Recombination within the complex locus *His(2-6)* containing genes for five histone H1 subtypes in pea

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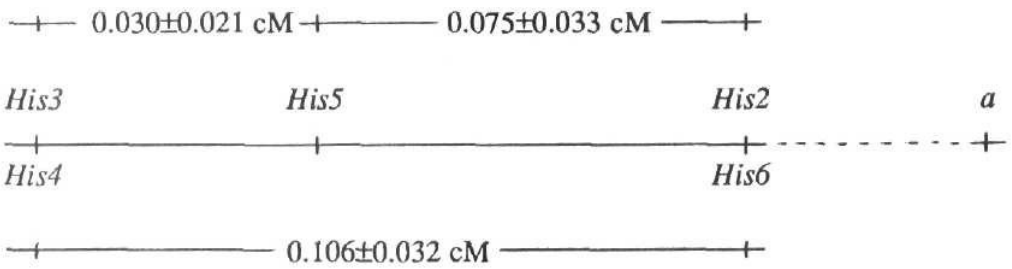
It is now reliably established that the pea genome contains at least 7 genes that encode histone H1 proteins. They are mapped to three loci: *His1* in linkage group V (4), and *His(2-6)* and *His7* in linkage group I (1, 3). Locus *His(2-6)* consists of 5 closely clustered genes situated within 4.1±1.5 cM of the anthocyanin gene, *a* (1).

This paper describes an attempt to register recombination events between the genes of locus *His(2-6)* and to determine its fine structure. Each gene of this locus has allelic variants. Their protein products are easily identified by electrophoresis in 15% polyacrylamide gel containing 8M urea/0.9M acetic acid. Isolation of histone H1 is described in (3). Following Berdnikov *et al* (2), the H1 allelic combination of a plant (the 'haplotype') is designated by a formula which in this case includes five positions, because it denotes the allelic states of five genes (*His2* to *His6*) encoding H1 subtypes 2 to 6. In this formula, the numerals denote allelic forms of the genes and their positions in the formula correspond to the gene number (the first position to *His2,* the second to *His3,* and so on). The allelic forms were numbered in accordance with their relative electrophoretic mobility. Among four variants of subtype 5 there are two with close electrophoretic mobility which were not resolved by Berdnikov *et al* (2). These two variants were denoted as 2' (the slow form) and 2 (the fast form).

The experiment involved more than 3000 individual F_2 plants from four independent crosses (see Table 1). Parental lines with particular haplotypes were obtained from the VIR collection: VIR6560 (haplotype *21133*) ; VIR4871 (*22122*) ; VIR5195 (*11123*) ; VIR5417 (*2212'1*) ; cultivar Torsdag (*21211*) ; a plant with haplotype *11223* was obtained from the F_2 progeny of cross VIR5195 (*11123*) with Sprint-1 (*21221*) (an extra rapid line derived in our laboratory from the cross Avanti x VIR7036).

The recombinants observed in these crosses are listed in Table 1. Taking into account the scarcity of recombinants, we combined data presented in the table for all crosses and mapped individual genes of the locus *His(2-6)* as follows:



We did not find recombinants between *His3* and *His4* or between *His2* and *His6.* For this reason, while combining the data from different crosses, we treated these genes pairs as single units, although in several cases only one gene of a pair had different alleles in parental forms.

The parental lines in cross 2 differed from each other also in alleles of the anthocyanin gene, *a* (the plants with *11223* had allele *A* and those with *2212'1* had allele *a*). The genotype for the anthocyanin locus was determined only in recombinants by their progeny. The genotype at the *a* locus occurred in parental combination with the corresponding alleles of *His2* and *His6* in all cases, but never with alleles of *His3* and *His4*. The result suggests that this histone cluster is oriented to the gene *a* by its *His2 His6* end.

Table. 1 Genotypes of F_2 plants with recombinant haplotypes for the *His2-6* gene cluster.

	Cross 1	Cross 2	Cross 3	Cross 4
Parents	*21133x21211*	*11223x2212'1*	*11123x21211*	*22122x21211*
Number of F_2	266	1716	763	568
Genotypes of plants with recombinant haplotypes*	none	*11223/**1212'3*** *2212'1/**21221*** *11223/**12123*** *2212'1/**1212'3***	*11123/**21111*** *11123/**21121***	*22122/**21212***

The recombinant haplotypes are printed in boldface

The data obtained in this study can shed light on an intriguing fact which was observed in extensive investigation of peas cultivated all over the Old World (1). No plant was found with the haplotype *22XX* (the haplotypic formula refers only to genes *His3* to *His6* because gene *His2* was represented chiefly by allele *2; X* means any allele), while haplotypes *12XX* and *21XX* were found to be abundant in the same regions. At the same time, the most common alleles of gene pairs other than *His3* and *His4* were found in all possible combinations. This might be explained in two ways: 1) very tight linkage and 2) some functional prohibition. The supposition that recombination was involved in formation of the diversity of haplotypes, being extremely rare or even impossible between *His3* and *His4* genes, remains only a first explanation.

Our map could be helpful while designing new combinations of histone H1 genes. It is very interesting to construct and examine a plant with haplotype *20000* (zero means that protein products of the corresponding genes are absent). We have crossed lines with *20101* and *21020* and have already obtained the combination *20100*.

1. Belyaev, A.I. and Berdnikov, V.A. 1981. Genetika (USSR) 17:498-504.
2. Berdnikov, V.A., Bogdanova, V.S., Rozov, S.M. and Kosterin, O.E. 1993. Heredity 71:199-209.
3. Kosterin, O.E. 1992. Pisum Genetics 24:56-59.
4. Rozov, S.M., Bogdanova, V.S. and Berdnikov, V.A. 1986. Genetika (USSR) 22:2159-2166.