A new allele at *Crd* disturbs development of the compound leaf

Berdnikov, V.A. and Gorel', F.L. and Kosterin, O.E.
Institute of Cytology and Genetics of Russian Academy of Sciences
Acad. Lavrentiev ave. 10, Novosibirsk 630090, Russia

Seeds of the SG stock were left to imbibe 0.1% EMS solution and planted. In the M_2 population a plant was found with leaflets reduced to a variable extent. Leaflets were sometimes reduced to a hair-like vein a few millimeters long or completely absent, the compound leaf being represented by a pair of stipules and a very thick and long (up to 30 cm) rachis which in its apical zone became a non-branching tendril (Fig. 1A). This plant as well as its descendants often displayed peculiar joints (marked with anthocyanin spots) in the leaf rachis, indicating the nodes from where the missing leaflets would have arisen. The stipules were large, with the margins tending to hang due to weak development of veins. The flowers also exhibited a number of anomalies: the number of sepals often were reduced to 4 or even 3, one or both alae usually were reduced or absent, the elements of the carina often were not fused, and the number of stamens were reduced to 7-8. Due to its resemblance to a whip, we called the new foliage phenotype *whip* (*wh*).

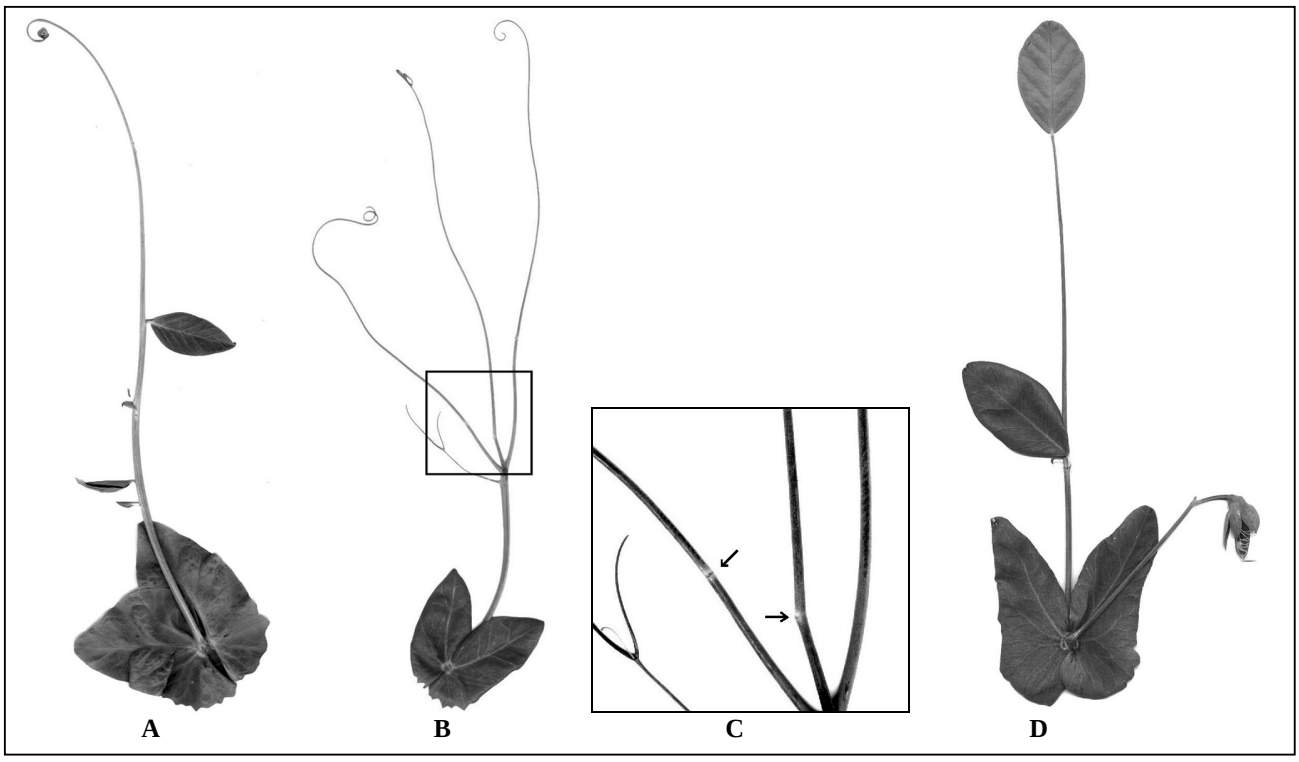

Fig. 1. [A] A compound leaf of a pea plant homozygous for the mutation crd^{wh}. *[B] A compound leaf of a pea plant with the genotype* crd^{wh} / crd^{wh} af/af. *The box indicates the area showed in [C] with magnification. [C] Joints (indicated by arrows) on the second order raches of the leaf of a pea plant with the genotype* crd^{wh} / crd^{wh} af/af *shown in [B]. [D] A compound leaf of a pea plant with the genotype* crd^{wh} / crd^{wh} tl^{w}/tl^{w}.

F_1 plants resulting from a cross of a mutant plant with the line WL1238 had normal leaves. Among 43 F_2 plants eight had phenotype *wh*, a ratio that does not contradict monogenic nature of inheritance of the mutant phenotype. In an *af/af* genotype the new mutation decreases the order and intensity of branching (Fig. 1B),

with the joints noticeable on the second order raches (Fig. 1C). Especially peculiar was the leaf appearance of the homozygote for the new mutation on the tl^w/tl^w background: a long rachis (lacking most of its lateral appendages) ending with a large lamina (Fig. 1D).

As a rule, plants possessing the new mutation exhibited reduced fertility, hampering genetic investigations. Nevertheless, after a series of crosses with various lines we obtained a relatively fertile line WHAF homozygous for the mutation and recessive markers *a*, *le* and *af*.

A comparison of *wh* plants with the mutation *crd* in the line Wt11300 (obtained from W.K. Sweicicki) revealed a number of similarities. In addition to the parallel in stipular morphology the raches of both mutations often have joints. Also in the flowers of Wt11300 one or both alae are often absent, the carina elements are sometimes free, the stamens as a rule are reduced in number and the fusing of their filaments into a stamen tube is disturbed. F_1 plants resulting from a cross WHAF x Wt11300 (*a, crd, le, Af*), had the *whip*-phenotype, indicating that the new mutation is a new allele of the locus *Crd*. We designate the new allele by the symbol crd^{wh}. It should be noted that the allele crd^{wh} disturbs plant development much more strongly than the allele *crd*, conferring to the pea plant a certain resemblance to *Lathyrus aphaca* L.

As demonstrated by Swecicki (2) the locus *Crd* is linked to *A* and *Aatp*, located on linkage group II. We obtained F_2 progeny from the cross WHAF (crd^{wh}, *a, His(2-6)*^{1021}, $His7^2$) and Yellow Crispa (*Crd, A, His(2-6)*^{1221}, $His7^3$) (the origin of Yellow Crispa is described in ref. 1) and mapped *Crd* with respect to *A* and *His(2-6)* (Table 1). (In this cross the markers *gp* and *cri* of linkage group V also segregated but did not show linkage to *crd*). The data of Table 1 allow the construction of the following map segment:

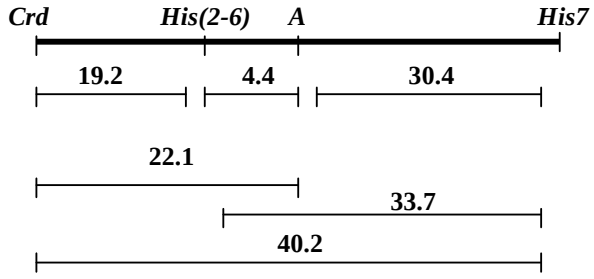

Table 1. Segregation of phenotypes in F_2 progeny of the cross WHAF (*His(2-6)*^{1021}, *a*, crd^{wh}, $His7^2$) x Yellow Crispa (*His(2-6)*^{1221}, *A, Crd,* $His7^3$). N=268.

Gene pair		Number of plants with designated phenotypes[1]						Joint Chi-sq.	Recomb fract. (%)	St. Error
		A/B	A/h	A/b	a/B	a/h	a/b			
a	crd	177	–	18	34	–	39	61.95***	22.11	2.94
a	His(2–6)	189	–	6	6	–	67	210.87***	4.44	1.29
a	His7	63	105	27	9	31	33	32.58***	30.43	3.27
crd	His(2–6)	180	–	31	15		42	78.80***	19.24	2.73
crd	His7	59	113	39	13	23	21	8.74	40.21	3.62
His(2–6)	His7	60	106	29	12	30	31	23.97***	33.70	3.40

[1]A,a - phenotype for the first gene; B,b - for the second gene; for codominant alleles in *His7* the capital B stands for the allele $His7^3$ linked to dominant alleles of other genes; h - heterozygous; capital letters stand for dominant alleles, the haplotype 1221 of the locus *His(2-6)* is dominant with respect to its counterpart 1021. Calculations were made using the maximum likelihood method using the program 'Cros'.

,**, - probabilities less than 0.01, 0.001 and 0.0001, respectively.**

The gene *Crd*, together with the genes *Uni*, *Af* and *Tl*, clearly are involved in the development of the compound leaf, with *Crd* apparently being responsible for its branching. *Crd* also appears to be necessary for normal development of the flower.

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1. Kosterin, O. E., Pukhnacheva, N.V., Gorel', F.L., Berdnikov, V.A. 1999. Pisum Genetics 31: 13-20.
2. Swecicki, W.K. 1989. PNL 21: 73-74.