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# Genetic Analyses of Durable Adult Plant Resistance to Stripe Rust and Leaf Rust in CIMMYT Wheat Genotype 11IBWSN50

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## ABSTRACT

The CIMMYT wheat genotype 11IBWSN50 exhibited high levels of resistance to Australian pathotypes of stripe rust and leaf rust pathogens. Genetic analyses based on $BC_1$- derived $F_2$ and/or $F_6$ and $F_7$ families demonstrated the digenic and trigenic control of stripe rust resistance against *Puccinia striiformis* f. sp. *tritici* (Pst) pathotypes 134 E16A+ and 110 E143A+, respectively. Digenic inheritance of adult plant stripe resistance was observed when $BC_1F_6$ families were tested in Mexico. Comparison of rust response data across different experiments indicated that at least one of the adult plant stripe rust resistance genes was not effective against the Pst pathotype 134 E16A+ and the Mexican Pst pathotype Mex96-11. Four independent genes controlled leaf rust resistance in 11IBWSN50. Genotype 11IBWSN50 was observed to carry *Lr13*, which was effective against the *Puccinia. triticina* pathotype used to create field epidemic in this study. Marker genotyping demonstrated the presence of *Lr34*/*Yr18* and *Lr46*/*Yr29* in 11IBWSN50. Pedigree information also supported the presence of these gene combinations. Genotype 11IBWSN50 carried another uncharacterised gene for adult plant leaf rust resistance. High levels of adult plant resistance against leaf rust and stripe rust pathogens in 11IBWSN50 makes this genotype a suitable source of resistance in wheat improvement programs.

**Keywords:** adult plant resistance, genetic analysis, marker genotyping, *Puccinia striiformis* f. sp. *tritici*, *Puccinia triticina*

## INTRODUCTION

Rust diseases have been and still are among the important constraints to wheat production globally. The most common and widely distributed of all three rust diseases is leaf rust (Roelfs *et al.* 1992; Park *et al.* 2002; German *et al.* 2007; Kolmer *et al.* 2007). In Australia, leaf rust can be found in all the wheat growing regions, but it reached epidemic levels in 1992, 1999 and 2000 crop seasons in Western Australia (Park *et al*. 2002). While stripe rust of wheat, caused by *P. striiformis* f. sp. *tritici* (Pst), causes severe damage to wheat production throughout the cool and humid wheat growing regions of the world, it was reported for the first time in Australia in 1979 (O'Brien *et al.* 1980). The stepwise pathotypic evolution of Pst in Australia is summarised in Wellings (2007). The detection of the Pst pathotype, 134 E16A+, in Western Australia for the first time in 2002 added to the existing pathotypic variation. The Pst pathotype 134 E16A+ observed to have adapted to relatively higher temperatures than those traditionally thought to be congenial for stripe rust development.

One of the major objectives of wheat breeding programs is to deploy genetically diverse resistances to rust diseases in new cultivars. Resistance to rust diseases in wheat can be classified into two broad classes, seedling or overall resistance; where plants exhibit resistance at the seedling stage and usually remain resistant to avirulent pathogen isolates for their entire growth cycle and adult plant resistance (APR); where plants are susceptible at the seedling stage but develop resistance during post-seedling stages (Bariana and McIntosh 1995). The latter type includes both hypersensitive (race-specific) or non-hypersensitive (non race-specific resistance) expression of resistance. The non-hypersensitive resistance, sometimes referred to as slow rusting, is considered more important due to its potential durability (Caldwell 1968; Johnson 1984). Durability can however be independent of the type of resistance.

Most of the catalogued rust resistance genes are of seedling type and confer race-specific hypersensitive responses (McIntosh *et al.* 2003). Genetic bases of seedling resistances have been widely studied and these are assumed to follow the gene-for-gene relationship (McIntosh and Wellings 1986). Such resistances are often short-lived. In contrast, very little is known about the genetic basis of APR to rust diseases. The CIMMYT wheat genotype 11IBWSN50 showed high levels of APR to both stripe rust and leaf rust diseases of wheat in Australia. The present investigation was planned to study the inheritance of APR to stripe rust and leaf rust in 11IBWSN50.

## MATERIALS AND METHODS

### Host material and field design

The CIMMYT wheat genotype 11IBWSN50 (Robin/Chanate/Bluebird/Nortano 67) was crossed with the stripe rust susceptible parent 'Avocet S'. The $F_1$ plants were backcrossed with 'Avocet S' to generate $BC_1F_1$ population The $BC_1F_1$ plants were selfed to obtain $BC_1F_2$ families. Twenty seeds of each $BC_1F_2$ family were screened for adult plant stripe rust response to study inheritance of resistance. Thirty seeds of each generation, $BC_1F_3$ and $BC_1F_4$, were grown in the field and bulk harvested during 2000 and 2001 crop seasons, respectively. Thirty $BC_1F_5$ seeds were sent to CIMMYT, Mexico for rust screening. This material was grown under quarantine regulations and the $BC_1F_6$ population was tested in Mexico. Two seeds from $BC_1F_5$ bulk were grown in the greenhouse at the Plant Breeding Institute, Cobbitty (PBIC), Australia and after germination only one plant was allowed to grow to produce the $BC_1F_6$ population. The $BC_1F_6$ families were screened in the 2002 crop season for adult plant stripe rust response variation and bulk

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harvested. Thirty seeds of $BC_1F_7$ were tested during the 2003 crop season.

The CIMMYT genotype 11IBWSN50 was crossed with the leaf rust susceptible genotype WAWHT1382 ('Cunderdin Sib') to generate a population segregating for leaf rust response. The $F_1$ plants were backcrossed with 'Cunderdin Sib' to obtain $BC_1F_1$. The $BC_1F_1$ individuals were grown in the greenhouse, harvested and threshed individually. Thirty seeds from each $BC_1F_2$ family were grown in the field and screened for leaf rust resistance. A single seed descent $F_8$ population (234 lines) derived from 11IBWSN50/Hartog cross was kindly provided by Dr M. Cooper, University of Queensland, Australia.

A 60 cm row of each test genotype (30 seeds/row) was sown in the field in blocks of 50 experimental rows. Each 50 row block was surrounded by a 30 cm strip of susceptible spreader. Parental genotypes were sown as controls.

## Pathogen material and epidemic development

*Puccinia striiformis* f. sp. *tritici* (Pst) pathotypes 104 E137A-, 108 E141A+, 110 E143A+ and 134 E16A+, and *Puccinia triticina* (Pt) pathotypes 104-1,2,3,(6),7,11 and 76-1,3,5,10,12 were used to test parental materials at the seedling stage. Seedling infection types (ITs) were scored on a 0 - 4 scale as described in McIntosh *et al.* (1995).

The Pst pathotypes 110 E143A+ (1999 and 2002) and 134 E16A+ (2003) were used for creating artificial epidemics at the PBIC field site. The Pst pathotype 134 E16A+ was detected in Western Australia in 2002 (Wellings *et al.* 2003) and was widespread throughout Australia in 2003 (Wellings 2007). These pathotypes were virulent on the seedling resistance gene *Yr6* carried by 11IBWSN50. Similarly, the Mexican Pst pathotype Mex96-11 was also virulent on *Yr6*. The Pt pathotype 104-1,2,3,(6),(7),11 was used to create leaf rust epidemic.

For creating artificial epidemics, urediniospores were suspended in light mineral oil (Pegasol®) and were misted over spreader rows using an ultra low volume applicator (Microfit®, Micron Sprayer Ltd.) on late afternoons when overnight dew formation was expected. Leaf rust and stripe rust susceptible infection spreader rows served as source of inoculum for epidemic development. Frequent irrigation was applied to maximize moisture levels within the canopy. Same procedure was followed to create leaf rust and stripe rust epidemics.

## Disease assessment

Stripe rust and leaf rust responses were assessed when the susceptible parent developed 80% or higher disease. Rust assessments were made following either a modified Cobb's scale which combines percent severity (0-100) with the response type (R, R-MR, MR-MS, MS, MS-S, S) (Peterson *et al.* 1948) or on a 1 - 9 scale (Bariana *et al.* 2004a), where 1 equals very resistant and 9 very susceptible.

## Marker genotyping

DNA from test samples was isolated according to Doyle and Doyle (1990). PCR amplification and gel electrophoresis details for the *Lr34*-linked marker, csLV34, are described in Lagudah *et al.* (2006). The marker csLV34 and a recently developed *Lr46*-linked CAPS marker, csLV46, (E.S. Lagudah pers. comm.) was used to detect the presence of *Lr34* and *Lr46*, respectively, in parental genotypes 11IBWSN50, 'Hartog', 'Cunderdin Sib' and 'Avocet S'. Genotypes 'Janz' and the chromosome 1B substitution line, Lal Bahadur (Pavon 1B), were used as positive controls for *Lr34* and *Lr46*, respectively.

## Statistical analysis

Based on the phenotypic scores, $BC_1$-derived lines were grouped into segregating ($BC_1F_2$) or resistant ($BC_1F_6$ and $BC_1F_7$) and susceptible classes. Chi-squared analyses were carried out to check the goodness-of-fit of the observed segregations with the expected ratios for different genetic models.

# RESULTS

## Seedling studies

Parental genotypes 11IBWSN50, 'Hartog', 'Avocet S' and 'Cunderdin Sib' were tested against different Pst pathotypes (**Table 1**). 11IBWSN50 and 'Hartog' produced low IT; N against the *Yr6*-avirulent Pst pathotype 104 E137A-. 'Hartog' remained resistant against the *Yr6*-virulent Pst pathotype 108 E141A+, whereas 11IBWSN50 produced a susceptible IT3+. Both 11IBWSN50 and 'Hartog' showed susceptible responses against *Yr6* and *Yr7*-virulent pathotypes 110 E143A+ and 134 E16A+. These results indicated the presence of *Yr6* in 11IBWSN50 and 'Hartog'. In addition, 'Hartog' carried *Yr7*. 'Avocet S' produced susceptible response IT3+ against all Pst pathotypes. Cultivar 'Hartog' produced ITXN against Pt pathotype 104-1,2,3,(6),(7),11, whereas 11IBWSN50 and 'Avocet S' produced slightly different but low IT23N. 'Cunderdin Sib' was susceptible (IT3+). All genotypes, except 'Hartog', produced susceptible seedling responses (IT3+) against Pt pathotype 76-1,3,5,10,12. 'Hartog' carries *Lr1* which is effective against this *Lr13*-virulent Pt pathotype. These results indicated the presence of *Lr13* in 11IBWSN50.

## Inheritance of adult plant resistance

### *Stripe rust*

Parents 11IBWSN50 and 'Avocet S' supported high levels of sporulation during the seedling stages. The resistant parent 11IBWSN50 expressed low stripe rust responses at the

**Table 1** Seedling responses of genotypes 11IBWN50, Hartog, Avocet S and Cunderdin Sib against *Puccinia striiformis* f. sp. *tritici* (Pst) and *Puccinia triticina* (Pt) pathotypes.

| Genotype | Pst pathotype | | | | Pt pathotype | | Postulated gene(s) |
|---|---|---|---|---|---|---|---|
| | 104 E137A- | 108 E141A+ | 110 E143A+ | 134 E16A+ | 104-1,2,3,(6),(7),11,13 | 76-1,3,5,10,12 | |
| 11IBWSN50 | ;N | 3+ | 3+ | 3+ | 23N | 3+ | *Yr6*, *Lr13* |
| Hartog | ;N | ;N | 3+ | 3+ | XN | 0; | *Yr6*, *Yr7*, *Lr1*, *Lr13* |
| Avocet S | 3+ | 3+ | 3+ | 3+ | 23N | 3+ | *Lr13* |
| Cunderdin Sib | - | - | - | - | 3+ | 3+ | - |

**Table 2** Adult plant stripe rust responses of the parental genotypes at different sites during different years.

| Site | Year | Pst pathotype | Genotype | Adult plant response[a] |
|---|---|---|---|---|
| PBIC | 1999 | 110 E143A+ | 11IBWSN50 | 10MR |
| | | | Avocet S | 100S |
| PBIC | 2002 | 110 E143A+ | 11IBWSN50 | 2 |
| | | | Avocet S | 9 |
| CIMMYT | 2002 | Mex96-11 | 11IBWSN50 | 10MR |
| | | | Avocet S | 100S |
| PBIC | 2003 | 134 E16A+ | 11IBWSN50 | 4 |
| | | | Avocet S | 9 |

*Two different scales are described in the material and methods section.

**Table 3** Adult-plant stripe rust responses of 11IBWSN50/2*Avocet S - derived families at PBIC and CIMMYT during different years.

| Site | Year | Rust response[a] | | $\chi^2$ | | No. of genes |
|---|---|---|---|---|---|---|
| | | R | S | 3:1 (2genes) | 7:1 (3 genes) | |
| PBIC | 1999 | 53[b] | 8 | 4.60* | 0.02 | 3 |
| PBIC | 2002 | 53 | 8 | 4.60* | 0.02 | 3 |
| CIMMYT | 2002 | 44 | 18 | 0.53 | 15.49** | 2 |
| PBIC | 2003 | 49 | 14 | 1.27 | 5.44* | 2 |

[a]The R category included families with stripe rust responses up to 7 or 80MS-S and the S category included families with stripe rust responses equivalent to the susceptible parent.
[b] Segregating.
* Significant at P = 0.05 and 1 d.f.
**Significant at P = 0.01 and 1 d.f.

late tillering to early jointing stages. The adult plant stripe rust responses of parental genotypes at different sites, during different years are given in **Table 2**. Under Australian conditions 11IBWSN50 exhibited adult plant stripe rust responses varying from 2 to 4 depending upon the pathotype used. At Mexico, it produced a score of 10MR. The susceptible parent 'Avocet S' showed susceptible responses (9 and 100S) at both places. The adult plant stripe rust segregation results scored during different years and at different locations are summarised in **Table 3**. Sixty one $BC_1F_2$ families derived from the cross 11IBWSN50/Avocet S were tested for stripe rust response variation in the field during 1999 crop season at PBIC against the Pst pathotype 110 E143A+. Chi-squared analysis of data conformed to segregation at three independent loci. Partitioning of 53 segregating families into two groups was performed for further validation of two genetic models. The first group included families segregating at three loci (7) and the second group included families segregating at 1-2 loci (45). Chi squared analysis using 1(7) : 6 (45) : 1 (8) model confirmed the involvement of three independent loci ($\chi^2$ = 0.71, non significant at P = 0.05 and 2 d.f.) in controlling low stripe rust response. Tests on $BC_1$-derived $F_6$ families at the PBIC during 2002 using Pst pathotype 110 E143A+ confirmed results from the 1999 crop season. The $BC_1F_6$ population was also tested at CIMMYT, Mexico and the Chi-squared analysis of data presented in **Table 3** indicated the presence of two APR genes for stripe rust resistance in 11IBWSN50. Similar results were obtained when $BC_1$-derived $F_7$ lines were tested against Pst pathotype 134 E16A+ at the PBIC during 2003.

### *Leaf rust*

Genotype 11IBWSN50 exhibited a resistant to moderately resistant response (10 R-MR) under field conditions. Seedling studies (**Table 1**) indicated the presence of *Lr13* in 11IBWSN50. *Lr13* was effective against the Pt pathotype 104-1,2,3,(6),7,11 used to create epidemic in the field. Parent 'Cunderdin Sib' was susceptible against this pathotype both at the seedling and adult plant stages.

Of 171 11IBWSN50/Cunderdin Sib-derived $BC_1F_2$ families, 15 showed homozygous susceptible responses equivalent to the susceptible parent 'Cunderdin Sib', when tested under field conditions. Chi-squared analysis of data (156 : 15) indicated segregation at 3 to 4 independent loci ($\chi^2_{7:1}$ = 2.19 and $\chi^2_{15:1}$ = 1.84, both non significant at P = 0.05 and 1 d.f.). Given that 30 seeds per line were sown, it was only possible to identify lines segregating at 1-2 loci. Based on phenotypic segregation the population was categorized into three components. The first category included lines that did not include any plant with leaf rust response level equivalent to the susceptible parent (segregating at >2 loci), the second category included lines that included one or more susceptible plants (segregating at 1-2 loci) and the third category included lines that were uniformly susceptible. After phenotypic partitioning, leaf rust response segregation did not conform to three gene model ($\chi^2$ 1:6:1 = 50.76, highly significant at P=0.01 and 2 d.f.), however, it was a good fit for four gene model ($\chi^2$ 5:10:1 = 1.85, non significant at P=0.05 and 2 d.f.) (**Table 4**).

**Table 4** Partitioning of 11IBWSN50/2*Cunderdin Sib ($BC_1F_2$) population into different classes based on phenotypic segregation for leaf rust response.

| No. of heterozygous loci | Observed frequency | Expected proportion[a] | Expected frequency | $\chi^2$ 5:10:1 |
|---|---|---|---|---|
| > 2 | 52 | 5 | 53.43 | 0.04 |
| 1-2 | 104 | 10 | 106.87 | 0.08 |
| Nil | 15 | 1 | 10.70 | 1.73 |
| Total | 171 | 16 | 171 | 1.85 |

[a] 5 (AaBbCcDd,+AaBbCcdd,+aaBbCcDd+AabbCcDd+AaBbccDd) : 10 (AaBbccdd+AabbCcdd+AabbccDd +aaBbCcdd+ aaBbccDd+aabbCcDd+Aabbccdd+aaBbccdd+aabbCcdd+aabbccDd) : 1 (aabbccdd).
Table value of $\chi^2$ at P = 0.05 and 2 d.f. = 5.99

**Table 5** Frequency of putative single gene lines in 11IBWSN50/Cunderdin Sib-derived $BC_1F_2$ population.

| Leaf rust response | Observed frequency | Expected frequency[a] | $\chi^2$ 1:2:1 |
|---|---|---|---|
| 10R - MR | 12 | 12 | 0.00 |
| 30-40 MR-MS | 28 | 24 | 0.66 |
| 60-70MS | 8 | 12 | 1.33 |
| Total | 48 | 48 | 1.99 |

[a] Based on the assumption that two APR genes produce similar response of 30-40MR-MS.

Genotypes putatively segregating at a single locus were examined further. Three types of response patterns were observed. **Table 5** lists the observed frequency of lines putatively segregating at a single locus. These response classes included 10R-MR, 30-40MR-MS and 60-70MS. The 10R-MR response was due to the presence of *Lr13* in 11IBWSN50. The other two types of low responses were attributed to the presence of APR genes. Almost double the number of lines showed a response of 30 to 40MR-MS indicating that two APR genes may have expressed a similar response.

### Tests on 11IBWSN50/Hartog–derived single seed descent (SSD) population

Genotypes 11IBWSN50 and 'Pavon 76' (a sister line of 'Hartog') were distributed in the same nursery and shared parents in common. A single seed descent population of 234 individuals derived from 11IBWSN50/Hartog was tested for adult plant stripe rust response variation in the field using Pst pathotype 110 E143A+. 11IBWSN50 and 'Hartog' were scored 2 and 4, respectively.

Almost equal number of lines were scored equivalent to the scores of parents 11IBWSN50 and 'Hartog'. Approximately 50% of lines were scored 3, equivalent to mid parental value (**Fig. 1**). Five lines (score 1) were scored better than both the parents and two lines scored (score of 6) clearly higher than both parents indicating transgressive segregations in both directions. Seventeen lines were scored 5, which was close in response to parent Hartog. Genotypes 11IBWSN50 and 'Hartog' carry two to three genes (this study) and two genes (H.S. Bariana unpublished results) for stripe rust resistance, respectively. Assuming genetic independence of resistance genes carried by 11IBWSN50 and

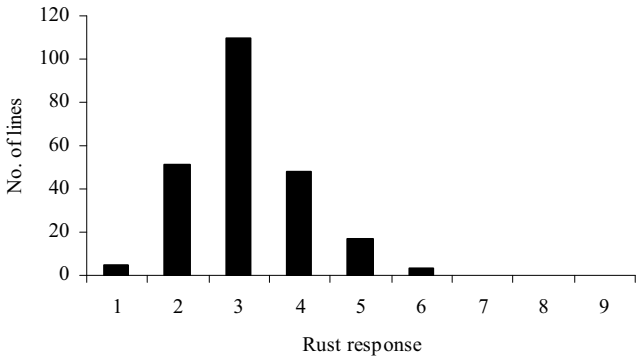


**Fig. 1** Frequency distribution of SSD lines derived from the cross 11IBWSN50/Hartog when tested against Pst pathotype 110 E143A+ under field conditions.

**Table 6** Genotypic status of parental genotypes with respect to markers csLV34 and csLV46.

| Marker/genotype | Marker allele[a] |
|---|---|
| **csLV34** | |
| Janz | b |
| 11IBWSN50 | b |
| Hartog | a |
| Cunderdin Sib | a |
| Avocet S | a |
| **csLV46** | |
| Lal Bahadur(Pavon 1B) | b |
| 11IBWSN50 | b |
| Hartog | b |
| Cunderdin Sib | a |
| Avocet S | a |

[a] b = present and a = absent

'Hartog', segregation at 4 to 5 independent loci in this population will be expected. Based on five gene model, a ratio of 31 resistant: 1 susceptible (score 9), would be expected. Absence of any susceptible segregants indicated that two genotypes share gene (s) in common.

### Marker genotyping of parental material

Genotypes 11IBWSN50 and 'Janz' amplified the *Lr34*-linked 'b' allele at the *XcsLV34* locus, whereas 'Hartog', 'Avocet S' and 'Cunderdin Sib' amplified the 'a' allele (**Table 6**). These results suggested the presence of *Lr34*/*Yr18* in 11IBWSN50. The 'b' allele at the *Lr46*-linked marker locus *XcsLV46* was amplified when DNA templates from 11IBWSN50 and the *Lr46* control Lal Bahadur (Pavon 1B) were used. The alternate allele 'a' was detected in 'Avocet S' and 'Cunderdin Sib'. These results indicated the presence of *Lr46*/*Yr29* in 11IBWSN50.

## DISCUSSION

Genotype 11IBWSN50 displayed high levels of APR to both leaf rust and stripe rust under Australian conditions since its distribution in the 11th International Bread Wheat Screening Nursery during 1976 together with 'Pavon 76'. Genetic analysis of adult plant stripe rust resistance against Pst pathotype 110 E143A+ indicated the presence of three APR genes in 11IBWSN50, whereas involvement of only two APR genes for stripe rust resistance was evident when Pst pathotype 134 E16A+ was used. Results from CIMMYT, Mexico also indicated the presence of two genes for APR to stripe rust. It appeared from this observation that one of the APR genes for stripe rust resistance was either not effective against Australian Pst pathotype 134 E16A+ and the Mexican Pst pathotype Mex96-11 or it produced near-susceptible responses when present alone. On comparing the stripe rust responses of homozygous susceptible lines from CIMMYT, Mexico with the $BC_1F_6$ responses, it was observed that 10 additional lines that produced a stripe rust response of 100S in Mexico exhibited a response of 80MS-S against Pst pathotype 110 E143A+ in Australia. Such observations were also made on other genetic populations (Diamondbird/Janz and Sunco/Tasman) segregating for adult plant stripe rust response (Bariana *et al.* 2004b, 2006). Genetic analysis of leaf rust resistance indicated the involvement of four genes for resistance. One of the genes was *Lr13* and the remaining three genes conditioned APR.

The CIMMYT cultivars 'Pavon 76' (Vcm//Cno/CC/3/Kal/Bluebird) and 'Parula' (Fkn/3/2*Frocor//Kenya-Ad/Gabo-54/4/Bluebird/Chanate) share pedigree with 11IBWSN50 (Robin/Chanate/Bluebird/Nortano 67). 'Bluebird' is the common parent among 11IBWSN50, 'Pavon 76' and 'Parula', whereas the parent 'Chanate' was only shared by 11IBWSN50 and Parula. Both 'Pavon 76' and 'Parula' carry the chromosome 1BL located stripe rust/leaf rust QTL, which was designated *Yr29*/*Lr46* and in addition 'Parula' carries *Yr18/Lr34* gene combination (Singh *et al.* 2005). Lagudah *et al.* (2006) reported a robust PCR based marker that was shown to detect the presence of *Lr34* in a range of germplasm (Singh *et al.* 2007; Kolmer *et al.* 2008). The amplification of *Lr34*-linked PCR product also indicated the presence of *Lr34/Yr18* gene combination in 11IBWSN50. The presence of *Lr46*/*Yr29* was expected in 11IBWSN50 based on pedigree information and absence of any stripe rust susceptible segregate among 11IBWSN50/Hartog (a sister line of 'Pavon 76') $F_8$ lines. 11IBWSN50 was also found to be positive for markers reported to be linked with the gene combination *Lr46*/*Yr29*. Identity of the third gene for leaf rust resistance remains unknown. Chromosome 7B of cultivar 'Parula' carries APR to leaf rust (R.P. Singh unpublished). 11IBWSN50 and 'Parula' share two parents, 'Bluebird' and 'Chanate', in common. Genotype 11IBWSN50 may also carry the chromosome 7B located leaf rust resistance gene.

This study demonstrated the marker based confirmation of APR genes in test genotypes. The availability of markers closely linked with APR gene combinations *Lr34/Yr18* and *Lr46/Yr29* proved very useful in determining the identities of genes carried by 11IBWSN50. Markers linked with several seedling stripe rust and leaf rust resistance genes have been reported by various workers and primer details are listed in Bariana *et al.* (2007). Pyramiding of seedling and APR genes can be assured in future wheat cultivars using a combination of molecular marker and phenotypic screening technologies.

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