Characterization of Topiary (*top*) an Architectural Mutant of Common Bean

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ABSTRACT. Plant breeders are interested in developing upright common beans (*Phaseolus vulgaris* L.) to reduce diseases and permit mechanical harvest, and improve seed quality. Morphological and genetic characteristics of an architectural mutant in common beans were studied. The mutant had shiny, dark green leaves, overlapping leaflets, and short petioles. Branching was nearly absent, resulting in single stemmed plants. Although mutant plants carried *Fin* for indeterminacy, and plants progressed in flowering from lower to higher nodes, the terminal node was reproductive. This represents a new form of determinacy in common bean. Inheritance studies demonstrated that the mutant syndrome was controlled by a single recessive gene. Allelism tests between the mutant and overlapping leaflets (*ol*), and dark green savoy leaf (*dgs*) showed that the mutant was not allelic to either locus. The trait was designated as Topiary with the gene symbol *top*, describing its compact and neat appearance. Linkage was tested between *top* and growth habit (*fin*), shiny leaves, cross-sectional shape of pods, striped pod (*C prpst*), and pod suture strings. All genes segregated independently. The genetic merit of the Topiary mutant for improving common beans needs to be investigated, especially the value of single stem growth habit combined with an upright plant habit.

Plant breeders have been interested in using architectural traits to avoid disease, and to improve grain quality, lodging resistance, and yield (Coyne, 1980). Plant architecture may be critical to success of dry bean cultivars (*Phaseolus vulgaris* L.) in various cropping systems (Kelly and Adams, 1987). Varieties in the kidney market class are determinate because growers require a bean that matures uniformly and quickly. The indeterminate vine architecture characteristic of small red, pinto, pink and great northern market classes is associated with higher yields compared to determinate types (Myers, 1992). Growers in the western United States have used cultivars with a floppy vine (type III) habit because these types produce the highest yields, and upright architecture is not needed to avoid foliar diseases. Midwestern growers have greater foliar disease problems, and have preferred upright short vine cultivars that sacrifice some yield potential, but avoid disease. A prostrate growth habit creates considerably more risk of harvest losses from white mold [*Sclerotinia sclerotiorum* (Lib.) de Bary] (Kelly and Adams, 1987), and Coyne (1980) suggested that severity of white mold could be reduced considerably by developing dry edible beans that have an upright architecture with porous canopy.

Upright plant architecture allows use of direct harvest systems with narrow row spacing, high plant populations, and a flat planting surface. Narrower rows and higher plant populations cause pods to form higher on the plant and allow better competition with weeds. Compared to traditional production systems, less energy is used when direct harvest is incorporated (Smith, 1996).

Four principal growth habits were identified by researchers at Centro Internacional de Agricultura Tropical (CIAT) based on

determinate or indeterminate habit, number of nodes, internode length, climbing ability, and degree and type of branching. Growth habits are Type I, determinate bush; Type II, indeterminate short vine; Type III, indeterminate prostrate nonclimbing vine; and Type IV, indeterminate climbers (Fernandez, et al. 1986). Another growth habit category not included in this classification is the determinate climber (Deboucq et al., 1988). The mutant trait described herein affects plant architecture. The objectives of this study were to perform a genetic analysis of the mutant trait, including inheritance, linkage, and allelism studies, and to characterize the morphology of the mutant.

Materials and Methods

The mutant line used in this study was first observed and selected in 1995 in the small red (dry bean) breeding line 611413 from the cross 'UI 35'/'NW 59'/92001 by J.R. Myers at the University of Idaho (UI) Kimberly Research and Extension Center, Kimberly, Idaho. UI 35 is a small red bean cultivar released in 1959 by the UI (LeBaron, 1959). NW 59 is also a small red cultivar developed by the USDA-ARS at Prosser, Wash. (Burke, 1982). The breeding line 92001 was used in the UI breeding program, and derived from the cross 'UI 36'/6917 where UI 36 is another small red cultivar (Dean and LeBaron, 1964) and 6917 is a large seeded purple mottled cranberry type breeding line of the Andean center of origin. Seeds from fertile plants with strong expression of the mutant syndrome were harvested to initiate the line. In three generations of self-pollination, the line was stable and true breeding. The four parental lines were chosen to represent different bean types and were crossed to the mutant to study its inheritance. 'Oregon 91G' is a Type I bush blue lake green bean developed at Oregon State University (Baggett et al., 1981). 'Minnette' is a Type I small sieve green bean obtained from Harris Moran Seed Company, Modesto Calif. Genetic stock 5-593, obtained from Mark Bassett, University of Florida, Gainesville, also has a Type I growth habit. 'UI 906' is a Type II upright, early maturing black bean developed in the UI dry bean breeding program (Myers et al., 1991). Table 1 summarizes phenotypic characteristics of the parents used in this study.

Mutant plants were crossed, using standard emasculation

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Table 1. Characteristics of the parents used in a genetic analysis of a mutant in common bean.

Line	Growth habit ^a	Allele at <i>Fin</i> locus	Market class	Flower color	Pod cross-section	Seed luster	Seed color	Fiber in pod suture
Oregon 91-G	Type I	<i>fin fin</i>	Green bean	White	Round	Dull	White	Absent
Minuette	Type I	<i>fin fin</i>	Green bean	White	Round	Dull	White	Absent
5-593	Type I	<i>fin fin</i>	Genetic stock	Purple	Flat	Shiny	Black	Present
UI-906	Type II	<i>Fin Fin</i>	Black bean	Purple	Flat	Dull	Black	Present

^aType I = determinate bush, type II = indeterminate upright short vine.

procedures (Bliss, 1980), with the four parent lines to produce crosses and reciprocals in Spring 1997. F₁ progeny were grown in the field and greenhouse to produce F₂ populations. A total of 576 F₂ seeds were planted in a greenhouse in Fall 1997, representing 144 plants per cross, including reciprocals. Data on normal or mutant type and growth habit type were evaluated in these F₂ populations. The F₂ plants were harvested individually when the pods and seeds were dry. All F₃ seeds taken from F₂ populations were field planted as 576 plots (families) in Summer 1998. In addition, 250 remnant F₂ seeds from each of eight crosses were planted. Data were collected for normal or mutant type from F₂ and F₃ populations.

Allelism tests were conducted to determine whether the new mutant was allelic to *ol* (*overlapping leaflets*), (Nagata and Bassett, 1984) and *dgs* (*dark green savoy leaves*), (Frazier and Davis, 1966). Seeds of genetic stocks PI 583648 carrying *ol* and PI 583622 with *dgs* were obtained from the Western Regional Plant Introduction Station, Pullman, Wash. The new mutant was crossed to the *ol* and *dgs* stocks in the greenhouse in Spring 1998. Eighteen F₁ plants of each cross combination and reciprocal were grown in the greenhouse in Summer 1998. Fifty F₂ plants of each cross combination and reciprocal were planted in the greenhouse in Winter 1999. The F₁ and F₂ populations were evaluated for traits associated with the three mutants, as well as other traits segregating in these crosses.

Chi-square tests for goodness of fit and homogeneity were used to examine segregation ratios in F₂ and F₃ populations (Mather, 1951; Ramsey and Schafer, 1997). Contingency chi-square test for independence (Everitt, 1977) was used to test for linkage in two point segregation data. The contingency chi-square test of independence makes no prior assumptions about segregation ratios and was the preferred method because inheritance of some traits was not known and/or some segregation ratios deviated from expected segregation ratios.

Results

MORPHOLOGICAL DESCRIPTION. We chose Topiary as the designation for the trait because of the resemblance of the mutant to shrubby from a topiary garden (Fig. 1A). The original genetic background of the mutant is the small red market class with

type III indeterminate growth habit, white flowers, medium-sized shiny red seeds, and flat, fibrous, stringy pods. Traits associated with the mutant phenotype include a single stem, dark green leaves that are thicker, smaller, and more brittle than normal leaflets, and determinate growth habit with long internodes. Long internodes and weak stems contribute to a floppy habit.

Fig. 1. The Topiary architectural mutant of common bean. (A) Growth habit of Topiary plants; (B) comparison of Topiary (above) and 'Minuette' (below) leaves showing differences in rachis, petiolule, and petiole lengths (leaflets have been separated from petiole); (C) leaf of the Topiary mutant showing reflexed terminal leaflet compared to the lateral leaflets; and (D) terminal node from a Topiary plant showing inflorescence development, and demonstrating that Topiary is determinate.

Table 2. F₂ segregation data for the Topiary common bean mutant crossed to tester lines and grown in the greenhouse (1997) and at the Oregon State Univ. Vegetable Farm (1998).

Cross ^z	No. of plants		χ^2 (3:1)	P
	Normal	Mutant		
Topiary mutant x 91G	213	69	0.042	0.83
91G x Topiary mutant	205	69	0.004	0.94
Topiary mutant x Minuette	196	61	0.219	0.63
Minuette x Topiary mutant	194	60	0.257	0.61
Topiary mutant x 5-593	197	56	1.108	0.29
5-593 x Topiary mutant	208	66	0.121	0.72
Topiary mutant x UI 906	218	68	0.228	0.63
UI 906 x Topiary mutant	224	71	0.136	0.71
Combined	1655	520	1.383	0.23
Homogeneity ^y			0.735	0.99

^zGreenhouse and field populations pooled by cross after chi-square test of homogeneity.

^yHomogeneity df = 7.

Terminal and lateral leaflets overlap as a result of a shortened rachis and the acute angle of lateral leaf petiolules (Fig. 1B). Lateral petiolules of the mutant averaged 3.0 ± 0.3 mm and the rachis averaged 20.0 ± 0.7 mm compared to 5.0 ± 0.3 mm and 35.0 ± 0.8 mm, respectively, for normal leaves of 'Minuette'. The mutant had 36.0 ± 0.7 mm petioles compared to 116.0 ± 1.1 mm for 'Minuette'. The terminal leaflet pulvinus may be abnormal because the terminal leaflet is sometimes reflexed below the plane of the lateral leaflets (Fig. 1C).

The terminal node is a reproductive bud (Fig. 1D), but unlike determinacy conditioned by *fin*, the Topiary mutant begins flowering at a lower node, and proceeds up the stem. Whereas plants with *fin* usually begin flowering at the terminal node, the terminal bud on Topiary is usually the last to open. The Topiary mutant flowers between the 4th and 21st node with time to bloom and node of bloom delayed by increasing daylengths. We do not know if photoperiod sensitivity is a pleiotropic effect of Topiary, or associated with the genetic background of the line.

INHERITANCE. Crosses between Topiary and four normal bean lines produced F₁ progeny with normal morphology and an indeterminate growth habit, indicating that the mutant trait is recessive. Because '91G', 'Minuette', and 5-593 possess *fin*, Topiary must have *Fin*. The F₂ and F₃ segregation data were tested against the expected ratios for a single recessive gene. The F₂ segregation data obtained from the greenhouse and the field supported an expected 3 normal : 1 mutant ratio (Table 2). The data were homogeneous, indicating that all crosses represented

the same population and no differences were observed between the crosses and their reciprocals. These results are consistent with the hypothesis that a single recessive gene controls the Topiary mutant. When F₃ families were tested for goodness of fit to an expected 1 normal : 2 segregating: 1 mutant ratio (Table 3), the data supported the expected ratio and were homogeneous. Within the segregating families, a 3:1 ratio of normal to mutant plants was observed (Table 3). These data were also homogeneous. The F₃ segregation results confirm the hypothesis that a single recessive gene controls the Topiary mutant.

TESTS OF ALLELISM. Because Topiary might be an allele at the *Fin* locus, we examined cosegregation of Topiary and *fin*. Growth habit conditioned by *Fin* segregated in three of the four crosses—'91G', 'Minuette', and 5-593 (Table 4)—but not with 'UI 906' (data not presented). Topiary and *fin* could be distinguished individually by their distinctive phenotypes. The double recessive plants were small and compact, and exhibited the determinacy pattern of *fin* with the leaf characteristics of Topiary. Thus, determinacy conditioned by *fin* appears to be epistatic to that of Topiary. *Fin* segregated as a single recessive gene and was independent of Topiary (Table 4). There were some apparent disturbances in the segregation ratios. Although one cross (5-593 x Topiary) deviated significantly from the expected ratio (fewer individuals than expected in the double recessive class were observed), the reciprocal fit the expected ratio. Two other crosses ('91G' x Topiary and 'Minuette' x Topiary) had near significant deviations from expected at $P=0.05$. In both cases, more individuals

Table 3. Segregation of F₃ families of the Topiary common bean mutant crossed to tester lines grown in 1998.

Cross	No. of families			χ^2 (1:2:1)	P
	Normal	Segregating ^z	Mutant		
Topiary mutant x 91G	17	33	16	0.030	0.98
91G x Topiary mutant	15	30	21	1.636	0.44
Topiary mutant x Minuette	21	28	14	2.284	0.31
Minuette x Topiary mutant	15	30	14	0.050	0.97
Topiary mutant x 5-593	23	33	10	5.121	0.07
5-593 x Topiary mutant	21	29	20	2.085	0.35
Topiary mutant x UI 906	17	31	17	0.138	0.93
UI 906 x Topiary mutant	18	24	21	3.857	0.14
Combined	147	238	133	4.162	0.12
Homogeneity ^y				11.041	0.68

^zSegregation within segregating families fit a 3:1 ratio (3271 normal:1146 mutant, $\chi^2 = 2.104$, $P = 0.14$; homogeneity $\chi^2 = 3.723$, df = 7, $P = 0.81$).

^yHomogeneity df = 7.

Table 4. Test of independence for *Topiary* and *Fin* in an F_2 population of common bean.

Cross	No. of plants				χ^2	<i>P</i>
	Normal <i>Fin</i> --	Normal <i>finfin</i>	<i>Topiary Fin</i> --	<i>Topiary finfin</i>		
<i>Topiary</i> mutant x 91G	38	12	10	7	1.842	0.17
91G x <i>Topiary</i> mutant	37	10	12	9	3.357	0.06
<i>Topiary</i> mutant x Minuette	30	22	5	7	1.011	0.31
Minuette x <i>Topiary</i> mutant	35	11	7	7	3.478	0.06
<i>Topiary</i> mutant x 5-593	43	14	8	5	1.034	0.30
5-593 x <i>Topiary</i> mutant	36	15	20	1	5.229	0.02
Combined ²	219	84	62	36	2.867	0.09
Homogeneity ³					13.084	0.02

²Segregation of *fin* fits a 3:1 ratio ($\chi^2 = 2.51$, df = 3, *P* = 0.11).

³Homogeneity df = 5.

than expected in the double recessive class were observed. An apparent systematic deviation when *Topiary* is the male in crosses is an artifact stemming from the use of contingency chi-square to test for independence of the traits (Table 4). When fit to a 9:3:3:1 ratio, these systematic deviations disappear. Overall, homogeneity chi-square was statistically significant, not permitting pooling of the data. The deviations were not consistent with the hypothesis of linkage, and the causes of these deviations are unknown.

Phenotypically, *ol* and *dgs* share some features of the *Topiary* mutant. *Topiary* and *dgs* both had dark green glossy leaves whereas *Topiary* and *ol* had overlapping leaflets. Expression of overlapping leaflets was less extreme for *ol* under Oregon greenhouse conditions compared to *Topiary*. The *ol* and *dgs* mutants showed normal growth habit and determinacy conditioned by *fin*, compared to the distinctive architecture of *Topiary*. All F_1 s from crosses of *Topiary* with *ol* and *dgs* produced progeny with normal phenotype with regard to the mutant traits. The F_1 progeny also exhibited a combination of traits (normal leaves, indeterminate climbing habit, and purple flowers) not found in either parent indicating that the progeny were the results of hybridization and not self-pollination. In the F_2 , we were able to distinguish three phenotypic classes (normal, *Topiary*, and *ol* or *dgs*), but did not observe individuals in the double recessive class. (Table 5). Populations were small but should have been sufficient to detect the double recessive.

LINKAGE. Independent gene segregation was tested between *Topiary* and flower color (*V* and *P*), pod color (*C prp*^u), pod cross-sectional shape (oligogenic inheritance), shiny leaves (genetic control unknown), and pod suture strings (oligogenic inheritance). The test of allelism between *top* and *fin* reported above also served as a test of linkage. No evidence of linkage was detected in any of the crosses (data not presented).

Discussion

The *Topiary* mutant has a complex of traits that distinguishes it from other bean mutants. Most prominent are shiny, dark green leaves on a shortened rachis, petiolules, and petioles that cause overlapping leaflets. These leaflets are thicker, more brittle and smaller than the leaflets of normal plants. The *Topiary* mutant begins blooming at a lower node, and proceeds to bloom in both directions, but mostly upward from that node. The terminal bud is reproductive rather than vegetative as is normally found in indeterminate lines. This is a new form of determinacy in common bean.

In crosses of *Topiary* to lines carrying *ol* and *dgs* for tests of allelism, the double recessive class was not observed. We suspect that epistasis masks expression of *Topiary* in the double recessive. Intuitively, we would expect *Topiary* to be epistatic to both *ol* and *dgs*, however, the small population size did not allow us to differentiate between 9:3:4 and 9:4:3 segregation ratios. These results indicated that the *Topiary* mutant is not allelic to *ol* or *dgs*. We propose the designation *top* as the gene symbol for this mutant. The gene symbol *top* is an abbreviation for *Topiary* describing the neat, compact appearance of this mutant.

Short petiole or petiolule traits have been studied in soybean [*Glycine max* (L.) Merr.] (Cary and Nickell, 1999; Kilen, 1983; You et al., 1998). The short-petiole trait of breeding line D76-1609 was inherited as a single recessive gene (Kilen, 1983). You et al. (1998) reported a new short-petiole mutant in the breeding line NJ90L-1SP. Genetic analysis showed a single locus inheritance when NJ90L-1SP was crossed to 'Nannong 86-4'. However, two-locus inheritance was found when NJ90L-1SP was crossed to a sister line, NJ90L-2. Tests of allelism conducted between the breeding lines NJ90L-1SP and D76-1609 indicated nonallelism because all F_1 plants had long petioles. The gene symbol *lps*₁ was

Table 5. F_1 and F_2 tests of allelism between *Topiary* and *ol*, or *dgs* common bean mutants.

Cross ²	No. of plants				Expected ratio ³	χ^2	<i>P</i>
	Normal <i>Ol/Dgs</i> — <i>Topiary Ol/Dgs</i>	Normal <i>ol/dgs</i>	<i>Topiary ol/dgs</i>				
<i>Topiary</i> x <i>ol F</i> ₁	36	0	0	0	1:0:0:0	0.0	1.0
<i>Topiary</i> x <i>dgs F</i> ₁	36	0	0	0	1:0:0:0	0.0	1.0
<i>Topiary</i> x <i>ol F</i> ₂	24	9	17	0	9:3:3:1	2.240	0.33
<i>Topiary</i> x <i>dgs F</i> ₂	22	12	16	0	9:3:3:1	3.051	0.22
Combined	46	21	33	0	9:3:4	4.698	0.10
					9:3:3	11.767	0.003

²Cross and reciprocal combined.

³For a 9:3:4 ratio, we assume that double recessive individuals are counted in the Normal *ol/dgs* class. The hypothesis for a 9:3:3 ratio is that the double recessive class is missing.

proposed for the recessive gene carried by D76-1609 and *lps₂* was proposed for the recessive gene discovered in NJ90L-1SP.

Cary and Nickell (1999) reported a mutant in the soybean line LN89-3502TP in which petiolules of the plant were shorter than normal and leaflet margins curled uniformly upward forming a cupped-shaped leaf. The trait was controlled by a single gene showing incomplete dominance, and was given the gene symbol *lc*.

The Topiary mutant arose spontaneously from an Andean x Mesoamerican cross (Gepts, 1988). Several mutations affecting growth habit, including multiple primary leaves, dwarf plant habit, and an *aphyllus* mutant (Lamprecht, 1958), have been observed from such crosses (J.R. Myers, unpublished data). The Andean and Mesoamerican centers of origin are separated by about 4000 km, which has allowed populations to diverge genetically. While not separate biological species, certain genetic incompatibilities such as dwarf lethal genes (Gepts, 1988) are manifested upon crossing. The Topiary mutant may represent another example of this Andean-Mesoamerican incompatibility.

In other plant species, mutations in the cytokinin and auxin pathways can cause abnormalities similar to those seen in Topiary (Dean, 1998; Estruch et al., 1993; Felix et al., 1996; Levy and Spena et al., 1991; Strabala et al., 1996). No mutant has been described that shows the complete set of abnormalities of Topiary although the Waldmeister mutant in *Arabidopsis thaliana* (L.) Heynh. converts indeterminate inflorescences into determinate ones as well as affecting leaf shape (Felix et al., 1996). The Topiary mutant may represent a mutation in a regulatory gene involved in fundamental metabolic processes, with effects on possibly more than one biochemical pathway.

Singer et al. (1990) studied a determinate mutant (*det*) of pea (*Pisum sativum* L.). They reported that the apparent terminal flower arises from an axillary meristem. The terminal meristem senesces and differentiates trichomes, forming a rudimentary stub in the same manner as axillary meristems of conventional (*Det*) plants. Thus, the effect of the *det* gene on inflorescence architecture results from early apical arrest rather than conversion of terminal meristem. To our knowledge, no studies in bean have examined the ontogenesis of determinacy conditioned by *fin*. We also do not know if Topiary conditions determinacy in a manner similar to *det* in peas.

The genetic merit of this mutant needs to be investigated using several breeding approaches. Because the Topiary mutant has a single stem, closer row spacing may be achieved for higher planting populations. However, some of the other pleiotropic effects of this recessive gene may be detrimental to economic use of the trait for common bean improvement. Overlapping leaflets could make favorable conditions for white mold development. If most flowers protrude beyond the foliage, this could affect pod set in hot climates and reduce yield. These effects need to be determined. Placed into an upright background with pod placement off the ground, Topiary may provide a plant type suitable for direct harvest. We do not know the effects of the gene for Topiary on yields in comparison to cultivars with normal growth habit. The transfer of Topiary into upright, near isogenic backgrounds and comparison to commercial cultivars is a goal of our program.

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