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A linkage map of diploid *Avena* based on RFLP loci and a locus conferring resistance to nine isolates of *Puccinia coronata* var. '*avenae*'

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Abstract An F_2 oat population was produced by crossing the diploid (n=7) species *Avena strigosa* (CI 3815) with *A. wiestii* (CI 1994), resistant and susceptible, respectively, to 40 isolates of *Puccinia coronata*, the causal agent of crown rust. Eighty-eight F_2 individuals were used to construct an RFLP linkage map representing the *A* genome of cultivated hexaploid oat. Two hundred and eight RFLP loci have been placed into 10 linkage groups. This map covers 2416 cM, with an average of 12 cM between RFLP loci. Eighty-eight F_3 lines, derived from F_2 individuals used to construct the map, were screened for resistance to 9 isolates of *P. coronata*. One locus, *Pca*, was found to confer a dominant resistance phenotype to isolates 203, 258, 263, 264B, 290, 298, 325A, and 345. *Pca* also conferred resistance to isolate 276; however, an unlinked second gene may also be involved.

Key words Genetics · Disease resistance · Monocots

Introduction

Puccinia coronata Corda var '*avenae*' W.P. Fraser and Ledingham, the causal agent of crown rust in oats, is one of the most important fungal pathogens of cultivated oat (*Avena sativa* L.). The host-plant response to this pathogen in oat is influenced by a specific gene-for-gene system (Simons et al. 1978; Nof and Dinoor 1981) similar to those documented for flax (Flor 1955), lettuce (Paran et al. 1991), maize (Hulbert and Bennetzen 1991), wheat (Milne and McIntosh 1990), and barley (Wise and Ellingboe 1985). The genetic control of resistance to crown rust in hexaploid oat has been reviewed (Marshall and Shaner 1992): 80 *Pc* genes conferring resistance to *P. coronata* have been named. However, allelic relationships are unclear, and their placement in the oat genome is unknown.

Investigations utilizing diploid *Avena* have been important sources of basic information and germ plasm. Genetic studies in diploid *Avena* identified single dominant genes for resistance to *P. coronata* among *A. strigosa* accessions CI 2630, CI 3815, and CI 7010 (Simons et al. 1959). Genes conferring resistance to three or more isolates were reported. Allelism tests indicated that the resistance genes in the three accessions were not allelic. Another study using CI 3815 observed a single gene conferring dominant resistance to one isolate, while resistance to two other isolates was determined by two independent dominant genes (Marshall and Meyers 1961). At least three loci in *Avena strigosa* conferring resistance to *P. coronata* have been previously observed. Resistance genes have been transferred from *A. strigosa* to *A. sativa* (Forsberg and Shands 1969; Rothman 1984; Sadanaga and Simons 1960). Several of the transferred genes confer resistance to isolates that are highly virulent on cultivated germ plasm and provide a degree of protection unavailable among hexaploid germ plasm.

The advantages of using diploid *Avena* to construct a linkage map and the value of such a map for investigating the genetics of hexaploid *Avena* have been described by O'Donoughue et al. (1992). In their investigation, a linkage map consisting solely of restriction fragment length polymorphism (RFLP) loci was developed from F_2 plants of an *A. atlantica*×*A. hirtula* population. To further investigate the genetic control of host-plant response to *P. coronata* in *Avena*, an RFLP map was constructed with a population from a cross between highly resistant and highly susceptible parents. A survey of infection types produced

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in response to inoculation with 47 isolates of *P. coronata* demonstrated that accession CI 3815 (A. *strigosa*) was resistant to 40 isolates and CI 1994 (*A. wiestii*) was susceptible to the same isolates (Wise and Gobelman-Werner 1993). We report herein the initial RFLP map and the placement of a locus conferring resistance to nine isolates of *P. coronata*.

Materials and methods

Plant material

The population was generated by crossing a USDA accession of *Avena strigosa* Shreb. (CI 3815) with a USDA accession of *A. wiestii* Steud. (CI 1994). Three F_1 seeds from a single panicle were self-pollinated to produce the F_2 generation used for mapping. A chi-square test of homogeneity verified the hypothesis that data from each of these plants could be combined into a single F_2 population ($0.90>P>0.70$). The DNA from 88 F_2 plants was used to construct the RFLP linkage map. The parents had been characterized for resistance to *P. coronata* (Simons et al. 1959; Wise and Gobelman-Werner 1993).

RFLP probes

One-hundred and seventy probes were isolated from a cDNA library constructed in the Unizap-XR phagemid vector (Stratagene, LaJolla, Calif.). The library represents genes expressed in the roots of 8-day-old etiolated oat seedlings (*Avena sativa* cv 'Lang'). Thirty probes were from other libraries. Sixteen CDO and 10 BCD probes were described by O'Donoughue et al. (1992) and identify RFLP loci on a map of a cross between diploid species *A. atlantica* and *A. hirtula*. The BCD, CDO, and 4 oat genomic clones (OGC) were provided by M. Sorrells (Cornell University). Probes were prepared and labelled as described by Veldboom et al. (1994).

DNA techniques

Total genomic DNA was isolated from leaves and stems of flowering F_2 oat plants. Methods for quantifying, digesting, separating, blotting, and hybridizing DNA were described by Veldboom et al. (1994).

Rust inoculum

Urediniospores were collected as previously described (Wise and Gobelman-Werner 1993). Isolates that were virulent on the greatest number of differentials and gave a distinct differential reaction between the *strigosa* parent (resistant) and the *wiestii* parent (susceptible) were chosen to increase the probability that these isolates would recognize single resistance genes in the mapping population.

Detection of *Pc* genes

Twenty-five seeds of each F_3 family were placed on moist filter paper at 4°C for 4 days to allow radicle emergence. This treatment resulted in uniform germination and growth prior to inoculation of seedlings. Imbibed seeds were planted in 20×30-cm test flats to produce 24 seedlings. 'Markton', 'CI 3815' (*A. strigosa*), and 'CI 1994' (*A. wiestii*) were included as controls. 'Markton' is a susceptible cultivar used to culture all *P. coronata* isolates at Iowa State University. At the one-leaf stage, seedlings were inoculated with a suspension of fresh urediniospores. Inoculations were conducted as described by Wise and Gobleman-Werner (1993).

Ten days after inoculation, seedlings were evaluated for their reaction to *P. coronata* using the standard crown rust infection type ratings (ITR) of 0, 1, 2, 3, or 4 as defined by Finkner (1954). Seedlings were evaluated individually to ascertain if the F_3 family was either homozygous resistant, heterozygous, or homozygous susceptible for the *Pc* gene identified by a particular isolate. A minimum of 16 plants was used to ensure 99% probability of observing a least one homozygous recessive individual in an F_3 family (Mather 1951). After the seedlings were evaluated, they were trimmed to a height of 2 cm. Four days later, newly emerged leaves were inoculated with a second isolate of *P. coronata*, again using fresh urediniospores.

Data analysis

Autoradiograms were scored independently by two experienced individuals. Genotypic data were entered into separate files and compared to identify errors. Chi-square goodness-of-fit values for segregation ratios were calculated using a program written using PC-SAS (K. Lamkey, personal communication). Linkage analysis was performed using "MAPMAKER" version 1.9 (Lander and Botstein 1987). Mapping procedures were described by Veldboom et al. 1994.

Results

Polymorphism within the mapping population

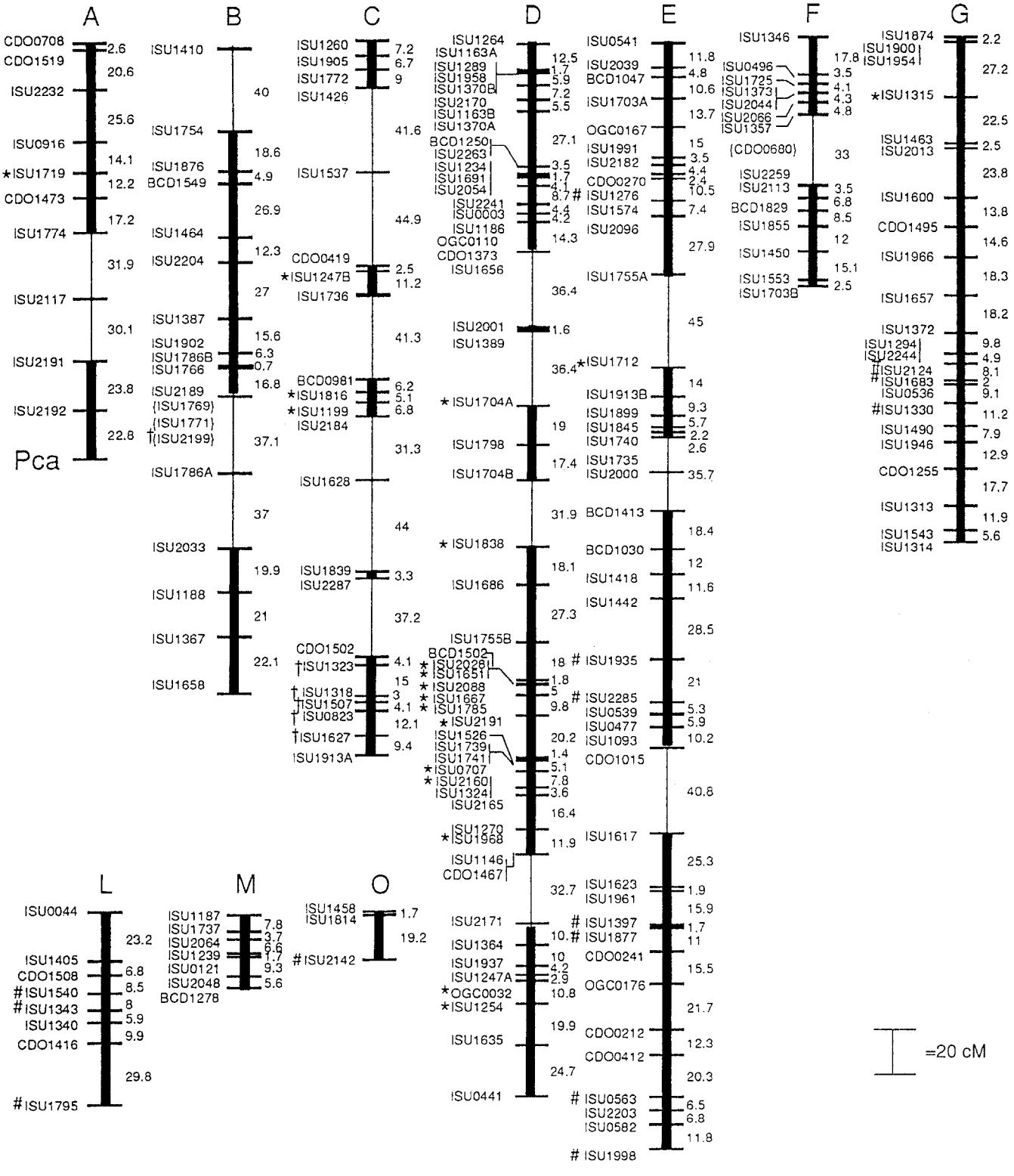
The parents were screened for RFLPs with 883 clones probed to DNA digested with two restriction enzymes. Of these clones, 681 detected low-copy sequences, and 202 detected moderately repetitive sequences. Of the 681 low-copy clones, 170 detected RFLPs between the resistant and susceptible parents. Of the 170 mapped ISU clones, 103 clones detected RFLPs with both enzymes, 35 detected RFLPs exclusively with *Hin*dIII, and 33 detected RFLPs solely with *Eco*RI. A total of 178 RFLP loci were detected by 170 ISU clones. Eight clones detected 2 loci identifying sequence duplications. After initial map construction, loci detected by 16 CDO, 10 BCD, and 4 OGC clones were placed into existing linkage groups identifying 30 additional loci.

Linkage map construction

The map is composed of 209 loci defined by 208 RFLPs and 1 locus for reaction to 9 isolates of *P. coronata*. Four RFLP loci were unlinked. Two-point linkage analysis was conducted on all 209 loci, and markers were sorted into distinct groups using an LOD score of 6.0 with a distance

Fig. 1 Linkage map of diploid *Avena* representing the *A* genome. With the aid of "MAPMAKER 1.9" (Lander et al. 1988) 208 RFLP markers and 1 locus (*Pca*) conferring resistance to *Puccinia coronata* were assigned to ten linkage groups (A–G, L, M, and O). *Numbers* on the *right* of a linkage group represent map distances in cM. Designations on the *left* are marker or gene names. Some allele frequencies displayed segregation ratios skewed toward the *strigosa* (*crosses*), *wiestii* (*#*), and heterozygote (*) genotypes, respectively. *Thin lines* represent regions between groups of markers linked by a LOD score greater than or equal to 3.0, but with a distance greater than 30 cM. *Thick lines* represent regions between markers linked by less than 30 cM at LOD 5.0

Avena strigosa x A. wiestii map



of 30 cM. This procedure produced 21 groups with 3 or more markers, 8 paired markers, and 21 unlinked markers. Three-point linkage analysis established 21 "framework" orders.

Linkage between the 21 unlinked markers, 8 paired markers and the 21 linkage groups was tested at a lower stringency (LOD=3, 30 cM). Four markers (ISU1383, ISU1780, ISU1792, and ISU1939) did not assort with any linkage groups. Fourteen of the previously unlinked markers and the 8 paired markers assorted with the existing 21 "framework" orders. Three of the previously unlinked markers formed a 22nd linkage group. Four "framework" orders linked to form groups C, D, and E. Two "framework" orders linked to form groups A, B, and F. When the same probes detected linked RFLP loci in two different mapping populations, the linkage group name designated by O'Donoughue et al. (1992) was used. The resulting map is composed of 10 linkage groups covering 2416 cM, with an average of 12 cM between loci (Fig. 1). The larger gaps, typically observed in intraspecific crosses, may reflect highly recombinogenic regions (Werner et al. 1992; Gill et al. 1991; Doebley and Stec 1991). If recombination distances greater than 30 cM (thin lines in Fig. 1) are discounted as overestimates, the map covers 1743 cM, a size observed for linkage maps of several diploid plant species including tomato (Tanksley et al. 1992), maize (Burr et al. 1988), and sorghum (Whitkus et al. 1992).

Of the 208 RFLP loci, 191 were defined by codominant alleles. Allelic ratios at most loci were in good agreement with expectations; however, at 39 loci codominant alleles segregated into genotypic ratios deviating from 1:2:1. Of these, 6 were skewed toward the homozygous *strigosa* genotype, 14 were skewed toward the homozygous *wiestii* genotype, and 19 were distorted toward the heterozygous genotype. Loci identified by alleles having distorted segregation ratios were observed on 7 of the 10 linkage groups (Fig. 1). Groups of 2 or more linked loci having segregation ratios distorted toward the same genotype were observed on linkage groups C, D, E, G, and L.

Eight clones detected RFLP loci that were duplicated in the genome. Three clones (ISU1163, ISU1370, ISU1704) detected duplicate loci that were linked within group D. One clone (ISU1786) detected 2 loci linked within group B. Four other clones detected duplicate loci in different linkage groups. Clones ISU1755, ISU1247, ISU1913, ISU1703 detected duplicate loci between linkage groups D and E, D and C, E and C, and E and F, respectively. Linkage group D demonstrated the most redundancy with at least one copy of 5 different duplicated loci.

Resistance to *Puccinia coronata*

Genotypes of F_2 individuals were determined from infection type reactions of F_3 families that were observed to be uniformly resistant, segregating in a ratio of 3 resistant to 1 susceptible individuals within the family, or uniformly susceptible, respectively. For 6 of the 9 isolates, segregation among F_3 families fit a 1 uniformly resistant : 2 segregating : 1 uniformly susceptible ratio at the 95% confidence level (Table 1). Segregation among F_3 families for isolates 264B and 290 fit a 1 resistant : 2 segregating : 1 susceptible ratio at the 90% confidence level. The hypothesis that a single dominant gene confers resistance to each isolate was rejected only for reaction to isolate 276. The segregation ratios among F_3 families for isolate 276 had a better fit to a 1 resistant : 8 segregating : 7 susceptible ratio. Linkage analysis placed resistance to all 9 isolates to a single region is at one end of linkage group A (Fig. 1).

Table 1 Segregations and chi-square goodness-of-fit tests of infection type on F_3 families derived from F_2 individuals[a] from a single cross between *Avena strigosa* and *A. wiestii*

Isolate	Order of inoculation[b]	Number of families			
		Resistant	Segregating	Susceptible	χ^2[c]
264B	1	15	51	12	8.14*
290	2a	10	49	19	7.61*
345	2b	14	43	18	2.47
325A	3a	19	42	19	0.08
203	3b	17	44	19	0.90
276[d]	4a	7	42	28	12.07**
263	4b	13	45	19	1.96
258	5a	16	40	16	1.42
298	5b	12	41	18	2.69

[a] DNA was extracted from the same F_2 individuals

[b] Different numbers indicate chronological order of inoculation of different flats of seedlings on different dates. Same numbers indicate identical flat inoculated on 1 day (a) with one isolate and then on another day (b) with a different isolate

[c] Chi-square values greater than or equal to this value would be expected by chance at probability (P):*P=0.05; **P=0.01. Chi squares were tested to a 1:2:1 ratio

[d] When tested to 1:8:7 ratio, χ^2=2.28; 0.30<P< 0.50

Discussion

Polymorphism within the mapping population

When compared to other interspecific crosses (O'Donoughue et al. 1992; Graner et al. 1991; Gill et al. 1991), a low level of polymorphism was observed. The root cDNA library yielded a majority of low-copy number clones (681 of 883) and 202 clones of moderately repetitive gene families. But only 171 of 681 low-copy clones (25%) detected RFLPs between the resistant and susceptible parents. This low level of polymorphism supports Ladizinsky's (1989) classification of *A. strigosa* and *A. wiestii* as morphological variants of the same biological species. An RFLP linkage map for diploid oat representing the *A* genome and covering 614 cM was developed by O'Donoughue et al. (1992) from a cross between *A. atlantica* and *A. hirtula*. The frequency of RFLPs between *atlantica* and *hirtula* detected with single digests of two enzymes (*Eco*RI and *Eco*RV) was 74%. In contrast, only 39%

of the clones detected RFLPs in the *strigosa/wiestii* cross using single digests of two enzymes. Thus, the parents used in our mapping study are more closely related and likely represent the same species.

Each enzyme detected nearly the same frequency of polymorphism. The observation that 109 of the 178 RFLPs detected by root cDNA probes were common to both enzymes suggests that 61% of the RFLPs are caused by mechanisms other than point mutations within the restriction endonuclease recognition sites. Insertions or deletions in DNA flanking the hybridization region are possible mechanisms (Gill et al. 1991, McCouch et al. 1988). Of the RFLPs 39% may have been caused by point mutations, since they were detected by only 1 restriction endonuclease.

Linkage map construction

The 7 largest linkage groups (A–G) range from 505 cM to 116 cM in length. These may represent the seven chromosomes of diploid *Avena*. Physical mapping using hexaploid monosomic stocks is in progress (Jellen et al. 1993). Of the 39 loci with alleles segregating in distorted ratios 33 were placed to 5 linkage groups (C, D, E, G, and L). Allelic frequencies at all loci of a "distortion cluster" were skewed toward the same genotype. Similar results were observed in RFLP linkage maps made from crosses of diploid oat (O'Donoughue et al. 1992), barley (Graner et al. 1991), and bean (Vallejos et al. 1992). Distortion clusters may result from selection occurring during several stages of the plant's life cycle (Zamir and Tadmor 1986). Inversions can also explain the appearance of distortion clusters (Vallejos et al. 1992).

Genetic distances in intra- and interspecific crosses

Greater recombination frequencies and, therefore, greater map distances have been observed for intraspecific crosses than for interspecific crosses of rice (McCouch et al. 1991), potato (Gebhardt et al. 1991), tomato (Rick 1969), and maize (Doebley and Stec 1991). Reduced recombination has been observed in interspecific crosses even when detailed cytogenetic analysis revealed normal pairing and chiasmata formation (Rick 1969).

To assess the possibility of different recombination frequencies in diploid oat crosses, 26 probes that detected RFLP loci on the *atlantica/hirtula* map were placed on the *strigosa/wiestii* map. Of 26 CDO and BCD probes from the *atlantica/hirtula* map, 11 detected loci that exhibited conserved linkage order in *strigosa/wiestii* linkage groups (Fig. 1, Table 2). The 3.6-fold reduction in recombination in the *atlantica/hirtula* cross for 5 syntenic loci on group E is consistent with the four fold decrease (2470 vs. 614 cM) in total length for the *atlantica/hirtula* map.

The difference in map sizes produced by two diploid oat crosses is consistent with previous comparisons of maps produced from intra- and interspecific crosses in maize. Doebley and Stec (1991) identified 8 pairs of markers that were linked by less than 25 cM on an interspecific maize-teosinte map. The same pairs of loci were linked by more than 40 cM on an intraspecific map. The diploid oat map (Fig. 1) depicts 20 regions linked by more than 30 cM (thin lines). These linkages have been constructed because the adjacent markers are at least 1000 times more likely to be linked to each other (LOD=3.0) than to any other markers on this map. Two markers linked by 32 cM on the *atlantica/hirtula* map (CDO1015, CDO0241) span a 97 cM region that includes a 40.8-cM gap (thin line) on linkage group E (Fig. 1). The possibility that the *strigosa/wiestii* map is constructed from an intraspecific cross while the *atlantica/hirtula* map is constructed from a much more divergent interspecific cross very likely accounts for much of the difference in map size.

Table 2 Comparison of recombination distances[a] in crosses of diploid *Avena*

Interval		Linkage group[b]	*strigosa/ wiestii*	*atlantica/ hirtula*
Locus 1	Locus 2			
CDO1473	CDO1519	A	70	70
CDO1502	BCD0981	C	134	43
CDO1467	BCD1502	D	78	8
BCD1413	CDO1015	E	113	6
CDO1015	CDO0241	E	97	32
CDO0241	CDO0212	E	37	31
CDO0212	CDO0412	E	12	3
CDO1495	CDO1255	G	117	56

[a] Recombination distances are calculated in cM using the Kosambi function (Kosambi 1944)

[b] When the same probes detected linked RFLP loci in two different mapping populations, the linkage group name designated by O'Donoughue et al. (1992) was used

Resistance to *P. coronata*

Resistance to isolates 203, 258, 263, 264B, 276, 290, 298, 325A, and 345 map to a single locus at the end of linkage group A. This locus is tentatively designated *Pca*, representing a major *Pc* locus from the *A* genome of *Avena*. The segregation pattern among F_3 families fit a ratio of 1 resistant : 2 segregating : 1 susceptible, consistent with a genetic model of a single dominant factor determining the resistant phenotype. Our observations agree with previously described reports of single genes conferring dominant resistance to *P. coronata* (Simons et al. 1959; Marshall and Meyers 1961). Resistance to isolate 276 may involve the *Pca* locus interacting with a second unlinked locus, because segregation ratios favor a two-gene model. Placement of resistance to isolate 276 in linkage group A im-

plies that at least one of the two genes may be at the same locus involved in resistance to 8 other isolates.

The lack of RFLP markers near the *Pca* locus was unexpected. This result may be a consequence of the kind of markers used to construct the map. Almost entirely, low-copy cDNA probes defined RFLP loci. The *Pca* locus may be inaccessible to this type of marker, perhaps due to a preponderance of repetitive sequences. Other marker systems such as randomly amplified polymorphic DNA (Williams et al. 1990) might identify markers in previously unmarked regions among repetitive sequences (Paran et al. 1991).

The genomes of tribe *Aveneae*, represented by *Avena* (oat), and tribe *Triticeae*, represented by *Hordeum* (barley), *Triticum* (wheat), and *Secale* (rye), share several features. All are members of the family *Gramineae* with a basic chromosome number of seven. DNA sequence homology is shared among barley, wheat, rye, and oat because some RFLP probes hybridize to genomic DNA across these genera (Hart and Gale 1990; Wang et al. 1992). Twelve barley cDNA clones detect RFLPs on the current map and 64 have been used by others (O'Donoughue et al. 1991). All four genera are parasitized by various species of *Puccinia*, and genes conferring resistance to them have now been placed on the genetic linkage maps of all four grasses (Sogaard and Weitstein-Knowles 1987; Milne and McIntosh 1990; Melz et al. 1992). Conservation of gene order among homoeologous chromosomes for loci encoding seed proteins, isoenzymes, and genes conferring resistance to obligate fungal biotrophs like *Puccinia* (rust pathogens) and *Erysiphe* (mildew pathogens) is observed for barley, wheat, and rye (Hart and Gale 1990; Milne and McIntosh 1990; Singh et al. 1990; Wang et al. 1992). Homoeologous relationships between chromosomes of *Avena* and the *Triticeae* are unknown. However, the linkage relationships identified by this study will contribute to a better understanding of host-pathogen interaction and the evolution of *Avena* and members of the *Triticeae*.

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