MAPPING OF A WHEAT-RYE TRANSLOCATION¹

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THE genetic distance of genes from their centromere remains undetected in conventional linkage studies. In hexaploid wheat (*Triticum aestivum* L.) these distances can be estimated by the use of telocentric stocks, as shown by SEARS (1962, 1963). The procedure involves crossing a normal stock having 21 pairs of chromosomes, bearing *A*, with a recessive stock in which the chromosome bearing *a* is telocentric for that arm. This F_1 is backcrossed as male to a normal recessive stock, and the recessive BC_1 plants are examined cytologically. As telocentrics compete poorly with normal chromosomes for transmission through the pollen, transmission of *a* usually necessitates its crossing over to the two-armed chromosome. Elimination of recessive BC_1 plants not possessing 21 pairs of normal chromosomes allows the frequency of crossing over between *A* and the centromere to be determined.

The character involved in the present study is referred to as pubescent peduncle or "hairy neck." This trait, which was derived from cultivated rye (*Secale cereale* L.), behaves as a simple dominant (DRISCOLL and SEARS 1963).

MATERIALS AND METHODS

The hairy-neck trait was derived from the Cornell Wheat Selection 82a1-2-4-7, a derivative of a wheat $\times$ rye cross. The character was backcrossed into the variety Chinese Spring. The hairy-neck gene (*Hp*, Hairy peduncle) was located on its specific chromosome by monosomic analysis. It was located on a particular arm of that chromosome by cytological examination of F_2 individuals following crossing with a stock that is telocentric for the arm concerned. Backcrosses to Chinese Spring were made with F_1 plants involving *Hp* and the telocentric, and non-hairy neck BC_1 plants were examined for chromosome complement. From these observations the linkage value was determined as described below.

RESULTS

Specific chromosome location of Hp: The backcross line involving *Hp* possesses 21 pairs of chromosomes, as does the F_1 between this line and normal Chinese Spring. Thus the segment of rye chromatin bearing *Hp* had spontaneously translocated to a wheat chromosome. This had previously been postulated by JENSEN and KENT (1952). Of the 12 chromosomes tested in the monosomic

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analysis, one, chromosome 4A, was found to bear *Hp*. The aneuploid F_2 population involving 4A segregated 47 *Hp*:1 *hp*, the one *hp* being a nullisomic. The pooled ratio of the other F_2 families was 206 *Hp*:68 *hp*, which is the closest possible fit to a 3:1 ratio. This is evidence of unimpaired male transmission of the translocation chromosome (the chromosome partly wheat, partly rye).

Specific chromosome-arm location of Hp: The line homozygous for *Hp* was crossed with an aneuploid stock of Chinese Spring which is telocentric for the left arm of chromosome 4A. Designations of left and right have been applied to the telocentrics of near-equal-armed wheat chromosomes, pending their identification as to long or short arms. The left arm of 4A is complementary to that reported by SEARS 1954. On selfing this heterozygote, *hp* plants were obtained that possessed an entire chromosome. Thus crossing over must have taken place between the translocation chromosome and the telocentric in the region between *Hp* and the centromere. This establishes that the rye segment must be attached to the left arm of 4A.

Desynapsis of the heteromorphic bivalent involving Hp: When *Hp* is not involved, normal pairing is observed between the two-armed 4A and left-arm telocentric 4A. However when heterozygosity for *Hp* is involved, pairing of these two chromosomes is not observed at metaphase I in all pollen mother cells (PMCs). The percentage of PMCs in which pairing was observed varied from plant to plant, a range of 29 to 56 per 100 cells being observed. Of a total of 551 PMCs, 40% exhibited synapsis. When unpaired, the two chromosomes were often co-oriented about the metaphase plate. Of 74 PMCs involving lack of pairing, 47% exhibited obvious co-orientation.

The low percentage of pairing at metaphase I was presumably due to the presence of the rye segment. Although this segment would not be expected to pair with the corresponding portion of the wheat chromosome, such pairing is conceivable, in which case the reduced pairing in the heteromorphic bivalent would be due to the rye segment's having replaced a wheat segment substantially longer than itself. This possibility is ruled out, however, by observations on an individual obtained in the course of the study that was ditelosomic and homozygous *Hp*. Here the telocentrics paired in nearly 100% of the PMCs. Also, the entire chromosome bearing *Hp* could not be detected to differ in length from its normal homologue.

The frequent co-orientation observed in the F_1 material suggests that the two chromosomes usually synapse but crossing over and chiasma formation do not always ensue; i.e., desynapsis is involved rather than asynapsis.

Linkage study: The F_1 possessing the heteromorphic bivalent with *Hp* on the two-armed chromosome was backcrossed as the male parent to Chinese Spring. Two hundred thirty-six BC_1 individuals were classified for the presence or absence of *Hp*. The observed ratio was 139 *Hp*:97 *hp*. The results of the cytological examination of the 97 recessive individuals are shown in Table 1. The first three types listed were considered to be authentic crossovers. The remaining three types were considered noncrossovers. The two monosomics in which the monosome was not dissimilar to 4A probably involved functioning of male

TABLE 1

Chromosome complement of the 97 non-hairy-neck BC₁ plants

Number	Chromosome complement
78	21"
1	21" + 2 isochromosomes
5	20" + 1' (monosome satellited—not 4A)
2	20" + 1' (monosome not dissimilar to 4A)
10	20" + heteromorphic bivalent involving one normal chromosome and one telocentric
1	20" + heteromorphic trivalent involving one normal chromosome, one telocentric and one isochromosome

gametes possessing neither chromosome 4A. Involvement of monosome 4A was confirmed in one of these cases by the phenotypic detection of nullisomic 4A in the selfed progeny. The ten plants possessing 20" + heteromorphic bivalent almost certainly involved instances of functioning of male gametes including the parental telocentric chromosome. The one individual with 20" + heteromorphic trivalent was probably of similar origin to the previous ten with an additional isochromosome having been derived from the telocentric. Thus of the 97 *hp* individuals, 84 involved functioning of male gametes possessing a two-armed chromosome bearing *hp*, i.e., involving crossing over.

Of the 139 *Hp* individuals in the BC₁ population a random sample of 20 was examined cytologically. As is seen in Table 2, 17 of these possessed 21", and one possessed a nonsignificant monosome. The individual possessing 20" + heteromorphic bivalent involved crossing over of *Hp* to the telocentric and subsequent inclusion of this crossover chromatid in a functioning male gamete. The individual possessing 20" + heteromorphic trivalent is looked upon as involving a male gamete that possessed both the normal and the telocentric 4A. Thus 18 of 20 male gametes possessed one entire chromosome 4A bearing *Hp* and no telocentric. Of 139 male gametes, 125.1 would be expected to possess this same constitution with respect to 4A.

In the PMCs of the male parent each crossover between the centromere and the *Hp* segment gives rise to one gamete with an entire 4A bearing *hp*, and one

TABLE 2

Chromosome complement of 20 hairy-neck BC₁ plants

Number	Chromosome complement
17	21"
1	20" + 1' (monosome satellited—not 4A)
1	20" + heteromorphic bivalent involving one normal chromosome and one telocentric
1	20" + heteromorphic trivalent involving two normal chromosomes and one telocentric

gamete with an entire 4A bearing *Hp*. Therefore *Hp* plants in excess of 84 must have involved gametes that were produced following failure of crossing over, these being $125.1 - 84 = 41.1$. As lack of crossing over in this region apparently results in desynapsis, which leads to lagging and loss of chromosomes, a correction factor must be applied to the figure of 41.1 in order to calculate the number of PMCs that were involved in giving rise to these 41.1 gametes. It may be assumed that failure of crossing over always leads to desynapsis. Following desynapsis the probability of a chromosome being included in a particular gamete is about $1/4$ (see SEARS 1954). Thus the probability of the entire chromosome being included and the telocentric excluded is $1/4 \times 3/4 = 3/16$. As each PMC gives rise to four gametes, this fraction is multiplied by 4 to give $3/4$. The figure of 41.1 is then divided by $3/4$ to give 54.8. Thus for 84 PMCs involving a crossover between the centromere and *Hp* there are 54.8 not involving such a crossover; i.e., 60.5% of the PMCs possessed a crossover in this region. The genetic distance between *Hp* and the centromere is half of 60.5; viz., of the order of 30 map units.

DISCUSSION

The amount of pairing of telocentric 4A with its homologue calculated from the genetic data was 60.5%, which is in rather poor agreement with the 40% observed cytologically. However, the cytological data were taken from different spikes than those used for making pollinations, and individual samples did show up to 56% pairing. It seems, therefore, that the data are in sufficiently good accord with expectation that they do not invalidate either of the two major assumptions involved in making the calculations, (1) that the rye segment is not intercalary and (2) that a one-to-one correspondence exists between chiasmata and crossing over.

A terminal position of the rye segment is more likely, since such a location would result from a reciprocal translocation requiring only two chromosome breaks, whereas an intercalary translocation requires three breaks. An intercalary position of the segment would make possible the occurrence of crossovers beyond the rye segment. In this case noncrossover chromatids would not have been subjected to univalent loss and the correction made for this would have given rise to a higher crossover value and a greater discrepancy between observed and expected pairing. Furthermore, the occurrence of chiasmata without detectable crossing over would have increased the amount of pairing required to yield the observed crossover frequency, adding still more to the discrepancy. Thus the data do not support an interstitial location for the rye segment.

Assuming that the rye segment is terminal, the reduced pairing of the substituted arm with the normal wheat arm is attributable to the reduced amount of wheat chromatin available for pairing and probably also to interference by the rye segment with pairing of the adjacent wheat chromatin.

The crossing over measured was not from the centromere to the actual locus of the *Hp* gene but to the proximal limit of the rye segment. If a mutation could be induced from *Hp* to some recognizably different allele, the *Hp*-centromere dis-

tance could be determined in material homozygous for the rye segment. In addition to allowing crossing over in the *Hp*-breakpoint interval, this would presumably also eliminate the interference effect. This distance might prove to be much greater than the 30% calculated in the present experiment, especially if intermediate markers were available to permit detection of double crossovers.

SUMMARY

The hairy-neck trait of the Cornell Wheat Selection 82a1-2-4-7, a derivative of a wheat $\times$ rye cross, was backcrossed into the wheat variety Chinese Spring. This trait is conditioned by a segment of rye chromatin that had spontaneously translocated to a wheat chromosome. By monosomic analysis it was found that the wheat chromosome involved was chromosome 4A. By use of a telocentric-4A stock it was determined that the rye segment is located on the left arm of 4A. Pairing in this arm is markedly reduced when the rye segment is heterozygous. Little or no crossing over occurs between the rye segment and the normal wheat homologue. By the telocentric linkage method it was calculated that the distance of the segment from the centromere is about 30 map units.

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