo56** (Rouse et al. unpublished) are both effective against TTKSK and linked to *Sr28* with similar map positions on chromosome 2BL. Whether *SrWeb* and *SrGabo56* are allelic or identical is not clear at present. Recombinants having *Sr28* and *SrGabo56* were developed and this linkage block is being further evaluated for potential to combine with one or more additional genes on chromosome 2BL (Rouse and Xu, unpublished). Deployment of two or more race Ug99-effective genes in coupling would simplify resistance breeding efforts and enable more complex pyramiding efforts.

Other resistance genes: Additional temporarily designated major genes preliminarily mapped and likely representing new sources of resistance include: *SrZelma*, *Sr1662*, *SrND643*, *SrTm4*, *SrB*, *SrC*, *SrSha7*, *SrNing* (Yu et al. 2009; unpublished). In addition, preliminary evidence indicates some genes previously characterized as ineffective against the race Ug99-complex, including *Sr12*, *Sr15*, and *Sr21*, may be moderately effective in certain environments and genetic backgrounds (Rouse unpublished). Characterizations of these genes are in variable stages of development. Additional novel sources of resistance are currently being characterized and introgressed from cultivated and wild tetraploids, *Ae. tauschii* and other *Aegilops* species, *D. villosum*, *T. monococcum*, and *Thinopyrum* species.

Adult plant resistance (APR) genes

Sr2: APR to Ug99-complex races conferred by *Sr2* on chromosome 3BS was validated in at least six recombinant inbred line populations characterized by CIMMYT (Bhavani et al. 2011), as well as in several other research efforts. An improved marker for *Sr2* is available (Mago et al. 2011), and continued efforts to develop “perfect” markers are underway. Significant interaction of markers linked to *Sr2* with markers linked to other resistance loci was detected in multiple association mapping panels (Yu et al. 2011, 2012). Many CIMMYT and other varieties internationally contain this gene in combination with other sources of resistance. *Sr2* is considered by many to be the foundation of APR breeding efforts.

Lr34/Yr18/Sr57: The pleiotropic effect of *Lr34*, located on chromosome 7DS, on stem rust APR has been noted in multiple publications, and supported by recent screening of *Lr34* loss-of-function mutants (Singh et al. unpublished). Interaction of *Lr34* with other loci contributing to adult plant resistance to Ug99-complex races was also recently documented (Kolmer et al. 2011; Yu et al. 2012), supporting earlier work by Kerber and others using North American *Pgt* races. Marker development (Lagudah et al. 2009) following cloning (Krattinger et al. 2009) now enables routine selection and detection of *Lr34* in diverse germplasm, with a couple of exceptions still under investigation. *Lr34* is common in CIMMYT-derived germplasm, but is also present in other germplasm internationally, including Chinese landraces.

Lr46/Yr29: QTL mapping of APR to Ug99-complex races in multiple populations in Kenya has detected consistent effects of a gene on chromosome 1BL, at a position consistent with the location of *Lr46* (Bhavani et al. 2011). Additional recent data suggests that *Lr46* contributes to stem rust APR, in a similar way to other “slow-rusting” genes (Singh et al. unpublished). DNA markers diagnostic for *Lr46* are not currently reported, but map-

based cloning of this gene is well advanced (Lagudah et al. unpublished). *Lr46* is probably common in CIMMYT and other germplasm.

Lr67/Yr46/Sr55: The recently identified *Lr67* locus confers a slow-rusting phenotype similar to *Lr34*, and its effect on stem rust APR was also validated (Herrera-Foessel et al. 2011; Singh et al. unpublished). Development of robust DNA markers linked to *Lr67* is underway.

Sr56: APR gene *Sr56* was located on chromosome 5B of cv Arina (Bansal et al. 2008; Bansal and Bariana, unpublished). QTL conferring resistance to race Ug99 were also consistently detected on chromosome 5B in both bi-parental (Bhavani et al. 2011) and association mapping (Yu et al. 2011, 2012). Based on these reports there may be at least two genes on 5B, and the relationship of *Sr56* and other QTL is not established. Continued mapping and marker development are in progress.

Ongoing characterizations of bi-parental and association mapping populations have indicated the presence of numerous other stem rust resistance loci, many likely contributing to APR. Seven consistent QTL were identified on chromosomes 1A, 2B, 3D, 4A, 5B, 6B and 7A in mapping populations screened in Kenya (Bhavani et al. 2011). Similarly, loci on chromosomes 1A, 1B, 2B, 4A, 5B, 6B and 7B were identified by association mapping of Ug99 resistance in spring and winter wheat germplasm from CIMMYT (Yu et al. 2011, 2012). The recent availability of DNA marker platforms for detailed rapid wheat genotyping is hastening characterization of these and other sources of resistance.

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