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# RFLP mapping of genes affecting plant height and growth habit in rye

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**Summary.** RFLP mapping of chromosome 5R in the $F_3$ generation of a rye (*Secale cereale* L.) cross segregating for gibberellic acid ($GA_3$)-insensitive dwarfness (*Ct2/ct2*) and spring growth habit (*Sp1/sp1*) identified RFLP loci close to each of these agronomically important genes. The level of RFLP in the segregating population was high, and thus allowed more than half of the RFLP loci to be mapped, despite partial homozygosity in the parental $F_2$ plant. Eight further loci were mapped in an unrelated $F_2$ rye population, and a further two were placed by inference from equivalent genetic maps of related wheat chromosomes, allowing a consensus map of rye chromosome 5R, consisting of 29 points and spanning 129 cM, to be constructed. The location of the *ct2* dwarfing gene was shown to be separated from the segment of the primitive 4RL translocated to 5RL, and thus the gene is probably genetically unrelated to the major GA-insensitive *Rht* genes of wheat located on chromosome arms 4BS and 4DS. The map position of *Sp1* is consistent both with those of wheat *Vrn1* and *Vrn3*, present on chromosome arms 5AL and 5DL, respectively, and with barley *Sh2* which is distally located on chromosome arm 7L (= 5HL).

**Key words:** RFLP – Rye – Dwarfism – Vernalisation – Genetic mapping

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## Introduction

Genetic mapping in rye (*Secale cereale* L.) (2n = 2x = 14) is of importance primarily for an understanding of the genetics of rye itself. Additionally, however, rye genes are a useful resource for wheat improvement. For example, the wheat/rye 1BL.1RS translocation, in which the rye segment carries genes for resistance to yellow rust (*Yr9*) (Mettin et al. 1973; Zeller and Fuchs 1983), leaf rust (*Lr26*) (Bartos et al. 1984), and stem rust (*Sr31*) (Hu and Roelfs 1986), may be associated with a positive effect on yield (Rajaram et al. 1983), though with a negative effect on bread-making quality (Zeller et al. 1982). The rye genome is also a constitutent of triticale, the wheat × rye hybrid.

Semi-dwarf gibberellin (GA)-insensitive wheats have been exploited worldwide, and have proven to be well-adapted to many environments (Gale and Youssefian 1985). For this reason rye collections were evaluated for similar genotypes, and two independent mutants, *compactum 2* and *1*, were selected (Börner and Melz 1988; Börner 1991). The genes determining this height reduction are on chromosome arms 5RL (*ct2*) and 7RL (*ct1*) (Sturm and Müller 1982; Melz 1989).

Among the most important genes for cereal production in cool climates, such as northern and central Europe, Asia and America, are those determining winter/spring growth habit. The spring growth habit gene (*Sp1*) in rye is located on the long arm of chromosome 5R (De Vries and Sybenga 1984; Melz 1989; Wricke 1991).

We report here experiments aimed at tagging the $GA_3$-insensitive dwarfing gene *ct2* and the spring growth habit gene *Sp1*, using RFLP techniques and to determine the genetic relationships of *ct2* and *Sp1* to their wheat and barley analogues.

## Materials and methods

*Plant material*

The primary mapping population consisted of 137 $F_3$ plants derived from a single $F_2$ plant of a cross between the variety 'Petka' (*Ct2*, *Sp1*) and the mutant 'Moskowskij Karlik' (*ct2*, *sp1*). The $F_2$ parent plant was heterozygous for both *ct2* and *Sp1*, as shown by segregation in the $F_3$ population. Five plants of 'Petka' ('P') and four plants of 'Moskowskij Karlik' ('MK') were included in the analysis. Use was also made of an $F_2$ population from a cross between the inbred lines 'DS2' and 'RxL10' ('D' × 'R'; described in Masojc and Gale 1991) to supplement the RFLP map.

*Morphological marker analysis*

Individuals of the $F_2$ and $F_3$ generations from the combination 'P' × 'MK' were classified for their response to exogenously applied $GA_3$ (Börner 1991). These determinations were confirmed by observations of adult plant height, for which the exploited population was scored (Fig. 1a). For *Sp1*, plants were grown without vernalisation in a glasshouse under continuous warm conditions. With this regime *sp1/sp1* genotypes failed to flower, but *Sp1/sp1* and *Sp1/Sp1* types were not inhibited (Fig. 1b). Putative *sp1* homozygotes (i.e., those which remained vegetative) were vernalised for 8 weeks at 4 °C, whereupon they reached flowering after transfer to warm conditions.

*DNA probes*

For the primary map, the probes used consisted of both anonymous [nine cDNAs, 14 single-copy and eight low-copy gDNAs, derived from various wheat libraries (Chao et al. 1989; Kam-Morgan et al. 1989; Cheung et al. 1992; Clark et al. 1992; Devos et al. 1992; Harcourt 1992)] and known-function sequences (sources of the eight used are given in the legend to Fig. 3). The probes were previously located (for low-copy clones at least one copy) to rye and/or wheat homoeologous group 5 chromosomes (Liu et al. 1992; Gale et al., unpublished). Chromosomal locations in rye were derived from analysis of the 'Chinese Spring' wheat/'Imperial' rye addition lines (Driscoll and Sears 1971), and wheat locations from the 'Chinese Spring' nullisomic-tetrasomic lines (Sears 1966). Arm locations in rye were inferred from those derived in wheat from the 'Chinese Spring' ditelosomics (Sears and Sears 1978).

*RFLP analyses*

Five grams of fresh leaf material from each plant were harvested before stem elongation, frozen in liquid nitrogen and freeze dried. DNA extraction, restriction enzyme digestion, agarose-gel electrophoresis, Southern blotting, probe labelling, and hybridisation were all as described by Devos et al. (1992). Nine different restriction enzyme digests were variously used: *Eco*RI, *Eco*RV, *Eco*RI + *Eco*RV, *Hin*dIII, *Dra*I, *Bgl*II, *Bam*HI, *Hae*III and *Taq*I. Map positions of polymorphic loci were derived by multipoint analysis using the computer programme 'Mapmaker' (Version 2.0) from E. S. Lander, Whitehead Institute of Biomedical Research, Cambridge/Mass. Normally a LOD score of $> 2.5$ was taken as the criterion for accepting a map position, but some loci were placed with lower LOD scores (as shown in Fig. 3). Recombination frequencies were transformed to centimorgans (cM) by the Kosambi function (Kosambi 1944).

## Results

Thirty-two of the 39 probes tested hybridised satisfactorily to 'P' and 'MK' DNA, although with variable strength. The individuals of both 'P' and 'MK' were

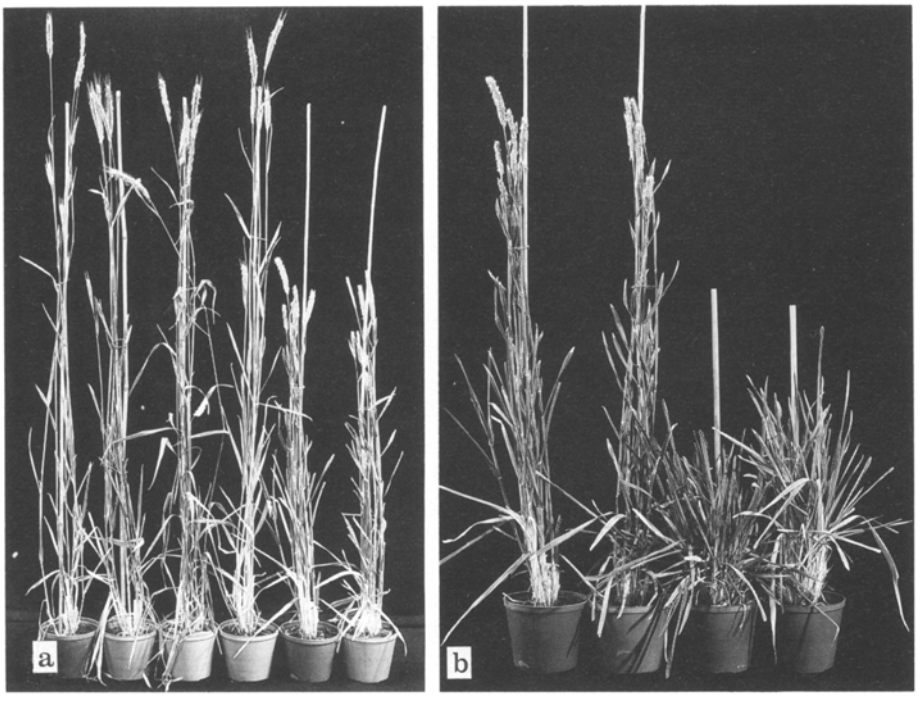


**Fig. 1.** Phenotypes of adult plants of (from left to right): **a**, 4 × *Ct2/.* and 2 × *ct2/ct2* genotypes; **b**, 2 × *Sp1/.* and 2 × sp1/sp1 genotypes (unvernalised plants)

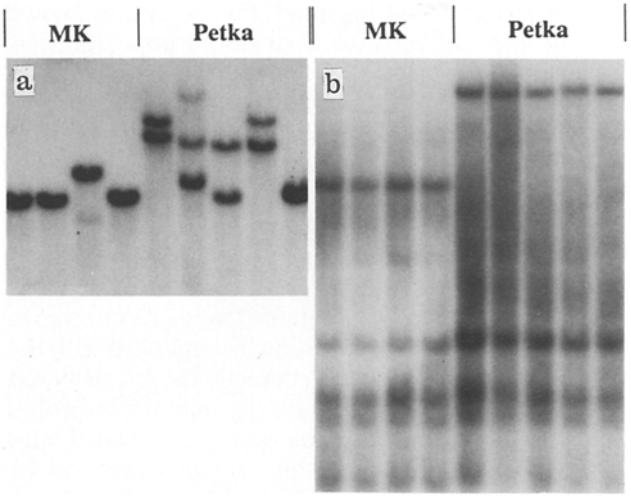


**Fig. 2.** Hybridisation pattern of DNA from different plants of the parental lines (*MK* = Moskowskij Karlik). **a**, digested with *Eco*RI and probed with PSR940; **b**, digested with *Hin*dIII and probed with PSR100

heterogeneous and/or heterozygous at all of the (RFLP) loci except *Xpsr100*. 'P' was more heterogeneous than 'MK'. For example, each of the five plants of 'P' tested gave a different hybridisation pattern when probed with PSR940 (Fig. 2a). PSR100 gave a uniform hybridisation pattern across each of the 'P' samples and each of the 'MK' samples (Fig. 2b). Simple segregating hybridisation patterns were produced in the $F_3$ population by 17 probes, and one, PSR120, detected two loci on 5R. Genotypes at these loci were scored in *Eco*RI and/or *Hin*dIII digests, giving either 1:2:1 (16 loci) or 3:1 (three loci) segregations. *Ct2/ct2* and *Sp1/sp1* segregated 3:1, as expected. All segregation ratios conformed to the expected values, as tested by $\chi^2$ ($P > 0.01$). Although in most cases analysis of the samples of 'P' and 'MK' showed the parental origin of the segregating alleles, this information could not be used because the recombination being analysed occurred in the gametes of an $F_2$ plant, which itself would not be expected to retain all the 'P' and 'MK' alleles in coupling. Thus, allocation of parental origin of alleles was inferred by choosing combinations which gave the lowest estimates of linkage.

**Table 1.** Linkage data for *ct2*, *Sp1* and their flanking markers

| Markers | Two-point linkage and standard error | Multi-point linkage |
|---|---|---|
| *ct2 – XEmpb* | 5.7% ± 2.4 | 5.2% |
| *ct2 – Xpsr79* | 11.5% ± 3.5 | 12.5% |
| *Sp1 – Xpsr426* | 5.8% ± 2.3 | 5.7% |
| *Sp1 – Xpsr120(2)* | 21.5% ± 4.4 | 18.8% |

The *ct2* locus maps between *Xpsr79* (or *Xpsr145*) and *XEmbp* (or *Xα-Amy-3*) and is tightly linked with *XEmbp* (5 cM), while the *Sp1* locus is well tagged (6 cM) by *Xpsr426* (Fig. 3). The two-point and multi-point linkage values, along with the associated standard errors, of *Xpsr79 – ct2 – XEmbp* and *Xpsr-120(2) – Sp1 – Xpsr426* are shown in Table 1. PSR120 is not a useful tagging probe, as it detects multiple loci, and thus in different genetic backgrounds it would not be straightforward to determine which *Xpsr120* locus is being assayed.

The 14 loci which failed to segregate in the 'P' × 'MK' population did so either due to fixation of alleles in the $F_2$ plant, or because the $F_1$ plant was itself homozygous at these loci. The latter possibility is unlikely for the majority of the loci, both because of the frequent polymorphism observed between 'P' and 'MK' individuals, and because on average 50% of alleles are expected to be fixed in any $F_2$ individual, conforming reasonably well with the observed 14 non-segregating and 21 segregating loci. Overall, the majority of the map distances between common points obtained in the two populations were highly comparable; therefore, the 'D' × 'R' map was used to interpolate the gaps in the 'P' × 'MK' map. Using the locations obtained from the 'D' × 'R' (Fig. 3) and wheat maps (Xie et al., unpublished), three of the non-segregating 14 loci can be shown to lie in a segment bounded by *Xpsr335* and *Xpsr911*, while three (all within the 4R/5R translocation segment) are distal to *Xpsr918*. Four other loci were mapped in 'D' × 'R': on 5RL, *Xksu26* is close to the centromere, *Ibf-R1* is distal to and linked by 7 cM to *Xpsr120(2)*, and *Xpsr1194* is close to *Xpsr79;* while on 5RS, *Xpsr929* lies proximal to *Xpsr628*. The combined map thus shows a group of seven loci (*Xpsr628* to *Xpsr100*) flanking the centromere and exhibiting very little recombination. The map positions in wheat or rye of the loci detected by the remaining non-polymorphic eight probes (PSR128, PSR940, PSR945, PSR1101, PSR1204, KSU58, and the known-function probes R5-8 and pACP11) are not known. The total distance mapped in 'P' × 'MK' is 124 cM, mostly involving the long arm of the chromosome, while the combined map of 5R now comprises 29 mapped points spanning 129 cM. Inferred arm locations for all loci conform with those obtained in wheat from ditelosomic analyses.

## Discussion

### *Use of $F_3$ populations in genetic mapping*

Although most genetic mapping experiments in plants use first-generation populations such as $F_2$ and BC1, or doubled haploids, where the level of heterozygosity

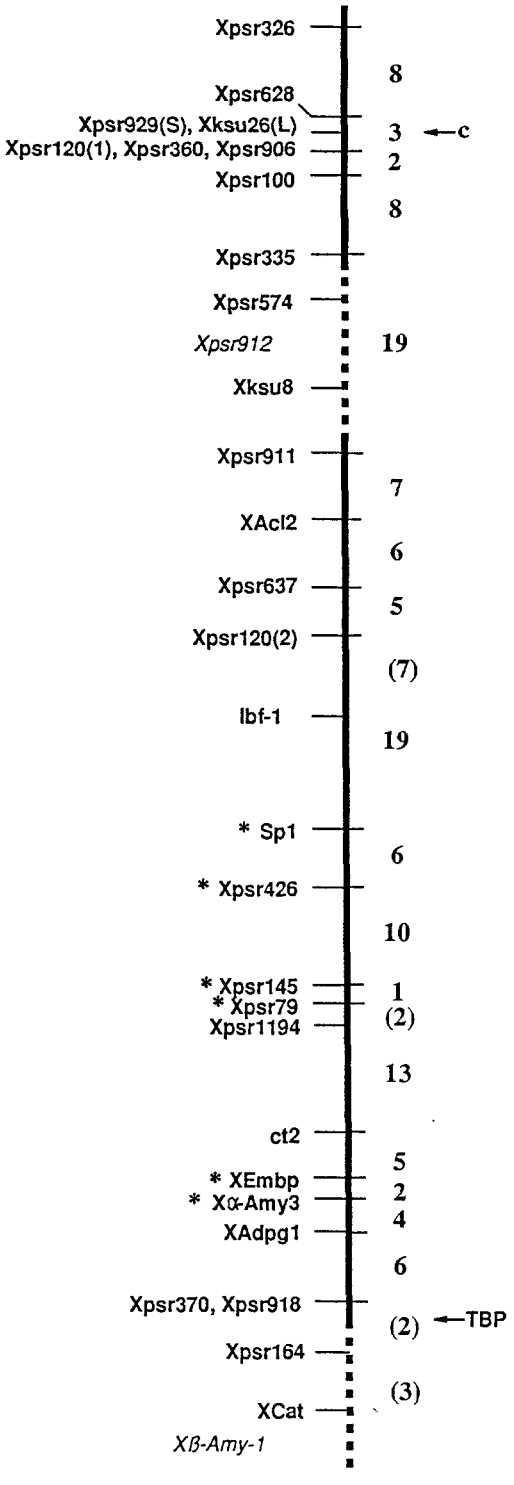


**Fig. 3.** Genetic map of chromosome 5R from the $F_3$ 'P' × 'MK'; map distances rounded to the nearest cM. c, centromere; TBP, 4R/5R translocation break point; *, preferred map locations with LOD differences < 2.5. The *broken lines* indicate the homozygous status of these regions in the $F_2$ parent plant. Loci with half marks (left side only) are interpolated from the $F_2$ of 'D' × 'R', interpolated distances shown in *parentheses*. Locations of *Xpsr912* and *Xβ-Amy-1* inferred from wheat maps. Sources of mapped known-function probes: ACPII (*XAc12*) leaf acyl-carrier protein II (Hansen unpublished); pGC19 (*XEmpb*) bZIP protein (Guiltinan et al. 1990); 33 (*Xα-Amy-3*) α-amylase-3 (Baulcombe et al. 1987); WL AGA 1 (*XAdpg*) ADP glucose pyrophosphorylase (Olivie et al. 1989); pCat2.1c (*XCat*) catalase (Bethards et al. 1987); pPS1 (*Xβ-Amy-1*) β-amylase-1 (Kreis et al. 1987). Unmapped known-function probes: R5–8 (*XCxp-3*) carboxipeptidase (Baulcombe and Buffard 1983); pACP11 (*XAc11*) leaf acyl-carrier protein I (Hansen 1987)

in the progenitor is maximal, this study has shown that it is possible to use a single $F_3$ population (as opposed to the bulk $F_3$ populations commonly used to reconstitute $F_2$ genotypes) for gene tagging, provided that the $F_2$ parent plant is heterozygous for the genes of interest. Despite the fact that an expected 50% of all loci will be homozygous in the $F_2$ plant, these are not likely to be in interest, as the majority will not lie within the segment containing the target gene. In subsequent selfing generations, provided that the target gene can be maintained in the heterozygous state, the number of segregating loci unlinked with the target will decrease by half, at exactly the rate achieved by backcrossing. In this way, the number of probes for which the full population needs to be tested falls, and those loci which continue to segregate will be increasingly more likely to be closely linked with the target. The process can be accelerated by deliberately selecting individuals homozygous at all loci removed from the target, but still heterozygous at those loci close to it. This tagging strategy requires, however, that each generation is bred from a single plant, and this can create difficulties in out-pollinating species, since a certain degree of self-compatibility is necessary.

All the probes (except PSR100) which detected segregating loci in the $F_3$ of 'P' × 'MK' also detected polymorphism among the small number of samples of the parental varieties 'P' and 'MK'. This is in contrast to wheat, where the level of polymorphism is generally low (Chao et al. 1989; Harcourt 1992), and is consistent with a correlation between the breeding system and the level of RFLP, whereby allogamous species (maize, rye) are highly polymorphic and autogamous ones (wheat, barley, tomato) are less polymorphic (Gale et al. 1990).

### *Relationships between GA-insensitive dwarfing genes in the Triticeae*

There does not appear to be any evidence of a genetic relationship between the GA-insensitive *Rht* genes of wheat, located on chromosome arms 4BS and 4DS (McVittie et al. 1978), and rye *ct2*. Chromosome 5R has been shown to contain a segment with homoeology to the *Triticeae* homoeologous group 4 chromosomes,

as evidenced from studies of chromosome pairing in wheat × rye hybrids (Naranjo et al. 1987) and of intrachromosomal mapping in wheat and rye (Liu et al. 1992). This segment cannot include the *Rht*-carrying region, since it is clear that the translocation involves a part of the long arm and not the short arm of the primeval homoeologous group 4 rye chromosome. Furthermore, the location of *ct2* on 5RL, but proximal to *XEmpb*, *Xα-Amy-3*, *XAdpgI*, *Xpsr370* and *Xpsr918* (markers also located on the long arms of the homoeologous group 5 chromosomes in wheat), indicates that it is far removed and proximal to the translocation breakpoint, and cannot therefore have originated from 4R, as far as current information can tell. In barley, the *gai* locus, which determines a GA-insensitive dwarf habit, is located on chromosome 2H (Hopp et al. 1982), and a further rye locus, *ct1*, is present on chromosome 7R (Sturm and Müller 1982; Börner 1991). Although chromosome 7R is known to carry a segment of the primeval 4R (Koller and Zeller 1976; Liu et al. 1992), this originates from 4RL and not 4RS. Thus, there does not appear to be a *Triticeae*-wide homoeoallelic series of GA-insensitive dwarfing genes, despite the strong intimation of its existence from the homoeologous locations of the wheat *Rht* loci. Some weight is given to this proposition by the fact that GA insensitivity is rare amongst the dwarf mutants observed to-date. Furthermore, a recent study has located factors on wheat chromosomes 5B, 7A and 7B which promote GA insensitivity, possibly representing homoeoloci of rye *ct2* and *ct1*, respectively (Börner et al. 1992b).

Endogenous levels of $GA_1$ in wheat lines isogenic for *Rht1* and *Rht3* are 4.5-fold and 25-fold higher, respectively, than in equivalent tissues of isogenic *rht* lines (Lenton et al. 1987) but, in contrast, no such increase was evident when $F_3$ lines homozygous for *ct2* or *Ct2* were compared (Börner et al. 1992a). However, levels of endogenous GAs in lines carrying the weaker allele *Rht1S* (Worland and Petrovic 1988) have not been investigated, and therefore it is difficult to determine relationships between *Rht* and *ct2* based on biochemical phenotypes.

### *Synteny of vernalisation genes in the Triticeae*

Major genes determining a vernalisation requirement are located on the homoeologous group 5 chromosomes in wheat (Pugsley 1972), barley (Nilan 1964, cited in Søgaard and von Wettstein-Knowles 1987) and rye (De Vries and Sybenga 1984). Thus it is plausible that a homoeoallelic series is present: if so, this would provide the opportunity to use a linked marker found in one species as a tag in one or both of the two other species. While *Sp1* is now mapped (and closely linked to *Xpsr426-5R*), none of the wheat genes *Vrn1* (5AL), *Vrn3* (5DL) or *Vrn4* (5B) have yet been linked to any RFLP marker. However, both *Vrn1* and *Vrn3* are known to be unlinked to their respective centromeres (Law et al. 1976), and the former is well separated from *β-Amy-A1* (Ainsworth et al. 1983), all of which is consistent with the position of *Sp1* reported here. In barley, *Sh* (*Vrn-1*) is present on chromosome 4L (=4HL), linked to the *β-Amy-H1* locus (Forster and Ellis 1991). Although *β-Amy-R1* is on 5RL in rye (Ainsworth et al. 1987) it is unlikely that *Sh* is a homoeoallele of *Sp1*, because *Sp1* is not located within the 4R/5R translocation segment. *Sh2* however, is, on barley chromosome 7, a member of the *Triticeae* homoeologous group 5 chromosomes. Its intrachromosomal location with respect to RFLP markers has not been reported to-date, but its position can be inferred to be distal on 7L from maps involving a number of morphological markers (Søgaard and von Wettstein-Knowles 1987), again consistent with the position of *Sp1*. Thus, the genetic data support the proposition that wheat *Vrn1*, *Vrn3*, and possibly *Vrn4*, rye *Sp1*, and barley *Sh2*, form a homoeoallelic set. The RFLP mapping of *Vrn1*, currently being undertaken, should serve to verify or exclude this.

The protein locus *Ibf-R1* is proximal to *Xpsr426-5R*, and linked to it by 13 cM (Liu et al. 1992), and is 7 cM distal to *Xpsr120(2)* (Fig. 3). This suggests that *Ibf-R1* would be a good candidate for tagging *Sp1*. However, Ibf analyses of the 'P' × 'MK' population appeared to give a highly distorted segregation pattern. Therefore, *Ibf-R1* could not be unequivocally scored and was not incorporated in the 'P' × 'MK' map. Work is now in progress in sister populations to estimate the linkage relationship of *Sp1* to *Ibf-R1*.

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