

The problem of leaflet dentation inheritance in peas

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The dominant allele of the locus *Td* determines a weak leaflet dentation in peas. Lamprecht (3) located this gene on linkage group IV about 33 cM from *le* and 36 cM from *z*. At the present time, linkage group IV is broken into two parts without observable linkage between them (7). The gene *z* belongs to group IVA and gene *le* to group IVB.

Marx (5) did not find linkage between *Td* and *z*, but demonstrated linkage (15 cM) between *Td* and *b* of group III. More recently Grajal-Martin and Muehlbauer (2) and Polans (6) obtained additional evidence that *Td* is in linkage group III between genes *st* and *Lap-1* (the latter is close to *b*). The plant materials used in the two latter studies (2, 6) were obtained originally from G. A. Marx and N. F. Weeden. So, in most crosses the gene *Td* was the same and, as a result, it was mapped in the same chromosome. Joint segregation between *Td* and *le*, which was studied by Lamprecht (3), was not investigated in the experiments mentioned above. Grajal-Martin and Muehlbauer (2) offered two possible explanations as to why *Td* mapped to group IV in Lamprecht's study and group III in the other studies: either 1) there are genomic rearrangements in some pea lines involving *Td* or 2) there are two different genes for leaflet dentation each with a similar phenotypic expression. Polans (6) favoured the first explanation. To further examine the problem I decided to use lines from other sources to answer the question of how many *Td* genes there are in the pea genome and where they are localized.

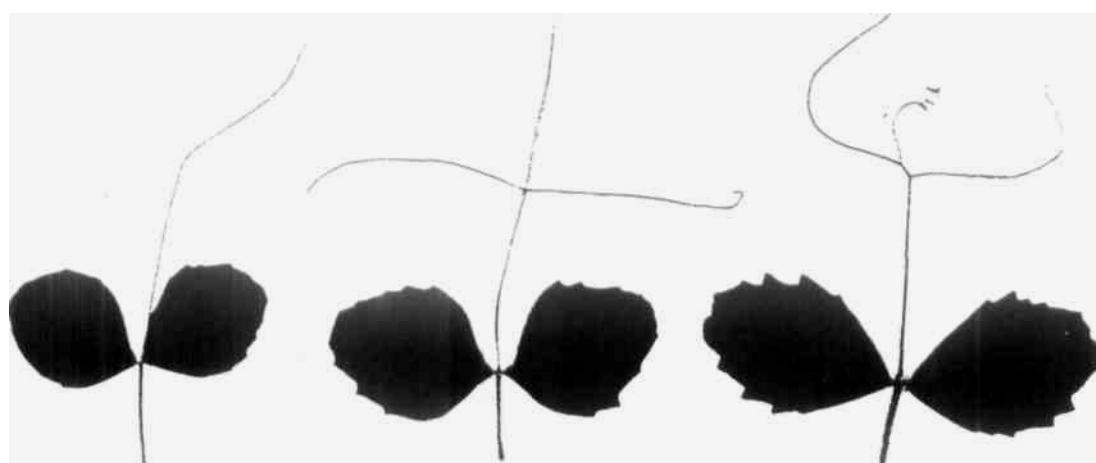
Two pea lines with weak leaflet dentation, WIR4907 (*Pisum sativum* ssp. *asiaticum*) and WIR319 (*Pisum sativum* ssp. *sativum*) (Fig. 1), were crossed with a standard marker line, WL1238 (= JI73). To distinguish the gene responsible for leaflet dentation in lines WIR319 and WIR4907 from the gene used by Marx, it seemed necessary to use another symbol, for example, *Td'*. Both crosses produced fully fertile hybrids. In *F*₁ plants, the gene *Td'* showed incomplete dominance. Among *F*₂ progeny, heterozygous plants could be distinguished from dominant homozygous plants. Segregation of *Td'/Td':Td'/td:td/td* *F*₂ plants of cross WIR319 x WL1238 was 24:48:25 (Chi-sq. = 0.03, P>0.9) indicating that the leaflet dentation in WIR319 is determined by a single gene.

Segregation analysis of two *F*₂ progenies for *Td'* and several markers is shown in Table 1. The data were analysed using the computer program CROSS. All individual segregations were in accordance with a 3:1 ratio (P>0.05). In the cross WIR4907 x WL1238, *Td'* was estimated to be located about 20 map units from *le* and, at the same time, 32 map units from gene *b*. The linkage *Td'-le* is highly significant (P<0.0001) while the *Td'-b* linkage is scarcely significant (P<0.01). It is difficult to explain the linkage with *b* confidently. One can only assume that an unknown gene near *b* has an influence on the expression of gene *Td'* from linkage group IVB. The *F*₂ data from the cross WIR319 x WL1238 clearly indicate that *Td'* is associated with *le* but not with *b*. As can be inferred from the segregation of *Td'*, *le* and *Np*, these genes are arranged in the following order: *Np* — 23 — *le* — 17 — *Td'*.

Thus, in lines WIR319 and WIR4907 *Td'* is located on the linkage group IVB. The gene *Td'* of these lines seems to be not the same as in line A886-193 used by Marx (5). The line A886-193 is derived from *Pisum abyssinicum* where the stipules and leaflets become dentate at node 6 or 7 and in all succeeding leaves. The lines WIR4907 and WIR319 have

Table 1. Joint segregation analysis for *Td'* and *le*, *b* and *Np*.

Cross*	Gene pair		Phenotypic classes				Joint		Recomb.	
	Cross*	X	Y	XY	Xy	xY	xy	Chi-sq	Prob.	fract.
A	<i>Le</i>	<i>Td'</i>	74	17	4	19	34.7	<0.0001	20.2	4.3
	B	<i>Td'</i>	62	18	16	18	10.2	<0.01	31.7	5.5
B	<i>Le</i>	<i>Td'</i>	69	11	3	14	26.8	<0.0001	16.7	4.2
	B	<i>Td'</i>	53	21	19	4	1.1	>0.05	-	-
	<i>Np</i>	<i>Td'</i>	58	16	14	9	2.8	>0.05	-	-
	<i>Le</i>	<i>Np</i>	68	12	6	11	19.1	<0.0001	22.8	5.0

*A. Cross WIR4907 {*Td'*, *Le*, *B*} x WL1238 {*td*, *le*, *b*}; n = 114B. Cross WIR319 {*Td'*, *Le*, *B*, *Np*} x WL1238 {*td*, *le*, *b*, *np*}; n = 97Fig. 1. Left to right: toothed leaves from the 6th node of pea lines WIR4907 and WIR319 (gene *Td'*), WL6 (gene *Td*) and WL1325 (gene *Ser*).

dentate leaflets only at nodes 6, 7, 8 and sometimes an occasional separate tooth on upper nodes.

The line WL6 from the Nordic Gene Bank has a classic *Td* phenotype. Its leaflets are toothed at nodes' 6 to 9 and leaflet dentation is a little deeper than in lines WIR319 and WIR4907 (Fig. 1). A test cross WTR319 x WL6 was made to verify if the leaflet dentation genes of these lines are the same or not. Under field conditions among 176 F₂ plants, 13 plants were without leaflet dentation (Chi-sq. (15:1) = 0.39, P>0.5). The remaining 163 plants differed as to the tooth intensity. One could see plants with weak, normal, strong and very strong leaflet dentation. The experiment was repeated in the greenhouse. 113 F₂ plants of the same cross were examined with respect to the degree of leaflet dentation at nodes 5 to 9. The F₂ plants were confidently divided into 5 phenotypic classes with very strong, strong, normal, weak, and without dentation, respectively. The numbers in the classes were 14:29:40:21:9. These numbers are in reasonable agreement with the theoretically expected ratio 1:4:6:4:1 (Chi-sq. = 8.7, P>0.05) for leaflet dentation being controlled by two independently segregating genes with partial dominance and additive effects.

Support for this result was found in the review by Blixt (1). He reported that besides the gene *Td* in the pea genome there is a semi-dominant gene, *Int (incrementum)*, which determines, together with *Td*, leaflet dentation of the *scalaris forma* type. This gene was described by Lamprecht (4). Its location is unknown.

Another gene coding for a saw-toothed leaflet dentation is the semi-dominant gene *Ser*. Its map location is also unknown. The *serratus* dentation was first described by Sutton in 1914 in *Pisum abyssinicum*. The line WL1325 from the Nordic Gene Bank expresses the classic *Ser* phenotype (Fig. 1), with leaflets dentate at nodes 5 to 9 and weak teeth on the following leaves.

The crosses WL6 x WL1325 and WIR319 x WL1325 were made. The resulting hybrid plants were fully fertile. Plants without toothed leaflets appeared in both F₂ populations. The toothed/without teeth plant ratio was 125:10 (Chi-sq. = 0.31, P>0.5) in the former cross and 209:18 (Chi-sq. = 1.1, P>0.2) in the latter cross. Judging from the number of plants with untoothed leaflets, which constituted about 1/16 part of analysed F₂ plants, these genes segregate independently. Thus, two different genes for "Td-phenotype" are present in the pea genome. They segregate independently from each other and from gene *Ser*. Both these genes, *Td'* of WIR319 and *Td* of WL6, have phenotype expression differing from the expression of *Td* reported by Marx. Perhaps *Td* of WL6 is not the same as *Td* of line A886-193 of Marx. Further genetic experiments are necessary to make clear the genetics of leaflet dentation in pea.

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