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Flowering and branching in *Lathyrus odoratus* L.: loci *sp* and *b*

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Summary. A second flowering gene, *Sp*, which influences sensitivity to photoperiod, is identified in the sweet pea, *Lathyrus odoratus* L. Genes *Sp* and Dn^h act in a complementary manner to confer the summer-flowering phenotype and a near obligate long day requirement for flowering in the unvernalized state. Mutations *sp* and Dn^i each diminish the response to photoperiod, and genotypes *sp* Dn^h and *Sp* Dn^i confer a spring-flowering phenotype. Response to photoperiod is further reduced in genotype *sp* Dn^i, which flowers only marginally later than the day-neutral or winter-flowering phenotype characterized by genotypes *Sp dn* and *sp dn* (gene *dn* is epistatic to the gene pair *Sp*/*sp*). Like Dn^i, gene *sp* reduces basal branching, while a branching gene, here resymbolized *b*, is shown to delay flowering in certain circumstances. Gene *dn* largely prevents basal branching in either *b* or *B* plants, but *dn b* plants do produce lateral shoots from the upper nodes, leading to a novel phenotype. The implications of the interactions between genes *sp*, Dn^i, *dn* and *b* are discussed with respect to the control of flowering and branching.

Key words: *Lathyrus odoratus* L. – Flowering – Branching – Photoperiod – Vernalization

Introduction

In the sweet pea, *Lathyrus odoratus* L., the allelic genes *dn*, Dn^i and Dn^h confer the flowering phenotypes DN, LDI and LDH, respectively (Ross and Murfet 1985a). DN cultivars are essentially day-neutral (winter-flowering), while the LDI (spring-flowering) and LDH (summer-flowering) types are quantitative long day plants with LDH lines exhibiting the greater response to photoperiod. In this paper, we identify and characterize a second gene controlling the response to photoperiod, and report on the interactions between the alleles of the two flowering gene loci.

The genes *dn*, Dn^i and Dn^h also exert a pleiotropic effect on branching in the sweet pea (Ross and Murfet 1985a). In short days, the tendency for lateral bud outgrowth increases in the sequence DN, LDI and LDH, with LDH plants branching profusely from the basal nodes. The "bush" or "erect" mutant (Bateson et al. 1908; Punnett 1925) is also described as branching profusely from the lower nodes, and this paper examines the interactions between the "bush" mutant and the flowering genes.

Materials and methods

Seven pure lines were used in this study. Line 4 was derived from cultivar 'Little Sweetheart' (W. Blom and Son, Australia) and is a dwarf (genotype *l*, Ross 1986), bush line with an LDI flowering phenotype. The flowering genotype remains to be determined here. The single gene pair that controls the normal non-bush/bush difference (F_2/f_2) of Punnett (1925) is resymbolized here as *B*/*b* following the system adopted by Scott-Moncrieff (1936) and Ross (1986). Other lines used were 5 (phenotype LDH, tall, non-bush; genotype Dn^h *L B*), 3 (LDI, tall, non-bush; Dn^i *L B*), and 26 (DN, tall, non-bush; *dn L B*). Line 9 (LDI, non-bush; Dn^i *B*) is of intermediate height but carries gene *L*. Two new lines, 37 (from cross 3 × 4) and 38 (from cross 5 × 4), were developed during the course of this work. Sweet peas are entirely self-pollinating under our conditions, and all lines are genetically homozygous. The flowering and branching characteristics for six of these lines are illustrated in Fig. 1. The phenotypes DN, LDI and LDH are defined in relation to the behaviour of specified type lines, respectively lines 14, 9 and 5 (Ross and Murfet 1985a). However, other lines may satisfactorily be used as representatives of these classes, and in Fig. 1, lines 26 and 3 provide data typical of the DN and LDI classes, respectively.

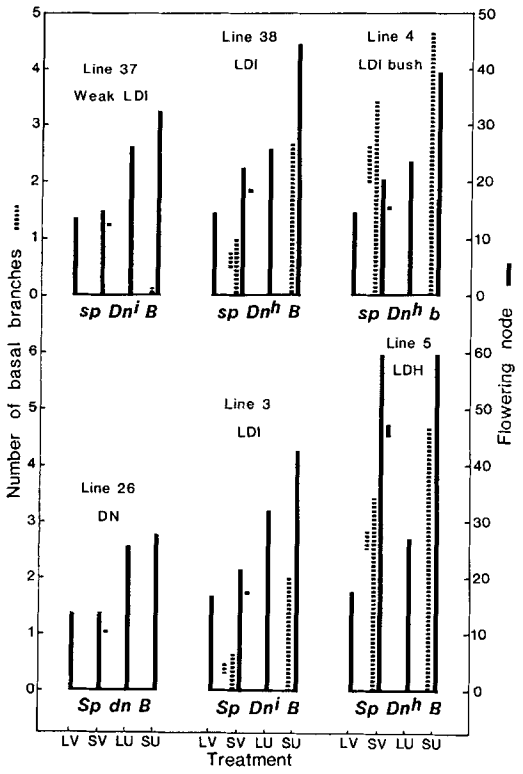

Fig. 1. Effect of photoperiod ($L=24$ h; $S=8$ h) and vernalization (V = vernalized for 4 weeks; U = unvernalized) on flowering node and number of basal branches (primary lateral branches from nodes 1–6 longer than 5 mm on day 44) in six pure lines differing with respect to the flowering genes *Sp/sp* and *Dn^h/Dn^i/dn*, which determine the phenotypes LDH/LDI/DN, and the branching gene pair *B/b* determining the non-bush/bush difference. The s.e. of the mean is shown for the *SV* treatment. $n=6-8$ except for *lines 4* and *5* where $n \geq 4$. The *line 4* plants were grown in a separate experiment to the other lines

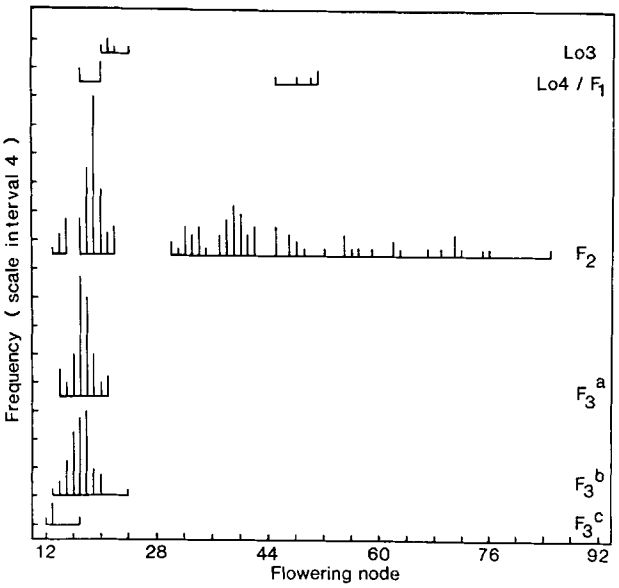

Fig. 2. Distribution of flowering node values for the parents and the F_1, F_2 and F_3 progeny of cross 3 (*Sp Dn^i*) × 4 (*sp Dn^h*). All plants were grown in an 8 h photoperiod, following 28 days of vernalization. The parents and F_1 were grown together, and the F_2 and F_3, in subsequent plantings. F_3 progeny were derived from F_2 plants positively identified by backcrossing. *a*, progeny from 9 *sp Dn^h* F_2 plants with flowering node values 18–20; *b*, progeny from 8 *Sp Dn^i* F_2 plants with flowering node values 17–19; *c*, progeny from 1 *sp Dn^i* F_2 plant (progenitor of line 37) with flowering node 15

The plants were grown in a heated greenhouse as described previously (Ross and Murfet 1985a). During each 24 h cycle, all plants received 8 h of natural light followed by 16 h in chambers (at 16°–17 °C) maintained in darkness (short day conditions) or illuminated by 40 W incandescent bulbs providing an intensity of 3 μmol m^{-2} s^{-1} at pot top (long day conditions). The vernalization treatment consisted of exposing the germinating seeds, after imbibition for 24 h, to a temperature of 3°–4 °C for 28 days.

Hybridization was performed as described by Ross and Murfet (1985a). The following crosses were examined: 3 × 4 (Fig. 2) and 4 × 5 (Table 1, Fig. 3) F_1–F_3 under short day, vernalized (SV) conditions; 4 × 26 (Table 2, Figs. 5 and 6) F_1 and F_2 under SV conditions, and F_3 and F_4 from LDI and DN F_2 plants under short day, unvernalized (SU) conditions; 4 × 37 (text) and 9 × 37 (Fig. 4) F_2 under SU conditions. In addition, F_2 plants from cross 3 × 4 were genotyped by backcrossing. For simplicity, in segregating progenies the notation *B* segregates implies both *B/B* and *B/b* plants.

Flowering node was used as the main index of flowering and defined as the number of the first node on the main stem to bear a flower initial, regardless of whether or not that initial subsequently developed into an open flower. In certain rare cases, as indicated in the text, the number of expanded leaves present at the time of death was used in place of flowering node. All node counts began with the cotyledons as zero. Plant age was measured from the end of the vernalization treatment as day 0. Branching was quantified by either counting the number of lateral branches longer than a certain length (usually 1 cm) or by summing the lengths of individual laterals at specified nodes to give the "total lateral length" per plant (see Ross and Murfet 1985a). Plants lacking vigour were excluded from analyses of branching and internode length. Following the final measurement of branching, lateral branches were removed at regular intervals to ensure the active growth of the main stem. This was particularly necessary for LDH types, in which case laterals were removed approximately once weekly.

Results

Genetic control of the line 4 flowering phenotype: the mutant allele sp

Lines 4 (genotype unknown) and 3 (genotype *Dn^i*) both show flowering behaviour (Fig. 1) typical of the LDI phenotype. However, cross 4 × 3 produced an LDH F_1 and approximately 9/16 LDH plants in F_2 (Fig. 2). Thus, the mutant gene causing the LDI habit in line 4 cannot be allelic with *Dn^i*. Cross 4 × 5 (LDH, *Dn^h*) produced an LDH F_1, the F_2 segregated in accord with a 3 LDH : 1 LDI ratio (observed numbers 64 and 23,

Table 1. Effect of segregation at the *sp* and *b* loci on lateral outgrowth, internode length and flowering of F_2 plants from cross 5 (*Sp Dn*^{h} *B*) × 4 (*sp Dn*^{h} *b*). The plants were grown in an 8 h photoperiod following a 28 day vernalization

Genotype	Phenotype	Leaves expanded on day 22			Stem length between nodes 1 and 8 (cm)[a]			Total lateral length from nodes 2 and 3 on day 22 (mm)			Flowering node		
		Mean	s.e.	*n*	Mean	s.e.	*n*	Mean	s.e.	*n*	Mean	s.e.	*n*
Sp Dn^h *B*	LDH Non-bush	7.24	0.11	42	14.28	0.23	37	34.67	2.97	44	46.02	1.30	50
sp Dn^h *B*	LDI Non-bush	7.36	0.13	14	16.93	0.61	9	12.93	3.08	14	20.71	0.41	14
Sp Dn^h *b*	LDH Bush	6.92	0.18	13	12.12	0.27	14	75.89	8.79	14	60.07	4.41	14
sp Dn^h *b*	LDI Bush	7.00	0.00	5	16.43	0.74	4	29.84	20.7	5	18.13	0.48	8

[a] Dwarf (*l*) segregates were excluded from analysis of stem length

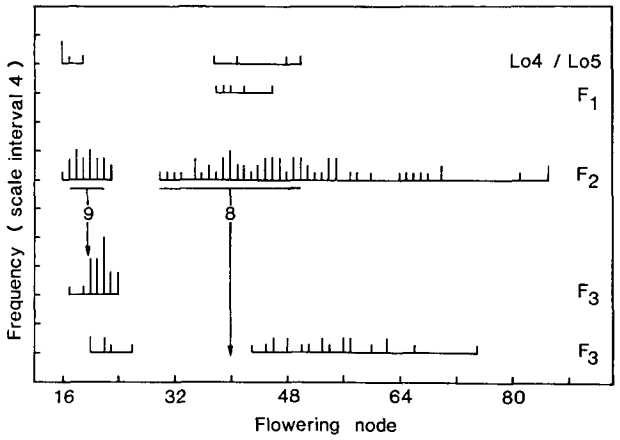

Fig. 3. Distribution of flowering node values for the parents, and the F_1, F_2 and F_3 progeny of cross 5 (*Sp Dn*^{h}) × 4 (*sp Dn*^{h}). All plants were grown in an 8 h photoperiod following 28 days of vernalization. The *arrows* and their *associated numbers* indicate the origin of the F_3 and the number of progenies involved. The parents and F_1 were grown together, and the F_2 and F_3 in subsequent plantings

$\chi_1^2 = 0.10$), and the LDI segregates bred true in F_3 (Fig. 3). The above results show that the LDI phenotype of line 4 is conferred by a recessive allele of a previously undescribed gene, designated here *sp* (spring-flowering). Mutation at this locus, as at the locus *dn*, appears to have occurred spontaneously. The complementary dominant genes *Sp* and *Dn*^{h} together confer the LDH phenotype, while genotypes *sp Dn*^{h} and *Sp Dn*^{i} result in an LDI phenotype.

Effects of gene sp on branching and internode length

In the 4 (*sp Dn*^{h} *b*) × 5 (*Sp Dn*^{h} *B*) F_2, *sp B* segregates branched less from the basal nodes than *Sp B* segregates, as indicated by the highly significant difference ($P < 0.001$) between the means for total lateral length on day 22 (Table 1). Plants of genotype *sp* also possessed significantly ($P < 0.001$) longer internodes between nodes 1 and 8 than did *Sp* segregates (Table 1). These effects appear to have occurred before flower initiation in the *sp* plants (see argument by Ross and Murfet 1985a). Genes *Dn*^{i} and *dn* have been shown to exert pleiotropic effects on branching and internode length (Ross and Murfet 1985a), and it is suggested that gene *sp* acts in a similar manner.

Genotypes sp Dn^h*, sp Dn*^{i} *and sp dn*

The F_2 of cross 3 (*Sp Dn*^{i}) × 4 (*sp Dn*^{h}) (Fig. 2) consisted of 72 LDH plants, 55 LDI plants and 9 plants with low flowering node values (13–15) almost within the DN range under these conditions since accompanying line 26 plants (phenotype DN, genotype *Sp dn*) flowered at nodes 10–13. These numbers are in close agreement with a 9 : 6 : 1 ratio ($\chi_2^2 = 0.61$), and backcrossing indicated that the three phenotypic groups corresponded to genotypes *Sp Dn*^{h} (LDH), *Sp Dn*^{i} and *sp Dn*^{h} (LDI), and *sp Dn*^{i} (earlier than LDI). In the F_3, descendants of known *sp Dn*^{h} F_2 plants exhibited a flowering node distribution similar to that of the F_3 plants produced by known *Sp Dn*^{i} F_2 individuals (Fig. 2), and LDI F_3 plants of genotype *sp Dn*^{h} could not be distinguished from LDI F_3 plants of genotype *Sp Dn*^{i} on the basis of general appearance, degree of branching, internode length (before and after flower initiation) or flowering time. Thus, genes *sp* and *Dn*^{i} exert very similar phenotypic effects. This conclusion is further supported by data (Fig. 1) for lines 38 (*sp Dn*^{h}) and 3 (*Sp Dn*^{i}), which indicate that these two genotypes respond in a similar manner to photoperiod and vernalization, and exhibit a similar pattern of basal branching.

The combined effect of genes *sp* and *Dn*^{i} appears to be greater than the effect of either gene acting alone, i.e. *sp Dn*^{i} plants tend to flower at a lower node than *sp Dn*^{h} or *Sp Dn*^{i} plants. However, the distinction between double recessive and single recessive types was not clear in

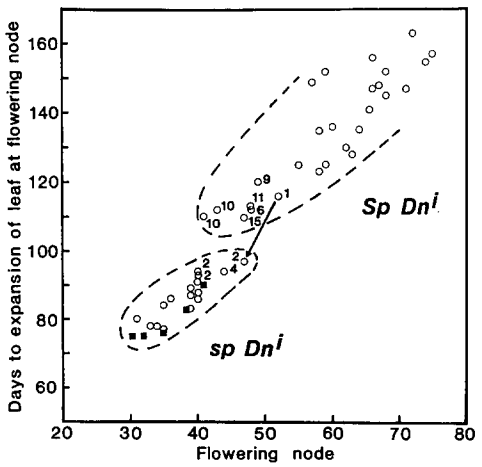

Fig. 4. The time of expansion of the leaf at the flowering node plotted against flowering node for line 37 (■) and for F_2 segregates (o) from cross 37 (*sp Dn*^{i}) × 9 (*Sp Dn*^{i}). The putative boundaries of the *sp* and *Sp* classes are indicated by *broken lines*. For marginal plants, the number of lateral branches greater than 1 cm in length on day 55 is shown. Fifteen F_2 segregates and all line 9 plants flowered later than the limits of the figure. The plants were grown in an 8 h photoperiod without vernalization

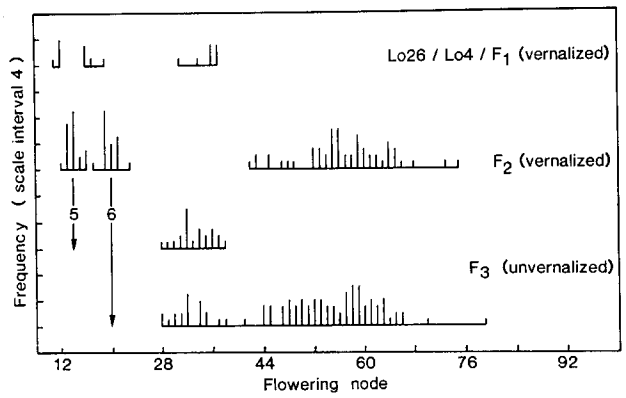

Fig. 5. Distribution of flowering node values in an 8 h photoperiod for the parents and the F_1, F_2 and F_3 progeny of cross 26 (*Sp dn*) × 4 (*sp Dn*^{h}). The parents and F_1 were grown together, and the F_2 and F_3 in subsequent plantings. The *arrows* and their *associated numbers* indicate the origin of the F_3 and the number of progenies involved

the F_3 of cross 3 × 4 where all plants were vernalized. In contrast, segregation for the gene pair *Sp/sp* could be observed on a *Dn*^{i} background in the unvernalized F_2 of cross 37 (*sp Dn*^{i}) × 9 (*Sp Dn*^{i}), particularly when three indices were used to discriminate among the segregates (Fig. 4), e.g. segregates of genotype *sp Dn*^{i} produced fewer basal lateral branches than *Sp Dn*^{i} segregates. Indeed, in the comparison of pure lines (Fig. 1), *sp Dn*^{i} plants (line 37) resembled accompanying DN plants (line 26, *Sp dn*) since they produced few basal lateral branches, and showed no statistically significant response to photoperiod when vernalized and only a relatively small response to photoperiod in the unvernalized state.

Table 2. Effect of segregation at the *dn* and *b* loci on the branching of F_3 plants from cross 26 (*Sp dn B*) × 4 (*sp Dn*^{h} *b*) grown in an 8 h photoperiod without vernalization

Genotype	Phenotype	No. of lateral branches > 10 mm in length on day 49 from nodes 1–7			No. of lateral branches > 10 mm in length on day 49 from above node 7		
		Mean	s.e.	*n*	Mean	s.e.	*n*
Dn^h *B* (*sp*)	LDI Non-bush	5.51	0.16	89	0.02	0.02	89
Dn^h *b* (*sp*)	LDI bush	12.89	0.27	96	3.54	0.20	96
dn B (*Sp* or *sp*)	DN Non-bush	0.29	0.07	41	0.76	0.22	41
dn b (*Sp* or *sp*)	DN Aerial branches	1.27	0.31	22	4.86	0.55	22

The F_2 of cross 26 (*Sp dn*) × 4 (*sp Dn*^{h}) comprised 56 LDH, 19 LDI and 22 DN plants, which is in agreement with a 9 : 3 : 4 segregation ($\chi^2_2 = 0.28$, Fig. 5). In the F_3 generation (grown in short days without vernalization), DN F_2 segregates bred true, while some LDI F_2 segregates produced both LDI and DN types (Fig. 5; the lack of vernalization in the F_3 has substantially increased the flowering node of both types). Therefore, genotypes *dn Sp* (e.g. line 26) and *dn sp* were both phenotypically DN, indicating that gene *dn* is basically epistatic to the *Sp/sp* gene pair.

The mutant allele b (bush)

As expected, the F_2 generation of crosses 5 (*B*) × 4 (*b*), 3 (*B*) × 4 (*b*) and 26 (*B*) × 4 (*b*) segregated approximately 3 : 1 for *B* and *b* plants. The *B/b* gene pair segregated independently of genes at the *dn*, *l* and *sp* loci. Bush (*b*) segregates were generally recognizable because they produced, on average, at least twice as many lateral shoots as *B* segregates (Table 2). In addition, the laterals of *b* plants grew more upright, i.e. at a smaller angle to the vertically trained main stem, than did those of *B* plants, giving young plants a more upright appearance. Indeed, the bush mutant has also been referred to as "erect" (Punnett 1925). For example, in the 26 (*B*) × 4 (*b*) F_2, the mean angle between the longest lateral branch and the main stem on day 32 was 18.9° ± 1.2° ($n = 17$) for *b* LDH segregates, while for *B* LDH segregates, the angle was 39.9° ± 1.2° ($n = 39$) ($P < 0.001$). The profuse branching of *b* types was associated with a smaller main stem apical bud compared with normal plants.

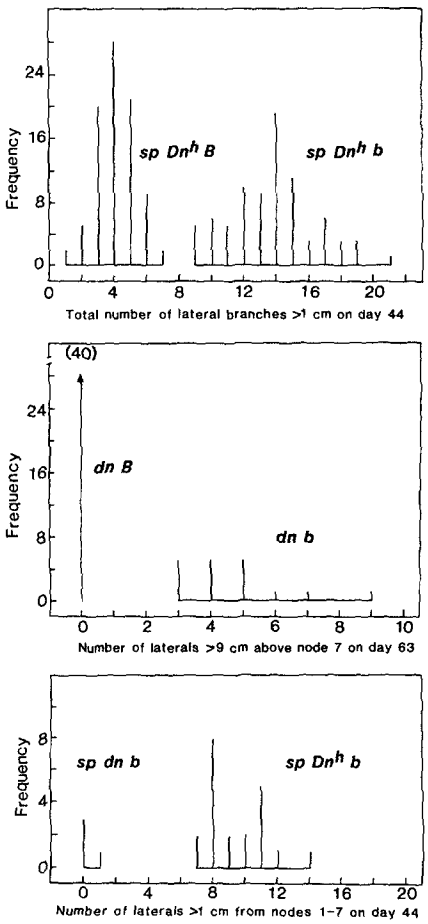

Fig. 6. Distribution of various indices of branching for F_3 plants from cross 26 (*Sp dn B L*) × 4 (*spDn*^{h} *b l*), showing the effects of the *B*/*b* difference on the branching of tall LDI (*sp Dn*^{h} *L*) plants (top), the *B*/*b* difference on the branching of tall DN (*Sp* or *sp, dn L*) plants (centre), and the *Dn*^{h}/*dn* difference on the branching of bush plants (background *sp b*) (bottom). The *dn b* segregates bred true in F_4. All plants were grown in an 8 h photoperiod without vernalization

Interaction of b with the flowering genes

Segregation of the *B*/*b* gene pair was clear in short days on either an LDH (vernalized or unvernalized) or an LDI (unvernalized) background. These conditions and genotypes are conductive to lateral outgrowth, and in these circumstances, gene *b* increased branching still further. Thus, bush (*b*) segregates were easily identified among LDH and LDI plants from cross 26 (*Sp dn B*) × 4 (*sp Dn*^{h} *b*) (e.g. Fig. 6 top, Table 2). While *b* plants could not be identified with certainty among *dn* segregates in the vernalized F_2 of cross 26 × 4, segregation of the gene pair *B*/*b* on a *dn* background could be observed clearly in the F_3 grown in short days without vernalization since *dn b* plants produced more aerial lateral branches (e.g. above node 7; Fig. 6 centre, Table 2) than *dn B* plants. However, gene *dn* markedly reduces the number of basal laterals in either *B* (Ross and Murfet 1985a) or *b* (Fig. 6 bottom) plants, and the two genotypes *dn B* and *dn b* could not be distinguished in the 26 × 4 F_3 on the basis of lateral outgrowth below node 7 since both genotypes exhibited little basal branching (Table 2). Thus, gene *dn* was largely epistatic to the gene pair *B*/*b* in terms of basal branching. On a *b* background, the effect of *dn*, compared with that of *Dn*^{h}, was to shift acropetally the zone of the most vigorous branching from the basal nodes (e.g. 1–7) to the more aerial nodes (e.g. above 7). The effect appears to be exerted before flower initiation in the *dn b* plants, since it was apparent when approximately 17 leaves had expanded (i.e. day 49; Table 2), whereas the mean flowering node of *dn b* plants was 35.59 ± 0.54. Thus, in short days, genotype *dn b* produced a novel phenotype consisting of very few basal branches, but at least several vigorous aerial lateral branches.

The effect of gene b (bush) on flowering

The presence of gene *b* did not change the flowering phenotype of *dn* segregates in cross 26 × 4; these plants remained DN. However, under certain circumstances, the presence of gene *b* resulted in a substantial temporal and plastochronic delay in flowering. For example, in the 5 (*Sp Dn*^{h} *B*) × 4 (*sp Dn*^{h} *b*) F_2 (grown in short days after seed vernalization), the mean flowering node of LDH *b* segregates was 31% greater than that of LDH *B* segregates ($P < 0.01$, Table 1). Consequently, *B* LDH plants produced visible flower buds more quickly than *b* segregates; for example on day 99, 74% of *B* LDH segregates, but only 7% of *b* LDH segregates, possessed visible flower buds. Similar results were observed in the LDH segregates of two other crosses: 3 (*B*) × 4 (*b*) (30% difference in flowering node; $P < 0.01$) and 26 (*B*) × 4 (*b*) (7.4% difference in flowering node; $P < 0.05$). In all progenies, however, there was some overlap between the flowering node values of *b* and *B* LDH segregates.

We suggest that the generally later flowering of *b* compared with *B* LDH segregates represents a pleiotropic effect of gene *b*. While the alternative hypothesis involving a flowering gene tightly linked to *b* cannot be discounted, this study has not revealed one unequivocal recombinant type.

A flower-delaying effect of gene *b* was also apparent in LDI segregates grown without seed vernalization, e.g. in the F_2 of cross 37 (*sp Dn*^{i} *B*) × 4 (*sp Dn*^{h} *b*), the mean flowering node of *sp Dn*^{h} *b* plants was 13% greater than that of *sp Dn*^{h} *B* plants ($P < 0.05$). However, the delaying effect of gene *b* was not manifest on an LDI background after seed vernalization. In fact, in vernalized progenies, LDI *b* segregates often flowered a little earlier than LDI *B* segregates (e.g. Table 1).

Discussion

In the sweet pea, two flowering gene loci have now been identified: *dn* (Little and Kantor 1941; Ross and Murfet 1985a), and *sp*. Genes *Sp* and Dn^h are complementary, and both must be present to confer the wild-type LDH (late-or summer-flowering) phenotype. This suggests that *Sp*, like Dn^h, controls a step in the biosynthetic pathway previously postulated to produce a flower inhibitor in short days in *Lathyrus odoratus* (Ross and Murfet 1985b). Genotypes *sp* Dn^h and *Sp* Dn^i each confer a similar LDI (spring-flowering) phenotype, and LDI plants still display a substantial response to photoperiod (e.g. Fig. 1). These facts suggest that the mutations *sp* and Dn^i impose only partial blocks in the biosynthetic pathway, and that *sp* and Dn^i each block production of the postulated flower inhibitor to a very similar extent. Genotype *sp* Dn^i confers a phenotype intermediate between LDI and DN, but possibly shows greater affinity with the DN class (Fig. 1). Thus, when present together, the two leaky mutations *sp* and Dn^i impede the pathway almost as much as the presence of the more severe mutation *dn*. The severity of the block imposed by *dn* is apparent from the essentially day-neutral habit which it confers (Ross and Murfet 1985a; Fig. 1) and the fact that *dn* prevents expression of the *Sp*/*sp* difference (Fig. 5).

There is long-standing evidence that garden peas (*Pisum sativum* L.) also produce a flower inhibitor in short days (Barber and Paton 1952; Murfet 1971; Murfet and Reid 1973), and two synthesis mutants in that species, *sn* (Barber 1959) and *dne* (King and Murfet 1985), appear to play a similar role to mutants *dn* and *sp* in sweet pea. Results from inter-generic grafts suggest that the same inhibitor pathway is common to at least three allied genera, *Lathyrus, Pisum* and *Vicia* (Ross and Murfet 1985; Murfet and Groom 1988), but the chemical nature of the inhibitor and the identity of the particular steps influenced by the several synthesis mutants remain to be determined.

Under the short day conditions used here, the flowering genes *Sp* and Dn^h are associated with increased basal branching and delayed flower initiation. It is suggested (Ross and Murfet 1985a) that this flowering delay may be due to reduced nutrition of the main shoot apical bud in profusely branching plants. This interpretation is further supported by the fact that the branching gene *b* is associated not only with increased branching but also with a reduction in the size of the apical bud and, in certain circumstances, a delay in flower initiation. Conversely, the action of factors which promote flowering in *L. odoratus* (such as gene *dn*) may involve a concentration of growth activity in the apical portion of the main stem. Consistent with this view is the observed effect of the flowering genes on the branching pattern of *b* plants (in short days): DN *b* plants tend to produce branches from the upper nodes, but not from the basal nodes. In contrast, lateral bud outgrowth in LDH and LDI *b* plants (as in LDH and LDI *B* plants) tends to occur more from the basal than the upper nodes. Thus, the observations reported here lend support to theories which assign a regulatory role to nutrient diversion in the control of branching and flowering (Phillips 1975; Sachs and Hackett 1969, 1977).

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