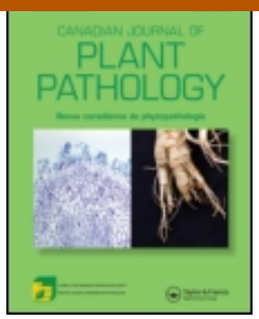

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Genetics and resistance/Génétique et résistance

A resistance gene to *Ustilago nuda* in barley is located on chromosome 3H

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Abstract: Loose smut of barley is a common disease which can be controlled using resistant varieties. Information on the chromosome location of loci controlling loose smut resistance and the development of molecular markers to aid in selection for these genes can be beneficial in the resistant variety development process. The objectives of this work were to determine the resistance or susceptibility of doubled haploid barley lines arising from a cross of the varieties 'Steptoe' and 'Morex' to *Ustilago nuda*, the causal agent of loose smut of barley, and map the chromosome location of the loose smut resistance locus in 'Morex'. The reaction to *Ustilago nuda* of the doubled-haploid barley plants was determined by inoculating spikelets of each line at anthesis by injection of a teliospore suspension using a needle inoculation method. Mature seeds from the inoculated spikelets were grown to determine the percentage of plants that developed with smutted heads. The lines were classified as susceptible if greater than 10% of the plants were smutted. The loose smut resistance locus from the resistant source 'Morex' was mapped using an existing DNA marker map of the 'Steptoe'/'Morex' population. The distribution of the resistant and susceptible progeny from the loose smut testing fit a single gene model. The resistance gene was mapped to chromosome 3 (3H).

Keywords: disease resistance, doubled haploids, loose smut, molecular markers

Résumé: Le charbon nu de l'orge est une maladie courante qui peut être contrée par l'utilisation de variétés résistantes. L'information relative à la localisation du loci responsable de la résistance au charbon nu sur le chromosome et le développement de marqueurs moléculaires servant à sélectionner ces gènes peuvent servir à développer des variétés résistantes. Le but de ces travaux était, d'une part, de déterminer la résistance ou la sensibilité des lignées d'orge diploïdes issues du croisement des variétés 'Steptoe' et 'Morex' avec *Ustilago nuda*, l'agent causal du charbon nu de l'orge et, d'autre part, de cartographier la localisation du site de résistance sur le chromosome de la variété 'Morex'. La réaction des plants d'orge diploïdes à *Ustilago nuda* a été déterminée en inoculant les épillets de chaque lignée au stade de l'anthèse en leur injectant une suspension de téléospores avec une aiguille. Arrivées à maturité, les graines provenant des épillets inoculés ont été semées afin de déterminer le pourcentage de plants dont les épis seraient charbonnés. Les lignées ont été classées « sensibles » si plus de 10 % des plants étaient charbonnés. Le site de résistance au charbon nu de la source résistante 'Morex' a été cartographié à l'aide d'une carte des marqueurs de la population 'Steptoe'/'Morex'. La distribution des descendants résistants et sensibles découlant des essais effectués avec le charbon nu correspond à un modèle à gène unique. Le gène de résistance a été cartographié sur le chromosome 3 (3H).

Mots clés: charbon nu de l'orge, haploïdes doubles, marqueurs moléculaires, résistance à la maladie

Introduction

Loose smut of barley (*Hordeum vulgare* L.), caused by *Ustilago nuda* (Jens.) Rostr., is a seed-borne disease found wherever barley is grown (Larter & Enns, 1962). It is a fungal infection which results in the inflorescence of the barley plant being largely replaced by sori containing

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teliospores of the pathogen (Bailey *et al*., 2003). This disease causes crop yield losses, but has little effect on seed quality. Yield loss is approximately equal to the percentage of infected plants within a field (Semeniuk & Ross, 1942; Morton, 1961).

Loose smut of barley is common in the northern Great Plains of the USA and the Prairie Provinces of Canada. This disease can be found in the majority of barley fields at levels of below 1% smutted plants, however, fields with 10–25% of the plants smutted can be found (Menzies *et al*., 1997; Popovic *et al*., 1998; B.J. Steffenson, unpublished data). The disease can be well controlled through the use of certified seed, smut-free seed (as determined using an embryo infection test), fungicidal seed treatment and resistant cultivars (Bailey *et al*., 2003).

The most economical and environmentally benign way of controlling loose smut of barley is the use of resistant cultivars. Genetic studies have found that resistance to *U. nuda* is generally conferred by single, dominant, independently inherited genes (Schaller, 1949; Metcalfe & Johnston, 1963; Metcalfe, 1966). However, the incorporation of loose smut resistance genes into new barley cultivars can be an arduous procedure because of the time and labour required for testing barley lines for resistance. The development of molecular markers and information on the chromosome location of loci controlling resistance to loose smut could be beneficial in the development of resistant cultivars.

The development of molecular genome maps of various crop plants has been useful in mapping genes to specific chromosome locations. One of the first and most widely studied molecular maps in barley is the 'Steptoe'/'Morex' population (Kleinhofs *et al*., 1993) developed by the North American Barley Genome Mapping Project (NABGMP). 'Steptoe' and 'Morex' were selected as parents in the mapping population because of their diversity in agronomic traits and good DNA polymorphism (Kleinhofs *et al*., 1993). 'Steptoe' is a high yielding, six-rowed feed-type barley derived from Washington selection 2546 and 'Unitan' (Muir & Nilan, 1973). 'Morex' is a Midwestern six-rowed malting-type barley derived from 'Cree' and 'Bonanza' and is known to carry resistance to loose smut (Rasmusson & Wilcoxson, 1979). 'Morex' is thought to have inherited one gene for loose smut resistance (the *Run1* gene) from 'Trebi' (Livingston, 1942; Schaller, 1949; Skoropad & Johnson, 1952). The objective of the present work was to assess the resistance of doubled-haploid plants from the 'Steptoe'/'Morex' population to *U. nuda* and use this information to map the loose smut resistance locus.

Materials and methods

A population of 97 doubled-haploid lines (Kleinhofs *et al*., 1993) was assessed for loose smut reaction. These lines were grown in 15-cm pots in growth cabinets at 16/22 °C day/night temperatures with 15 h light and 9 h dark. There were four lines per pot. Three seeds were sown per line and each line was allowed to develop two to three spikes. Two to three spikes of each doubled-haploid line were inoculated at anthesis by injection of a water suspension of teliospores of *U. nuda* isolate 01483 (1 g of teliospores L^{-1}) into the florets (filling the florets) using a 5 mL syringe with a 21–24 gauge, 2.5-cm needle (Menzies *et al*., 2009). Isolate 01483 of *U. nuda* was employed because of the differential reactions it elicited when inoculated to 'Morex' and 'Steptoe' (0% and 56% smutted plants grown from inoculated seed of the respective parents) in preliminary experiments. After seed maturation, the inoculated spikes from each line were harvested and threshed to collect the inoculated seed. The inoculated seed was then planted in soil beds in greenhouses (18/25 °C day/night, 16 h light/8 h dark) and the percentage of smutted plants from each doubled-haploid line assessed after spike emergence. In general, a minimum of 15 plants was required for a smut reaction assessment. The doubled-haploid lines were considered resistant if 10% or less of the plants were smutted and susceptible if greater than 10% of the plants were smutted. A χ^2 test was used to test the goodness of fit of the phenotypic data for Mendelian segregation.

The computer program MAPMAKER (version 2.0) and the phenotypic data on the resistance or susceptibility of the doubled haploid lines were used to map the loose smut resistance locus from the resistant source 'Morex' onto an existing DNA map of the 'Steptoe'/'Morex' population (Kleinhofs *et al*., 1993). Linkage maps were constructed based on a LOD (logarithm of odds) threshold of 3.0 and maximum Kosambi distance of 40 cM.

Results and discussion

Fifty-two of the inoculated plants had 0% of their progeny infected (Fig. 1) and were considered resistant, while 45 of the inoculated plants had greater than 10% of their progeny infected and were considered susceptible. A 10% division between resistant and susceptible reactions has been used previously in studies with *U. tritici* (Pers.) Rostr. and wheat (Heyne & Hansing, 1955; Nielsen, 1987; Knox *et al*., 2008). A system in which only a 0% infection level is considered resistant has also been used in studies with *U. tritici* and wheat (Knox *et al*., 2008; Randhawa *et al*., 2009) and *U. nuda* and barley (Eckstein *et al*., 2002).

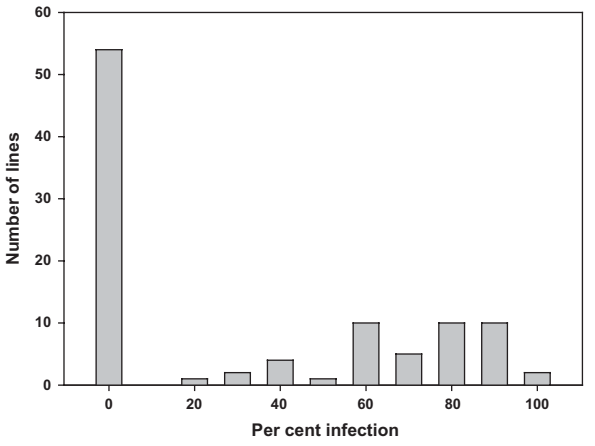

Fig. 1. The per cent infection of 97 doubled haploid lines from a population of the cross 'Steptoe'/'Morex' (Kleinhofs *et al*., 1993) inoculated with isolate 01483 of *Ustilago nuda*. The scale for per cent infection is 0 for 0% smutted plants, 10 for > 0 to 10% smutted plants, 20 for > 10 to 20% smutted plants, continued to 100 for > 90 to 100% smutted plants. Inoculation of 'Morex' resulted in 0% smutted plants and inoculation of 'Steptoe' resulted in 56% infected plants.

Either system would not have resulted in differences in the number of resistant or susceptible lines in this study. The results of the χ^2 test were in agreement with a single gene model (P = 0.477). The F_1 lines were not available for testing; thus, we cannot state if the resistance gene is inherited in a dominant or recessive manner.

The resistance gene identified in 'Morex' was mapped to Chromosome 3 (3H) bin15 in the *Glb4* to *iBgl* interval on the 'Steptoe'/'Morex' DNA map of Kleinhoffs *et al*. (1993). Previous mapping efforts for the *Run1* gene placed it on chromosome 1 (7H), linked to a stem rust resistance gene and a starch type gene (Shands, 1964; Franckowiak, 1997a, 1997b). Pomortsev *et al*. (2000) reported the loose smut resistance gene *Run6* was located on the long arm of barley chromosome 3 (3H), linked with a pubescence leaf blade gene. Their work involved the Canadian variety 'Keystone' as the donor for the *Run6* resistance gene. 'Keystone' (Johnston & Metcalfe, 1961) and 'Bonanza' (Wolfe *et al*., 1980) have the cultivar 'Jet' (C.I. 967) in both of their backgrounds. *Run6* was derived from 'Jet' (Skoropad & Johnson, 1952), so it is possible that Morex has inherited the *Run6* resistance gene through its parent 'Bonanza', and we have mapped *Run6*. We have given the gene of interest in this study the temporary locus symbol of *RunMx* (*Mx* referring to the resistant source 'Morex'). We have not conducted allelism studies with Morex and the source of *Run6*, so we cannot positively conclude that we have mapped the *Run6* gene. It is highly unlikely that we have mapped the *Run1* gene which has been previously reported to be the gene for loose smut resistance in 'Morex' (Livingston, 1942; Schaller, 1949; Skoropad & Johnson, 1952).

Numerous additional DArT (Diversity Arrays Technology), SNP (Single Nucleotide Polymorphism), EST (Expressed Sequence Tags) and TDM (Transcript Derived Marker) markers have been added to the original 'Steptoe'×'Morex' DNA map of Kleinhoffs *et al*. (1993) over the last few years (Rostoks *et al*., 2005; Wenzl *et al*., 2006; Marcel *et al*., 2007; Stein *et al*., 2007; Varshney *et al*., 2007; Potokina *et al*., 2008; Close *et al*., 2009). Some of these researchers published raw data that we used to expand the chromosome 3H bin15 map and identify closely linked and co-segregating markers (Fig. 2). These

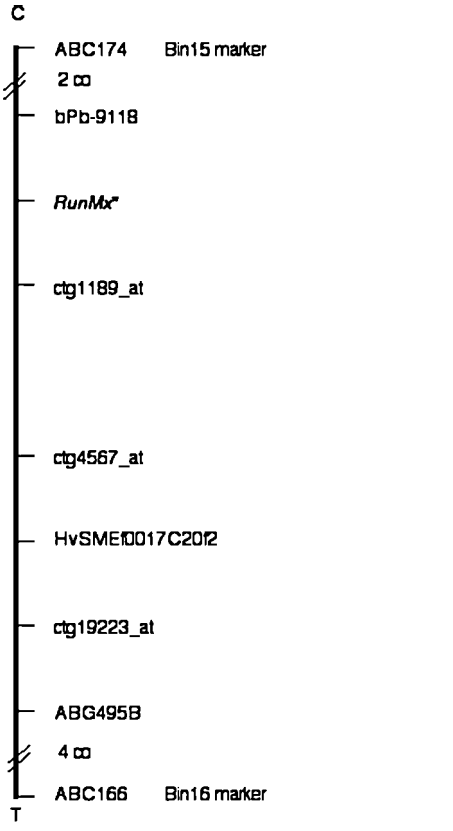

Fig. 2. The *RunMx* locus was integrated in the 'Steptoe'×'Morex' map of chromosome 3H (Kleinhoffs *et al*., 1993). Additional markers were mapped based on published raw data mapped on the 'Steptoe'×'Morex' doubled haploid population by Wenzl *et al*. (2006) (bPb-XXXX markers), Potokina *et al*. (2008) (ctg-xxxx markers), Close *et al*. (2009) (2-xxxx markers). The SSR markers are from Stein *et al*. (2007) (GBMxxxx and GBMSxxxx, 'Igri'×'Franka' population; EBmacxxx, 'Steptoe'×'Morex' population), Szucs *et al*. (2009) (Bmacxxx, OWB population).

Table 1. Molecular markers co-segregating with the barley loose smut resistance gene *RunMx* and their putative function.

Marker	Putative function/marker type
Glb4	b-glucanase
ctg20832_at	catalytic hydrolase (*Zea mays* 7e-08)
ctg25183_at	no significant homology
2_1272 (ctg10154_at)	Os01g0939600 protein
2_1376 (ctg11326_at)	cytosolic acetyl-CoA carboxylase
bPb-9599	DArT, sequence information contact 'a.kilian@diversityarrays.com'
bPB-2888	DArT, sequence information contact 'a.kilian@diversityarrays.com'
GBMS038	SSR, for primer sequence contact graner@ipk-gatersleben.de
GBM1288	SSR, for primer sequence contact graner@ipk-gatersleben.de
Bmac0144k	SSR, for primer sequences (Ramsay *et al*., 2000)
EBmac0541	SSR, for primer sequences (Ramsay *et al*., 2000)

could be used to develop PCR-based markers for molecular marker-assisted selection of *RunMx*. Co-segregating markers (Table 1) in a small population such as used here are not likely to identify gene candidates. Nevertheless, they provide a reference to potential collinearity regions in rice or *Brachypodium* which may result in identification of gene candidates. Unfortunately, if *RunMx* is the *Run6* loose smut resistance gene, its usefulness in breeding programmes in the northern great plains of the USA or the prairie provinces of Canada would be limited. The 'Jet' resistance, which included the *Run6* gene, was effective in Canada from 1961 to the mid-1970s, but in 1974, Thomas (1974) reported the occurrence of races of *U. nuda* which could overcome this resistance. The frequency of *U. nuda* collections virulent on barley lines possessing the *Run3* and *Run6* genes was reported as high (41–89%) into the 1990s in western Canada (Thomas & Menzies, 1997), suggesting that these genes are of little value in this area.

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