Flowering in pea: a mutation from *Lf*^{d} to *lf*^{a} and a summary of induced *Lf* mutations

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Four alleles *Lf*^{d} > *Lf* > *lf* > *lf*^{a} have been identified at the *Lf* (late flowering) locus which shows close linkage with the basic gene for anthocyanin production, *A* (5, 7, 21). These four alleles result in minimum flowering nodes of 15, 11, 8 and 5, respectively, counting from the first scale leaf as node 1 (10). The actual flowering node observed depends on the background for the other flowering genes and the environmental conditions used (10, 14). As a guide, the values in Table 1 give the flowering node ranges usually observed in summer field conditions at Novosibirsk, Russia, and under an 18 h photoperiod in the glasshouse at Hobart, Tasmania, for plants with the background *E Sn Dne Ppd.* This background is found in many domestic cultivars (14). The genotype at the *Hr* locus has little effect on the flowering node under an 18 h photoperiod (6). However, under mild (> 17°C) temperatures and 8 h short day conditions, plants with genotype *lf e Sn Dne Ppd Hr* may produce in excess of 50 vegetative nodes (6). Thus the *Lf* alleles do not determine the maximum flowering node.

The *Lf* gene is about ten times as susceptible to mutation as any of the other major flowering genes in pea (14) and 21 induced mutations have now been identified at this locus (Table 2). The very early flowering mutant XVIII/17 was induced in cv. Vesna by 10 krad of gamma radiation from a ^{60}Co source (M. Vassileva, pers. comm.). On the basis of allelism tests, Uzhintseva and Sidorova (18) concluded that line XVIII/17 was an *lf*^{a} mutant. However, they did not report the genotype of the initial line, Vesna.

We have now obtained results (Table 3) which indicate that Vesna carries the *Lf*^{d} allele. Under an 18 h long day photoperiod (see Table 1 for details), Vesna tended to flower 2-4 nodes later than the standard late (L-type; 10) line, L24. Line 24 carries the same *Lf* allele as the *Lf* type line, L65E, and it has white flowers (*a*). In the F_2, there was a strong association between white flowers and late flowering, and coloured flowers and very late flowering (Table 3), as would be expected if Vesna carried the *Lf*^{d} allele in coupling phase with *A*. There were two obvious recombinants out of 60 F_2 plants which leads to a recombination fraction of 3.3 ± 2.4%. This value is slightly less than the usual value of around 8-10%. The proposed *Lf*^{d}/- segregants overlap the *Lf/Lf* segregants at nodes 18 and 19 but the *Lf* alleles are known to display incomplete dominance (1, 5, 7, 11) and *Lf*^{d}*/Lf* heterozygotes may well account for this overlap. Under the 18 h photoperiod, Vesna tended to flower about two nodes earlier than the type line, WL1771 (= Hobart line 16), and the *Lf/Lf* segregants in the F_2 tended to flower 2 to 3 nodes earlier than the *Lf* parent, L24. These results can be explained if Vesna carries a polygenic background which modifies the expression of the *Lf* alleles toward earliness. Mutant XVIII/17 flowered at node 7 (Table 3) which is consistent with genotype *lf*^{a} (7) as concluded by Uzhintseva and Sidorova (18).

Table 1. Usual flowering node range for plants homozygous for alleles *Lf* ^{d}, *Lf, lf* or *lf* ^{a} grown under summer field conditions at Novosibirsk, Russia (18) or in the glasshouse at Hobart, Tasmania, under an 18 h photoperiod (natural daylight extended before dawn and after dusk by light from a 1:1 mixture of 40 W white fluorescent tubes and 100 W incandescent globes providing 25 µmol m^{-2} s^{-1} at pot top). The temperature in the glasshouse is usually maintained above 13°C. Node counts start from the first scale leaf as node 1 and the flowering gene background is taken as *E Sn Dne Ppd* and *Hr* or *hr*.

Conditions	Genotype			
	Lf^{d}/*Lf*^{d}	*Lf/Lf*	*lf/lf*	*lf*^{a}/*lf*^{a}
Novosibirsk: summer field	20-22	13-16	10-11	7-9
Hobart: glasshouse 18 h	20-24	13-19	9-13	6-8

Table 3. Node of flower initiation data for the standard *Lf* ^{d} line (WL1771), early flowering mutant XVIII/17 (ex Vesna), cv. Vesna (*A*), the standard late (L-type) line L24 (*Lf a*), and F_1 and F_2 populations from the cross Vesna x L24. The plants in the last five rows were grown simultaneously. All plants were grown in the glasshouse under an 18 h photoperiod. Node counts started from the first scale leaf as node 1. The brackets indicate the suggested F_2 segregation for *Lf/Lf* and *Lf*^{d}/- plants.

Line or Cross	Node of flower initiation																	
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
WL1771															1	7	6	5
XVIII/17	3																	
Vesna															2	1		
L24											2	2						
F_1															1	2		
Vesna														1	3			
L24												1	3					
F_1														2				
F_2 (*a/a*)							[1	1	2	5	3	2	1]		[1]			
F_2 (*A/-*)							[1]					[3	13	14	8	5]		

Table 2. A summary of mutations identified at the *Lf* locus.

Mutation type	Initial line	Mutant line	Mutagenic agent	Author mutant	Allelism tests
Lf^{d} -> *Lf*	'Dominant'(WL1771)	WL1770	Neutrons	20	8
Lf^{d} -> *lf*	"	WL1769	Neutrons	20	8
Lf^{d} -> *lf*^{a}	Vesna	XVIII/17	10 krad gamma	19	16, 18
Lf -> *lf*	Torsdag	K319	NEU	17	9, 18
	"	K320	NEU	17	18
	"	K320/1	NEU	17	18
	"	K326	NEU	17	18
	Falensky 42	K398	EMS	17	18
	Porta	Wt11790	200 r Nf	15	11
	"	Wt11791	200 r Nf	15	11
	Paloma	Wt1795[b]	NEU	15	13
	Ranny Zeleny	R9	Callus	2	12
	Ramonsky 77	I/178	100 r Nf	19	1
Lf -> *lf*^{a}	Dippes Gelbe Viktoria	46c	X rays	3	8
	Parvus	P745d	DES	4	8
	"	L629	NMU	17	18
	Torsdag	K2	Gamma	17	9, 18
	"	K578	EMS	17	18
	Falensky 42	K400	EMS	17	18
	Saratovsky mestniy	K418	EMS	17	18
	Kaliski	Wt11796	500 r Nf	15	13

[a] DES = diethyl sulphate, EMS = ethyl methane sulphonate, NEU = nitroso ethyl urea, Nf = fast neutrons, and NMU = nitroso methyl urea.

[b] This mutant allele falls between *lf* and *lf*^{a} (13).

The data in Table 2 now include examples of forward mutation at the *Lf* locus of the type Lf^{d} to *Lf*, Lf^{d} to *lf*, *Lf* to *lf*, *Lf* to lf^{a}, and the most extreme case Lf^{d} to lf^{a}. No examples of back mutation have yet been observed. The agents used to induce these mutations include physical and chemical mutagens, and in one case (2) the mutation arose in callus culture. With a score of 1 for each step down in the allelic series Lf^{d}, *Lf*, *lf*, lf^{a}, physical agents achieved a mean score of 1.67 ± 0.24 (n = 9) and chemical agents a mean of 1.45 ±0.16 (n= 11). These two means are not significantly different (P > 0.3) and bearing in mind that the three treatments to initial lines with the top allele Lf^{d} are all with physical agents, there is no evidence that radiation has caused any more severe change than chemical agents. However, the two cases of gamma radiation have both resulted in large changes from Lf^{d} to lf^{a} and *Lf* to lf^{a}.

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