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Genetic mapping of *Dn7*, a rye gene conferring resistance to the Russian wheat aphid in wheat

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Abstract The Russian wheat aphid is a significant pest problem in wheat and barley in North America. Genetic resistance in wheat is the most effective and economical means to control the damage caused by the aphid. *Dn7* is a rye gene located on chromosome 1RS that confers resistance to the Russian wheat aphid. The gene was previously transferred from rye into a wheat background via a 1RS/1BL translocation. This study was conducted to genetically map *Dn7* and to characterize the type of resistance the gene confers. The resistant line '94M370' was crossed with a susceptible wheat cultivar that also contains a pair of 1RS/1BL translocation chromosomes. The F_2 progeny from this cross segregated for resistance in a ratio of 3 resistant: 1 susceptible, indicating a single dominant gene. One-hundred and eleven RFLP markers previously mapped on wheat chromosomes 1A, 1B and 1D, barley chromosome 1H and rye chromosome 1R, were used to screen the parents for polymorphism. A genetic map containing six markers linked to *Dn7*, encompassing 28.2 cM, was constructed. The markers flanking *Dn7* were *Xbcd1434* and *XksuD14*, which mapped 1.4 cM and 7.4 cM from *Dn7*, respectively. *Dn7* confers antixenosis, and provides a higher level of resistance than that provided by *Dn4*. The applications of *Dn7* and the linked markers in wheat breeding are discussed.

Keywords Genetic mapping · RFLP · Insect resistance · Wheat breeding · Russian wheat aphid · Antixenosis

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Introduction

The Russian wheat aphid (RWA, *Diuraphis noxia*, Mordvilko) is one of the most destructive pests in wheat and small-grain cereals in several areas of the world (Archer and Bynum 1992). The RWA was introduced to the United States in 1986 via the Texas Panhandle (Stoetzel 1987). The pest causes leaf rolling and streaking, head trapping, and even death in heavily infested plants (Quick et al. 1991). Direct economic losses in small grains incurred from reduced yield and increased-production costs in the United States from 1985 to 1995 were estimated to be >$485 million (Morrison and Peairs 1998; Webster et al. 2000).

The use of resistant varieties is the most effective means of controlling this pest. For almost two decades, there has been a worldwide effort by wheat breeders to identify and incorporate new sources of genetic resistance to the RWA (Du Toit 1987, 1989). The first sources of resistance to RWA were identified from wheat that originated from countries where the pest is endemic, namely the former Soviet Union, the Balkans, Iran, Turkey and throughout the rest of the Middle East (Harvey and Martin 1990; Zemetra et al. 1990; Du Toit 1992). Dominant RWA resistance genes have been identified in wheat germplasm accessions including *Dn1* in PI 137739, *Dn2* in PI 262660 (Du Toit 1989), *Dn4* in PI 372129 (Nkongolo et al. 1991b), *Dn6* in PI 243781 (Saidi and Quick 1996), *Dn8* and *Dn9* in PI 294994, and *Dnx* in PI 220127 (Liu et al. 2001). PI 292994 was first hypothesized to contain a single dominant gene called *Dn5* (Marais and Du Toit 1993), but later shown to contain more than one gene in some plants. Three modes of inheritance were observed in PI 292994: a single

dominant gene, two dominant independent genes, or one dominant and one recessive gene conferring resistance to RWA (Zhang et al. 1998). All these resistance genes have been genetically mapped using molecular markers (Ma et al. 1998; Myburg et al. 1998; Venter and Botha 2000; Liu et al. 2001, 2002; Miller et al. 2001).

RWA resistance has also been found in related species of wheat. A recessive gene *Dn3* was identified in *Aegilops tauschii* line 'SQ24' (Nkongolo et al. 1991a). Resistant accessions were found in *Triticum monoccocum* (Du Toit 1987). In triticale, Nkongolo et al. (1992) identified four resistant Russian accessions, PI 386148, PI 386149, PI 396150 and PI 386156, which all showed a superior level of resistance compared to resistant wheat lines (Nkongolo et al. 1992, 1996). The resistance gene in PI 386150 was determined to come from chromosome 4R of *Secale montanum* Guss. (Nkongolo et al. 1996).

A dominant gene for RWA resistance, *Dn7*, was transferred from chromosome arm 1RS of rye (*Secale cereale* L.) into a wheat background via the 1RS/1BL chromosome translocation of wheat cultivar 'Gamtoos' (Marais et al. 1994). The resultant wheat line contains *Dn7*, as well as resistance genes for leaf rust (*Lr26*) and stem rust (*Sr31*) (Marais et al. 1994). The 1RS chromosome from 'Gamtoos' also contains resistance genes for stripe rust (*Yr9*) and powdery mildew (*Pm8*) (Friebe et al. 1989; Baum and Appels 1991). All four resistance loci are tightly linked with each other (Singh et al. 1990). *Dn7* was linked to *Lr26* with a distance of 14.5 ± 3.9 cM (Marais et al. 1998).

Host resistance to the RWA is based on tolerance, antixenosis or antibiosis (Webster et al. 1987). Tolerance is the ability of the plant to grow when infested with aphids. Antixenosis refers to non-preference by aphids for a host and is measured by the number of adult aphids per plant (Kogan and Ortman 1978). Antibiosis is measured by a significantly reduced fecundity in aphids (i.e. the number of nymphs per aphid) grown in a plant and can occur together with tolerance or antixenosis. The incorporation of different types of resistance would provide plants with a wider range of responses to the aphid.

The objectives of this study were to genetically map *Dn7* using DNA markers and to characterize the type of resistance conferred by this gene.

Materials and methods

Plant materials

Seeds of RWA resistant wheat line '94M370' [(CS/Turkey77//CS-Imperial addition 6R) = F_2 plant with 42 = t1RS/3/Gamtoos/4/Inia66/5/3/3*W84-17)] (Marais et al. 1994) and RWA susceptible wheat cv 'Gamtoos' were obtained from Dr. Frans Marais (University of Stellenbosch, Republic of South Africa). The 1RS/1BL chromosome in '94M370' came from 'Gamtoos' and *Dn7* was transferred to this chromosome through a recombination with the 1RS telosome from Turkey77. '94M370' and 'Gamtoos', both containing 1RS/1BL translocation chromosomes, were crossed, and an F_1 plant was selfed to produce F_2 progeny. One-hundred and ninety four F_2 plants were selfed to produce F_3 families, and 143 of these were used for mapping. RWA resistant wheat cultivars 'Halt' and PI 262660 were infested with RWA side by side with '94M370' to compare the levels of resistance of these lines. 'Halt' and PI 262660 contain the RWA resistance genes *Dn4* (Nkongolo et al. 1991b) and *Dn2* (Du Toit 1989), respectively. Wheat cv 'Carson' was used as a susceptible control for RWA screening.

RWA resistance phenotyping

The F_3 families were screened for their reaction to RWA infestation in replicated experiments over 2 years. For the first screening, 194 F_3 families were used. Because of the small seed supply of some F_3 families, only 143 families were re-screened for RWA reaction in the 2nd year. Seeds were planted in greenhouse flats in single rows consisting of 10–15 F_3 seeds per family and infested with aphid instars as described by Nkongolo et al. (1989). Individual seedlings within a row were scored and the average score per row was calculated. 'Carson' and 'Tam 107' served as susceptible controls while 'Halt' was used as the resistant control. The parents, '94M307' and 'Gamtoos', were also included.

The RWA damage was rated at 7, 14, 21 and 28 days after infestation. Leaf chlorosis, loss of chlorophyll and leaf rolling were the components of the rating system. Leaf chlorosis was based on a 1 to 9 scale (Quick et al. 1991), 1 being plants apparently healthy with very small isolated chlorotic spots or no spots at all, and 9 being dying or already dead plants. The second component measured the degree of leaf rolling. Seedlings showing chlorotic spots (scores 1–4) and no leaf rolling were recorded as resistant, whereas seedlings with leaf streaking (scores 5–9) and tightly rolled leaves were classified as susceptible. F_2 genotypes (homozygous resistant, homozygous recessive or a heterozygote) were inferred from the segregation of the F_3 plants. Scores were averaged between the two replications within a year, and between the 2 years to come up with the RWA resistance genotype for each individual.

Type of resistance conferred by Dn7

The level of resistance conferred by *Dn7* was compared with resistance from two previously characterized genes, *Dn4* and *Dn2* (Ma et al. 1998; Liu et al. 2001, 2002). '94M370', 'Halt', 'PI262220', and the susceptible cultivars, 'Carson' and 'Gamtoos', were grown in 6-inch pots, with one plant per pot. Five plants for each genotype (five replications) were grown, and the pots were randomized in the greenhouse. Each pot was infested with 40 aphids. The number of aphids on each plant was counted 7 days after infestation and the average was determined for each genotype.

RFLP probes

Probes for RFLP markers previously mapped in wheat chromosome group 1, rye chromosome 1R and barley chromosome 1H were used in this study. These included genomic clones from *Aegilops tauschii* (KSU) (Gill et al. 1991), wheat genomic (WG and WRGA) and cDNA (PSR) clones (Devos and Gale 1993), rice genomic clones (RZ) (Causse et al. 1994), rye cDNA clones (IAG) (Philipp et al. 1994); pSec (Hull et al. 1991), barley genomic (ABC, ABG, MWG) and cDNA (ABC, BCD, CMWG) clones (Graner et al. 1991; Heun et al. 1991; Kleinhofs et al. 1993; Lapitan, unpublished), and oat cDNA clones (CDO) (Heun et al. 1991). Probes were labeled with ^{32}P by random priming according to Feinberg and Vogelstein (1983).

DNA isolation, Southern blotting and hybridization

Equal amounts of tissue were bulked from 10 to 15 F_3 plants per F_3 family. Tissue was collected from 2-week-old plants. DNA isolation was performed according to Ma et al. (1998). DNA concentrations were quantified utilizing a TKO 100 Hoefer

fluorometer (Hoefer Pharmacia Biotech, San Francisco, Calif.), standardized with calf thymus DNA (Gibco Invitrogen Corporation, Carlsbad, Calif.).

Four restriction enzymes, *Eco*RI, *Eco*RV, *Hin*dIII and *Xba*I, were used to cut genomic DNA from '94M370' and 'Gamtoos'. Blotting and hybridization were as previously described (Ma et al. 1998), except that hybridizations were conducted in a hybridization incubator (Robbins Scientific, Sunnyvale, Calif.) (Model 400). Membranes were exposed to Phosphor-Imager Screens (Molecular Dynamics, Sunnyvale, Calif.) for 2 to 7 days depending on the relative intensity of the signal. Images were scanned utilizing a Storm Scanner (Molecular Dynamics, Sunnyvale, Calif.). Digital images were visualized using the Image Quant software program (Molecular Dynamics, Sunnyvale, Calif.).

Statistical analysis

Chi-square analysis was performed on the segregation data for RWA resistance against a single, dominant-gene model. Chi-square analysis was also performed on the segregation data for the DNA markers. The accuracy and efficiency of marker-assisted selection for *Dn7* using the flanking markers were calculated using the empirical formula proposed by Peng et al. (2000).

Genetic mapping

One hundred and eleven RFLP markers were tested for polymorphisms between '94M370' and 'Gamtoos'. Probes showing polymorphisms were hybridized to Southern blots containing restriction-enzyme digested DNA from 143 F_3 families. Construction of the genetic map was performed using Mapmaker V. 2.0 (Lander et al. 1987) at a LOD value of 3.0. Map distances (centimorgan, cM) were calculated using the Kosambi function (Kosambi 1944).

Cytogenetic analysis

Root tips were collected from germinating seeds of '94M370' and 'Gamtoos', pretreated with ice-cold water, and fixed in 3:1 95% ethanol-glacial acetic acid. Chromosome spreads were prepared as described by Lapitan (1996). The C-banding technique was performed according to Friebe et al. (1989).

Results

Inheritance and type of resistance conferred by *Dn7*

Prior to making the cross between the parents '94M370' and 'Gamtoos', C-banding experiments were conducted on metaphase chromosome spreads of both lines to confirm the presence of a pair of chromosome 1RS/1BL. A pair of 1RS/1BL translocation chromosomes was identified in both lines based on C-banding patterns as previously described by Friebe et al. (1989) (data not shown).

The 143 F_3 families from the cross between '94M370' and 'Gamtoos' segregated for RWA resistance as follows: 47 homozygous resistant, 33 homozygous susceptible, and 63 heterozygotes. A chi-square test showed that the segregation ratio fits a one-gene genotypic segregation ratio (1:2:1) at $P = 0.10–0.25$, and a 3:1 resistant:susceptible phenotypic segregation ratio at $P = 0.6–0.7$. This indicates that a single dominant gene controls resistance to RWA.

The type of resistance conferred by *Dn7* was compared with resistance from two other genes, *Dn4* and *Dn2*. '94M370' showed a higher level of resistance compared

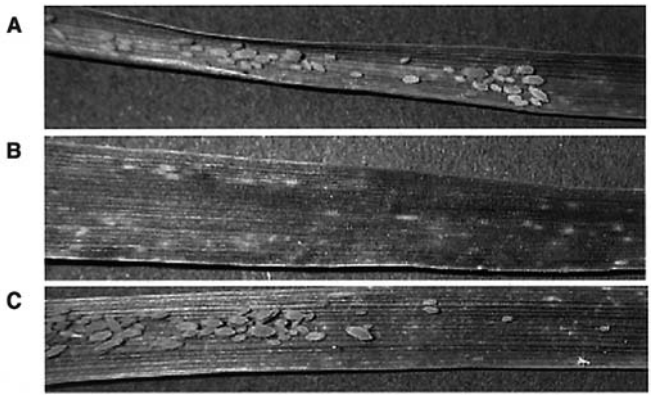

Fig. 1A–C Leaf sections of **A** 'Halt', **B** '94M370' and **C** 'PI262660', taken from plants 7 days after infestation with Russian wheat aphid

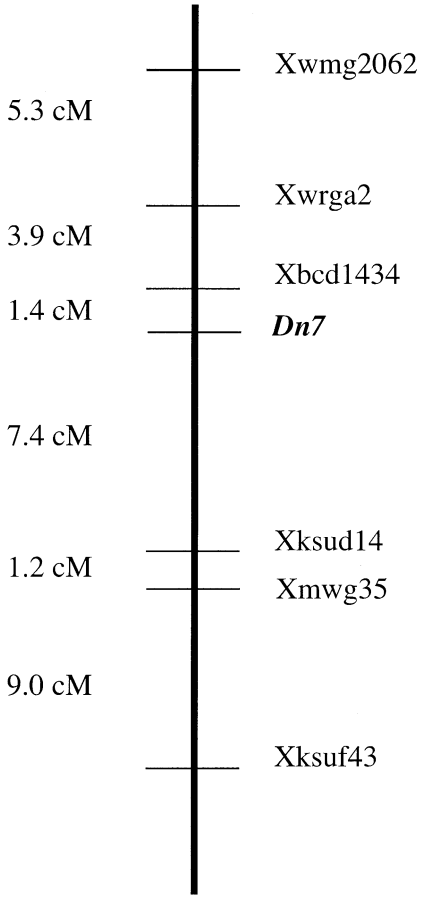

Fig. 2 Genetic map of *Dn7* showing six linked RFLP markers. The map is shown with the telomere side up and the centromere side down. Marker distances are not drawn to scale

Table 1 List of markers linked to *Dn7*, the size of polymorphic bands, linkage distances from *Dn7* and LOD values

Probe name	Size of polymorphic bands (in kb)	Linkage distance (in cM)	LOD score
Xmwg2062	13.0*	10.6	15.16
Xwrga2	23.0*	5.3	12.03
Xbcd1434	5.4*	1.4	24.01
Xksud14	4.4/4.0	7.4	35.99
Xmwg36	3.5*	8.6	19.13
XksuF43	23.0*	17.6	5.86

with 'Halt' (*Dn4*) and 'PI262660' (*Dn2*). On a rating scale of 1–9 as described above (1 = resistant, 9 = susceptible), '94M370' plants were scored as '1'. The plants showed no signs of leaf rolling or chlorosis, and showed an overall greater vigor than 'Halt' or PI '262660'. In addition, there were no aphids remaining on the plants 7 days after infestation, although leaf sections showed evidence of aphid feeding (Fig. 1B). 'Halt' and 'PI262660' were scored as '2', and '1', respectively, relative to '94M370'. 'Halt' exhibited mild leaf rolling (Fig. 1A). In addition, both 'Halt' and 'PI262660' harbored a large number of aphids (>100 per plant) 7 days after infestation (Fig. 1A, C). This suggests that resistance in '94M370' is based on antixenosis, whereas resistance in 'Halt' and 'PI 262660' is based on tolerance (Meyer et al. 1989; Smith et al. 1992). 'PI262660' was also reported to contain low-level antibiosis (Smith et al. 1992), which was not tested in this study.

Genetic mapping

Seventeen out of 111 RFLP clones (15%) detected polymorphisms between '94M370' and 'Gamtoos'. Of these, six markers were linked to *Dn7* (Fig. 2 and Table 1). The orientation of the linkage group in Fig. 2 was deduced based on comparison with previously published maps (Gale et al. 1995; Van Deynze et al. 1995; Boyko et al. 1999) (http://wheat.pw.usda.gov/ggpages/linemaps/Wheat/Trit1.html). The linkage group is shown with the short arm telomere on top and the centromere side at the bottom. The remaining 11 clones were not linked to *Dn7* or to each other at a LOD value of 3.0. The closest marker to *Dn7* was *Xbcd1434* at a distance of 1.4 cM. On the same side of the map, *Xwrga2* and *Xmwg2062* mapped 5.3 cM and 10.6 cM from *Dn7*, respectively. On the other side of *Dn7, Xksud14* was the closest marker at a distance of 7.4 cM. *Xmwg36* and *XksuF43* mapped 8.6 cM and 17.6 cM from *Dn7*, respectively.

Discussion

Genetics of *Dn7*

This paper reports the genetic mapping of *Dn7*, a rye gene on chromosome 1RS conferring resistance to the RWA (Marais et al. 1994). Because *Dn7* is present in a 1RS/1BL translocation chromosome, mapping was conducted in an F_2 population made from a cross between the resistant line '94M370' and a susceptible wheat that also contains a pair of 1RS/1BL chromosomes. The segregation of the F_2 progeny confirmed that resistance is controlled by a single dominant gene, consistent with previous results (Marais et al. 1994). Based on extensive synteny that chromosome 1R shares with homoeologous chromosomes in wheat and barley (Devos et al. 1992, 1993), RFLP markers previously mapped on wheat chromosomes 1A, 1B, 1D (Van Deynze et al. 1995), and barley chromosome 1H (Heun et al. 1991; Kleinhofs et al. 1993), were used, in addition to markers from chromosome 1R. The level of polymorphism (15%) observed between the parents was lower than that found between rye cultivars in other mapping studies. Korzun et al. (1998) and Ma et al. (2001) reported that 60% and 30.8%, respectively, of markers tested showed polymorphism between the rye parents used. The low level of polymorphism between '94M370' and 'Gamtoos' may be explained by the fact that these two share a common 1RS chromosome arm from 'Gamtoos' (Marais et al. 1994).

The genetic map of *Dn7* contains six RFLP markers spanning a total distance of 28.2 cM. One of the markers, *Xwrga2*, is a resistance-gene analog isolated from wheat using conserved sequence motifs within the nucleotide binding site – leucine rich repeat class of resistance genes (Spielmeyer et al. 1998). The markers *Xbcd1434, Xksud14, Xmwg36* and *Xksuf43* have all been previously mapped in wheat and have the same order as in the current map (Gale et al. 1995; Van Deynze et al. 1995; Boyko et al. 1999; http://wheat.pw.usda.gov/ggpages/linemaps/Wheat/Trit1.html).

Another RWA resistance gene, *Dn4*, was mapped on the short arm of the homoeologous wheat chromosome 1D (Ma et al. 1998; Liu et al. 2002). *Dn7* and *Dn4* share a common marker, *Xksud14* (Ma et al. 1998). More recent studies in our laboratory also showed linkage between *Dn4* and *Xbcd1434* and *Xwrga2* (unpublished data). These observations suggest that *Dn7* and *Dn4* may be orthologous. Mapping of additional markers may elucidate this question. If these loci are indeed orthologous, it will be interesting to determine the molecular basis for the difference in the type of resistance conferred by these two genes.

Application of *Dn7* and linked markers in wheat breeding

Rye has been a highly valuable source of genes for the enhancement of agronomically important traits in wheat. Rye chromosome 1R is one of the most-widely used sources of chromatin outside of the wheat genome for wheat improvement (see review by Baum and Appels 1991). However, chromosome 1RS also contains *Sec1* (Lawrence and Shepherd 1981), which codes for the rye endosperm protein, secalin. Secalin is highly undesirable in wheat because of the poor-dough qualities it produces for bread making. Dough derived from wheat cultivars containing the 1RS/1BL translocation is marked by stickiness, reduced strength and intolerance to overmixing (Dhaliwal et al. 1987; Graybosch et al. 1993).

It is possible to separate *Sec1* from the genes for disease resistance and yield, that are present in the 1RS arm as recently demonstrated (Lukaszewski 2000). The quality defect associated with the 1RS/1BL translocation was eliminated, while leaving the rust resistance gene complex intact by using a *ph1* mutant (Sears 1984) to induce homoeologous recombination between 1RS and wheat chromosome 1BS. 1RS/1BL translocations were recovered where *Sec1* was replaced by *Gli-1*/*Glu-3* loci from wheat. We are currently using this approach to separate *Dn7* from the *Sec1* locus in '94M370'.

The 'Kavkaz'-derived 1RS/1BL translocation in 'Gamtoos' is contained in several hundred wheat cultivars worldwide (Braun et al. 1998). Markers linked to the *Dn7* gene can be used in marker-assisted-selection to add *Dn7* to the repertoire of resistance genes already present in this translocation chromosome (Friebe et al. 1989; Baum and Appels 1991). PCR-based markers are ideal for marker-assisted selection. However, our attempts to identify single nucleotide polymorphisms in these markers were not successful. In the absence of PCR-based markers, RFLP markers still provide advantages over conventional screening methods. *Xbcd1434* showed a 99% accuracy of detecting resistance genotypes of *Dn7*. That is to say, 99.0% of the plants with the *Xbcd1434*-band were also resistant (either homozygous or heterozygous). Because it is a dominant marker, it can not distinguish the homozygotes from the heterozygotes. The other flanking marker, *Xksud14*, is a co-dominant marker and had a 97.5% accuracy of identifying homozygous-resistant plants. The efficiency of this marker (i.e., the number of plants that were homozygous for the marker among the homozygous-resistant plants) for identifying homozygous-resistant plants was 83.0%. When used together for marker-assisted selection, these two markers provide 100% and 82% accuracy and efficiency, respectively, for identifying *Dn7* homozygotes. In a conventional breeding process using selection based on aphid screening, the accuracy of obtaining the *Dn7* homozygous genotype in an F_2 generation is 33%. Using the flanking markers for selection, resistance to RWA could be fixed in the first segregating generation (F_2) without infestation with aphids.

Another advantage that marker-assisted-selection provides for breeding RWA resistance is an efficient way to pyramid two or more genes. *Dn4* has been incorporated into several wheat cultivars bred in Colorado (Haley, personal communication; Quick et al. 1996, 2001a, b, c), and the addition of *Dn7* to these cultivars would provide two types of resistance to the RWA. At present, pyramiding RWA resistance genes is difficult using conventional screening methods because there is only one aphid biotype in North America, although there are at least seven known biotypes world-wide (Puterka et al. 1992). Plants containing several RWA resistance genes may be better able to respond to the appearance of new biotypes. When conventional screening methods are used to pyramid two genes in a breeding program, resistant backcross progeny have to be selfed and segregation analysis performed to identify plants containing two resistance genes. Using DNA markers, this extra generation of selfing can be eliminated. The generation time required to produce cultivars containing two genes is therefore reduced by a half.

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