Characterization of Blossom-end Morphology Genes in Tomato and Their Usefulness in Breeding for Smooth Blossom-end Scars

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Abstract. Pointed blossom-end morphology may be used to reduce blossom-end scar size in large-fruited, fresh-market tomatoes (*Lycopersicon esculentum* Mill.). The usefulness of this characteristic has been limited due to persistence of pointedness on mature fruit, resulting in postharvest bruising, and to close association of pointedness with leaf curl, which may increase foliar disease problems. The inheritance of pointedness in three breeding lines (NC 140, Fla 890559-24, and Fla 894413-1) and four accessions with previously described blossom-end morphology genes [LA 2-5 with persistent style (*pst*), LA 986 with beaky (*bk*), LA 1787 with beaky-2 (*Bk-2*), and LA 2353 with nipple tip (*n*)] was investigated. In F_1 s and F_2 s of crosses with wild types, some pointedness was observed in heterozygotes, but the level of expression was generally close to wild type expression, except for LA 986. Consequently, *Bk-2* in LA 1787 was renamed *bk-2*. F_1 complementation tests were difficult to interpret. Wild types segregated in F_2 s of all complementation crosses, except for LA 986 $\times$ LA 2-5, a result indicating the presence of the same gene in these two accessions. Three new nipple-tip genes were named; *n-2* in NC 140, *n-3* in Fla 890559-24, and *n-4* in Fla 894413-1. None of the seven accessions tested had significant leaf curl. Early identification of mutant plants by the shape of the stylar base in flowers at anthesis was reliable only for *bk*. Various blossom-end morphology genes may be backcrossed into otherwise desirable breeding lines, and complementing parents may be intercrossed to obtain optimal smoothness in the hybrid without undesirable pointed mature hybrid fruit.

A common method in breeding for resistance to rough blossom-end scarring in large-fruited, fresh-market tomatoes is to select genotypes with a pointed blossom-end morphology. Unfortunately, in many breeding lines, pointedness is associated with adaxial leaf curl (Gardner, 1990, 1992), which may result in increased foliar disease problems (Gardner and Nash, 1987; Nash and Gardner, 1988). Pointedness is usually most pronounced in young, immature fruit and gradually disappears as the fruit matures. The expressivity of pointedness differs from season to season and, under undefined environmental conditions, pointedness may persist on mature fruit, leading to bruising at the blossom-end and postharvest decay. Expressivity of pointedness also varies with genetic background. Problems with leaf curl and persistence of pointedness prompted investigation of blossom-end morphology genes previously described in the literature and a search for new sources of pointedness to define alternative strategies for blossom-end scar improvement.

Several blossom-end morphology genes have been described in the literature. Nipple tip (*n*) produces a nipple-like protuberance on the blossom-end (MacArthur, 1934) and has been assigned to chromosome 5 (Mutschler et al., 1987). Segregation of 3 normal : 1 nipple tip in F_2 generations suggested a single recessive gene

(Young and MacArthur, 1947); however, Tikoo and Anand (1984) reported that nipple tip in their material was controlled by two different genes. In plants with persistent style (*pst*), styles remain attached to the ovary, resulting in strongly beaked fruit (Rick, 1945). Persistent style is mapped on chromosome 7 and is tightly linked to green stripe (*gs*) in repulsion phase (Rick, 1966). Beaked fruit (*bk*) is characterized by a prominent pointed beak on the blossom-end (Young and MacArthur, 1947) and has been located on chromosome 2 (Rick and Butler, 1956). Bouwkamp and Honma (1970) reported a second, dominant allele (*Bk-2*) associated with beaked fruit, but did not test allelism with *bk*, *n*, or *pst*.

Two breeding lines with pointed immature fruit, but without genetic leaf curl, were obtained from breeding programs at North Carolina State Univ. and the Univ. of Florida (NC 140, Fla 890559-24). Another breeding line, Fla 894413-1, has some leaf curl but less than NC 8276 from which its nipple-like fruit were derived. Fla 894413-1 represents a gene that is probably used in many breeding programs. The purpose of this study was to investigate the inheritance of pointedness in these new sources and to investigate the relationship between the blossom-end morphology genes in these new sources and the genes described in the literature. The usefulness of each blossom-end morphology gene for breeding toward smooth blossom-end scars is discussed.

Materials and Methods

Genetic material. Accessions with the four previously described blossom-end morphology genes were obtained from the Tomato Genetic Stock Center at Davis, Calif. (Table 1). LA 2-5 and LA 986 were characterized by prominent, pointed, columnar blossom-ends in immature and mature fruit. This blossom-end

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morphology was identified as p-type (Fig. 1). Both LA 2-5 and LA 986 had low fruit set. Pointedness due to *Bk-2* in LA 1787 was clearly distinguishable in immature fruit, but only moderately in mature fruit. LA 2353 (*n*) segregated ovate and round fruit shape, both with strongly pointed blossom-ends. Seed from plants with ovate fruit bred true and was selected for this experiment. The breeding lines NC 140, Fla 890559-24, and Fla 894413-1 had pointed blossom-ends, but no significant leaf curl, especially in the former two (Table 1). As mentioned earlier, Fla 894413-1 was derived from NC 8276, a line with pointed blossom-ends and genetic leaf curl. Pointedness was expressed most weakly in NC 140, in which it was confined to immature fruit only. The characteristic was more pronounced in Fla 890559-24 and Fla 894413-1 with some pointed mature fruit. LA 1787, LA 2353, and the three breeding lines had rounded blossom-ends less prominent than the p-type, which were identified as u-type (Fig. 1).

'Valerie' is a commercial F_1 hybrid with smooth blossom-end scars, even under environmental conditions promoting rough blossom-end scarring (Barten et al., 1992). 'Valerie' had pointed blossom-ends and a high degree of genetic leaf curl and was assumed to be homozygous for both characteristics, since both parents had pointed blossom-ends and severe leaf curl (R.B. Volin, personal communication). Leaf curl was characterized by adaxially curled leaf margins, frequently touching each other, and adaxially protruding midribs of the leaflets. Young and MacArthur (1947) reported the presence of leaf curl in their *n* source (T667V). In Fall 1989 and 1990, slight curling of the leaf margins was observed in LA 2353, however, leaf curl in LA 2353 was negligible compared to the leaf curl in 'Valerie' under Florida field conditions (Table 1).

Experimental procedure. The accessions in Table 1 were crossed with wild type breeding lines ('Florida MH-30', Fla 884068-1, 'Horizon', and Fla 7322), and, for six of these crosses, parents, F_1 s, and F_2 s were grown in Spring and Fall 1990. Generally, the results agreed between seasons, and two crosses for which F_2 seed was not available until Spring 1991 were grown in only one season. The genotypes in Table 1 were intercrossed in all possible combinations, and F_1 s and F_2 s were tested for complementation. Seven complementation crosses were evaluated in two seasons (Spring and Fall 1990) and, since conclusions agreed between seasons, the other crosses were evaluated in a single season. In Spring and Fall 1990 and Spring 1991, the experiment was conducted at Bradenton, Fla. The plants were grown in single 10-plant plots for parents and F_1 s and in single 30-plant plots for F_2 s. The plants were staked, tied, and watered by seepage irrigation. Fertilizers and pesticides were applied following recommended cultural practices. Indeterminate

plants were topped at ≈ 1.5 m. In Fall 1991, parents, F_1 s, and F_2 s of three crosses were grown nonstaked at Fletcher, N.C.

For each plant, the percentage of pointed fruit was calculated from observations on 10 immature (1 to 4 cm in diameter) and 10 mature fruit. For parents and F_1 s, data were averaged over 10 plants. F_2 segregation in wild type crosses was difficult to evaluate due to expression of pointedness in heterozygotes. To objectively

Fig. 1. p-Type blossom-end morphology in elongated fruit shape (**top**, LA 986) and u-type blossom-end morphology in round fruit shape (**bottom**, Fla 890559-24).

Table 1. Reported blossom-end morphology gene and several other characteristics for the accessions used in this experiment.

Accession	Source ^z	Blossom-end morphology gene	Average leaf curl ^y	Fruit shape	Other mutant genes ^x
LA 2-5	TGSC	Persistent style (<i>pst</i>)	1.0	Ovate	<i>d</i> , <i>s</i> , <i>sp</i> ⁺
LA 986	TGSC	Beaky (<i>bk</i>)	1.0	Pear	<i>d</i> , <i>p</i> , <i>s</i> , <i>r</i> , <i>Y/y</i> , <i>sp</i> ⁺
LA 1787	TGSC	Beaky-2 (<i>bk-2</i>)	1.7	Ovate	<i>en</i> , <i>sp</i>
LA 2353	TGSC	Nipple tip (<i>n</i>)	1.4	Ovate-round	<i>y</i> , <i>sp</i> ⁺
NC 140	NCSU	?	1.2	Round	<i>sp</i> ⁺
Fla 890559-24	UF	?	1.1	Round	<i>sp</i> ⁺ / <i>sp</i>
Fla 894413-1	UF	?	2.3	Round	<i>sp</i>
Valerie	RNK	?	4.5	Round	<i>sp</i>

^zTGSC = Tomato Genetic Stock Center, Davis, Calif.; NCSU = North Carolina State Univ.; UF = Univ. of Florida; RNK = Rogers NK Seed Co.

^yTen plants were rated individually on a scale from 1 to 5, where 1 = no leaf curl and 5 = severe leaf curl. Data were averaged over three seasons. Problems with tomato mottle geminivirus and physiological leaf curl may have affected the accuracy of the data.

^x*d* = Dwarf, *s* = compound inflorescence, *p* = peach, *r* = yellow flesh, *y* = colorless epidermis (*Y/y* = segregating), *en* = ensiform (sword-shaped sepals), and *sp* = self-pruning (*sp*⁺/*sp* = segregating).

identify mutant F_2 individuals, the minimum percentage of pointed fruit per plant in the mutant parent was established as the threshold value; plants with a lower percentage of pointed fruit were counted as wild types or heterozygotes and those with a higher percentage were counted as mutants. Subjective observations indicated that pointedness was more prominent in ovate and pear-shaped fruit than in round or oblate fruit. To aid in classification, fruit shape and type of blossom-end morphology (Fig. 1) were scored per plant. In F_2 generation allelism tests, the presence of wild types would indicate complementation between two different genes. Plants were counted as wild type when they had $\leq 15\%$ pointedness in round or oblate fruit and $\leq 35\%$ pointedness in ovate or pear-shaped fruit. For all but one complementation cross, these percentages were lower than the minimum percentage of pointed fruit per plant in the least pointed parent.

Gardner and Nash (1987) reported that plants with pointed fruit could be classified at anthesis by the shape and pubescence of the stylar base. In an attempt to characterize morphological traits associated with the mutant genes used in the current experiment, observations were made on the shape and pubescence of the stylar base and on the position of the separation between style and ovary using a stereomicroscope at $\times 25$. Flowers of parental and F_1 generations were investigated and, subsequently, the association of observed characteristics with mutant genes was evaluated in segregating F_2 generations.

Results

Inheritance of blossom-end morphology genes. All blossom-end morphology genes inherited as single recessives as indicated by F_2 segregation ratios, yet various degrees of pointedness were observed in F_1 s (Table 2). Intermediate expression of pointedness for

p-type blossom-end morphology genes *pst* (in LA 2-5) and *bk* (in LA 986) in heterozygous condition resembled the u-type blossom-end morphology. Mutant genes with a u-type blossom-end morphology had various levels of expression in heterozygous condition (Table 2). The F_1 s of wild type crosses with LA 2353 (*n*) and NC 140 had the lowest level of pointedness. *Bk-2* (in LA 1787) inherited recessively in this experiment (Table 2), in contrast with the report of Bouwkamp and Honma (1970). Henceforth this gene will be symbolized as *bk-2*.

There was only moderate environmental variation within each season, since the difference between average and minimum pointedness in the mutant parents was generally small (Table 2). Although the expressivity of pointedness varied somewhat between seasons and crosses, F_2 segregation ratios generally agreed between seasons and did not significantly deviate from 3 normal : 1 mutant. One exception was the F_2 segregation of 'Florida MH-30' $\times$ Fla 890559-24, which deviated significantly from 3 normal : 1 mutant in Fall 1990 but not in Spring 1990 (Table 2). Overrepresentation of mutants in Fall 1990 was probably due to grouping heterozygotes in the mutant class as a result of a low threshold value (Table 2). Pooled over seasons, the segregation was 41 normal : 18 mutant and a monogenic model was clearly accepted ($\chi^2_{(3:1)} = 0.95$, $P = 0.328$).

In spite of low expression of pointedness in NC 140 and a low threshold value, the F_2 with 'Horizon' segregated in a clear-cut 3 normal : 1 mutant ratio (Table 2). This agreed with observations on the F_2 of a cross between NC 902-1, a pointed breeding line derived from NC 140, and NC 50-7, a wild type grown in Fletcher, N.C. The segregation was 30 normal : 17 mutant with $\chi^2_{(3:1)} = 3.13$ ($P = 0.077$), accepting a monogenic model.

F_2 segregations generally deviated significantly ($\alpha = 0.01$) from 15 normal : 1 mutant (χ^2 values not shown), rejecting digenic

Table 2. Inheritance of blossom-end morphology in F_1 and F_2 generations of four accessions with described genes (LA 2-5, LA 986, LA 1787, and LA 2353 with *pst*, *bk*, *Bk-2*, and *n*, respectively) and three breeding lines (NC 140, Fla 890559-24, and Fla 894413-1) crossed with wild types ('Florida MH-30', Fla 884068-1, 'Horizon', and Fla 7322).

Cross ($P_1 \times P_2$) ^x	Season ^w	Pointed fruit (%) ^z			F_2 segregation			
		P_1	P_2	F_1	Threshold ^y (T, %)	+ : m (<T : $\geq$ T)	$\chi^2_{(3:1)}$	P
Fla MH-30 $\times$ LA 2-5 (<i>pst</i>)	S90	3	100(p)	21(u)	100(p)	26: 3	3.32	0.068
Fla MH-30 $\times$ LA 2-5 (<i>pst</i>)	F90	20	100(p)	17(u)	100(p)	26: 4	2.18	0.140
Fla MH-30 $\times$ LA 986 (<i>bk</i>)	S90	3	99(p)	84(u)	92(p)	23: 6	0.29	0.590
Fla MH-30 $\times$ LA 986 (<i>bk</i>)	F90	20	100(p)	74(u)	100(p)	25: 4	1.94	0.164
Fla MH-30 $\times$ LA 1787 (<i>Bk-2</i>)	S90	3	63(u)	13(u)	50	19: 8	0.31	0.578
Fla MH-30 $\times$ LA 1787 (<i>Bk-2</i>)	F90	20	70(u)	39(u)	55	21: 9	0.40	0.527
Fla 884068-1 $\times$ LA 1787 (<i>Bk-2</i>)	S90	4	63(u)	19(u)	50	20: 9	0.56	0.454
Fla 884068-1 $\times$ LA 1787 (<i>Bk-2</i>)	F90	15	70(u)	11(u)	55	24: 6	0.40	0.527
Fla MH-30 $\times$ LA 2353 (<i>n</i>)	S90	3	88(u)	6(u)	67	19: 8	0.31	0.578
Fla MH-30 $\times$ LA 2353 (<i>n</i>)	F90	20	77(u)	21(u)	65	20:10	1.11	0.292
Fla 884068-1 $\times$ LA 2353 (<i>n</i>)	S90	4	88(u)	6(u)	67	22: 6	0.19	0.663
Horizon $\times$ NC 140	F90/S91 ^v	6	20(u)	11(u)	17	24: 6	0.40	0.527
Fla MH-30 $\times$ Fla 890559-24	S90	3	52(u)	30(u)	44	24: 6	0.40	0.527
Fla MH-30 $\times$ Fla 890559-24	F90	20	46(u)	10(u)	35	17:12	4.15	0.042
Fla 7322 $\times$ Fla 894413-1	F90/S91 ^v	35	60(u)	35(u)	40	23: 7	0.04	0.842

^zBased on 10 plants and 20 fruit per plant—10 immature fruit (diameter 1 to 4 cm) and 10 mature fruit. Type of blossom-end morphology (Fig. 1) is indicated in parentheses.

^yMinimum percentage of pointed fruit per plant in mutant parent. F_2 plants with lower percentage pointed fruits are considered wild types (+), others are classified as mutants (m). (p) = only plants with p-type blossom-ends were rated as mutant.

^xThe notation does not always indicate the actual direction of the cross.

^wS90 = Spring 1990, F90 = Fall 1990, S91 = Spring 1991.

^vThe F_1 generation was grown in Fall 1990 and the F_2 generation was grown in Spring 1991. Parents were grown in both seasons.

models. Exceptions were 'Florida MH-30' x LA 2-5 (*pst*) with $\chi^2_{(15:1)} = 0.83$ ($P = 0.362$) in Spring 1990 and $\chi^2_{(15:1)} = 2.57$ ($P = 0.109$) in Fall 1990, and 'Florida MH-30' x LA 986 (*bk*) with $\chi^2_{(15:1)} = 2.82$ ($P = 0.093$) in Fall 1990. When data for 'Florida MH-30' x LA 2-5 (*pst*) were pooled over seasons, a digenic model was accepted over a monogenic model ($\chi^2_{(3:1)} = 5.43$; $P = 0.020$ and $\chi^2_{(15:1)} = 3.17$; $P = 0.075$). For 'Florida MH-30' x LA 986 (*bk*), pooling data over seasons resulted in rejection of a digenic model ($\chi^2_{(3:1)} = 1.86$; $P = 0.173$ and $\chi^2_{(15:1)} = 11.96$; $P < 0.001$).

Allelism tests for described genes. For LA 986 (*bk*) x LA 2-5 (*pst*), each plant in the parental, F_1 , and F_2 generations had 100% p-type blossom-ends (Table 3), a result indicating that LA 986 and LA 2-5 had the same blossom-end morphology gene. The F_2 of LA 986 x LA 2-5 segregated for fruit shape and *p*, confirming the identity of the cross. The blossom-end morphology of LA 986 (Fig. 1) and LA 2-5 was similar to that pictured for *bk* in Young and MacArthur (1947). Several characteristics of LA 2-5, such as *d*, *s*, and fruit shape did not match the description of the original *pst* source (E.A. Kerr, personal communication; Rick, 1945). Henceforth, it will be assumed that LA 2-5 had *bk* instead of *pst*. The higher expression of pointedness in the F_1 of 'Florida MH-30' x LA 986 than in the F_1 of 'Florida MH-30' x LA 2-5 (Table 2) could be explained by differences in genetic background and was probably associated with a more elongated fruit shape in the former F_1 .

In other complementation crosses involving *bk*, differences in the type of blossom-end morphology between parents suggested the presence of different alleles (Table 3). F_1 s of complementation crosses other than LA 986 x LA 2-5 had a high expression of u-type pointedness (Table 3) compared to the expression in F_1 s of corresponding wild type crosses in Table 2. This can be explained by the fact that the F_1 s in Table 3 had ovate fruit, whereas the F_1 s of wild type crosses in Table 2 had round fruit. High expression of u-type pointedness made F_1 complementation tests difficult to interpret. However, the expression of pointedness in F_1 s was lower than in their most pointed parent (Table 3), an indication of complementation between different genes or multiple allelism.

Segregation of wild types in F_2 s of all complementation crosses

except LA 986 x LA 2-5 confirmed control by different genes (Table 3). Low numbers of wild types were expected to segregate, since only 1 out of 16 F_2 plants was expected to have a wild type genotype. Significant deviation from a 15 pointed : 1 wild type ratio in F_2 s of LA 1787 (*bk-2*) x LA 2-5 (*bk*) and LA 2353 (*n*) x LA 1787 (*bk-2*) was due to overrepresentation of wild types. In these two crosses, low expression of pointedness in some heterozygotes may have resulted in more wild type phenotypes than expected.

Allelism tests for new breeding lines. A similar procedure was followed to test allelism of the blossom-end morphology genes in each of the three breeding lines with *bk*, *bk-2*, *n* and with each other (Table 4). The minimum percentage of pointed fruit per plant in the least pointed parent was higher than the 15% threshold for wild type expression in round-fruited plants, except for NC 140 x Fla 890559-24 (Table 4). In the F_2 of NC 140 x Fla 890559-24, wild types were classified based on expression of pointedness and shape and size of blossom-end scars.

Although high expression of pointedness hindered interpretation of F_1 complementation data, differences in expression between parents and expression of pointedness in F_1 s lower than in their most pointed parent indicated that different genes were involved. In all crosses, including those in which parents and F_1 s were similar in expression [e.g., all crosses involving LA 1787 (*bk-2*) and Fla 890559-24 x Fla 894413-1], enough wild types segregated in F_2 allelism tests to be certain of complementation between two different genes (Table 4).

Crosses with LA 986 generally had higher expression of pointedness in F_1 s and fewer wild types segregating in F_2 s than crosses involving LA 2-5 (Table 4). Apparently, LA 986 had a more favorable genetic background for expression of pointedness than LA 2-5 (Table 2). Crosses involving NC 140 had low expression of pointedness in the double heterozygotes (Table 4) and many wild types segregated in the F_2 s, except for NC 140 x LA 986 and NC 140 x LA 1787. Crosses with a high expression of pointedness in the double heterozygotes generally had fewer wild types segregating in the F_2 s (Table 4). Besides segregation of wild types in F_2 s,

Table 3. F_1 and F_2 allelism tests for described blossom-end morphology genes (*pst*, *bk*, *bk-2*, and *n*) in four accessions (LA 2-5, LA 986, LA 1787, and LA 2353, respectively).

Cross ($P_1 \times P_2$) ^w	Season ^v	Pointed fruit (%) ^z			F_2 segregation		
		P_1	P_2	F_1	Threshold ^y (%)	Total (no.)	Wild type ^x (no.)
LA 986 (<i>bk</i>) x LA 2-5 (<i>pst</i>)	S90	100(p)	100(p)	100(p)	100(p)	25	0
LA 1787 (<i>bk-2</i>) x LA 2-5 (<i>bk</i>) ^u	S90	63(u)	100(p)	59(u)	50	29	8
LA 1787 (<i>bk-2</i>) x LA 2-5 (<i>bk</i>) ^u	F90	70(u)	100(p)	48(u)	55	26	7
LA 1787 (<i>bk-2</i>) x LA 986 (<i>bk</i>)	S90	63(u)	99(p)	52(u)	---	---	---
LA 1787 (<i>bk-2</i>) x LA 986 (<i>bk</i>)	F90/S91 ^t	70(u)	100(p)	79(u)	55	29	4
LA 2353 (<i>n</i>) x LA 2-5 (<i>bk</i>) ^u	S90	88(u)	100(p)	72(u)	67	28	1
LA 2353 (<i>n</i>) x LA 2-5 (<i>bk</i>) ^u	F90	77(u)	100(p)	74(u)	65	29	2
LA 2353 (<i>n</i>) x LA 986 (<i>bk</i>)	S90	88(u)	99(p)	98(u)	67	29	2
LA 2353 (<i>n</i>) x LA 986 (<i>bk</i>)	F90	77(u)	100(p)	78(u)	65	57	1
LA 2353 (<i>n</i>) x LA 1787 (<i>bk-2</i>)	S90	88(u)	63(u)	49(u)	50	29	7
LA 2353 (<i>n</i>) x LA 1787 (<i>bk-2</i>)	F90	77(u)	70(u)	42(u)	55	28	5

^zBased on 10 plants and 20 fruit per plant—10 immature fruit (diameter 1 to 4 cm) and 10 mature fruit. Type of blossom-end morphology (Fig. 1) is indicated in parentheses.

^yMinimum percentage of pointed fruit per plant in least pointed parent.

^xPlants with $\leq 15\%$ pointed fruit in round and $\leq 35\%$ pointed fruit in ovate or pear-shaped fruit are considered wild types.

^wNotation does not always indicate the actual direction of the cross.

^vS90 = Spring 1990, F90 = Fall 1990, S91 = Spring 1991.

^tBased on information presented in this table and in the text, the blossom-end morphology gene in LA 2-5 was reassigned to *bk*.

^uThe F_1 generation was grown in Fall 1990 and the F_2 generation was grown in Spring 1991. Parents were grown in both seasons.

Table 4. F_1 and F_2 allelism tests for blossom-end morphology genes in three breeding lines (NC 140, Fla 890559-24, and Fla 894413-1) with described blossom-end morphology genes (*bk*, *bk-2*, and *n*) in four accessions (LA 2-5, LA 986, LA 1787, and LA 2353) and with each other.

Cross ($P_1 \times P_2$) ^w	Season ^v	Pointed fruit (%) ^z			F_2 segregation		
		P_1	P_2	F_1	Threshold ^y (%)	Total (no.)	Wild type ^x (no.)
NC 140 x LA 2-5 (<i>bk</i>)	F90	20(u)	100(p)	14(—)	17	27	16
NC 140 x LA 986 (<i>bk</i>)	F90	20(u)	100(p)	57(u)	17	26	2
Fla 890559-24 x LA 2-5 (<i>bk</i>)	S91	50(u)	100(p)	57(u)	---	---	---
Fla 890559-24 x LA 986 (<i>bk</i>)	F90	47(u)	100(p)	83(u)	35	27	4
Fla 894413-1 x LA 2-5 (<i>bk</i>)	S91	49(u)	100(p)	40(u)	---	---	---
Fla 894413-1 x LA 2-5 (<i>bk</i>)	F91	---	100(p)	49(u)	40	31	7
Fla 894413-1 x LA 986 (<i>bk</i>)	S91	49(u)	98(p)	74(u)	---	---	---
Fla 894413-1 x LA 986 (<i>bk</i>)	F91	---	100(p)	100(u)	40	33	5
NC 140 x LA 1787 (<i>bk-2</i>)	F90	20(u)	70(u)	41(u)	17	30	2
Fla 890559-24 x LA 1787 (<i>bk-2</i>)	S90	52(u)	63(u)	63(u)	40	27	8
Fla 890559-24 x LA 1787 (<i>bk-2</i>)	F90	47(u)	70(u)	51(u)	35	30	5
Fla 894413-1 x LA 1787 (<i>bk-2</i>)	F90/S91 ^t	60(u)	70(u)	46(u)	40	30	10
NC 140 x LA 2353 (<i>n</i>)	F90/S91	20(u)	77(u)	12(—)	17	28	18
Fla 890559-24 x LA 2353 (<i>n</i>)	S90	52(u)	88(u)	31(u)	40	29	7
Fla 890559-24 x LA 2353 (<i>n</i>)	F90	47(u)	77(u)	34(u)	35	29	8
Fla 894413-1 x LA 2353 (<i>n</i>)	F90/S91	60(u)	77(u)	46(u)	40	30	10
NC 140 x Fla 890559-24	S91	24(u)	50(u)	18(—)	---	---	---
NC 140 x Fla 890559-24	F91	10(u)	66(u)	10(—)	0	30	10 ^s
NC 140 x Fla 894413-1	F90/S91	20(u)	60(u)	27(—)	17	28	19
Fla 890559-24 x Fla 894413-1	F90/S91	47(u)	60(u)	53(u)	35	30	7

^zBased on 10 plants and 20 fruit per plant—10 immature fruit (diameter 1 to 4 cm) and 10 mature fruit. Type of blossom-end morphology (Fig. 1) is indicated in parentheses.

^yMinimum percentage pointed fruit per plant in least pointed parent.

^xPlants with $\leq 15\%$ pointed fruit in round and $\leq 35\%$ pointed fruit in ovate or pear-shaped fruit are considered wild types.

^wNotation does not always indicate the actual direction of the cross.

^vS90 = Spring 1990, F90 = Fall 1990, S91 = Spring 1991.

^tDue to germination problems, data for Fla 894413-1 were not available for Fall 1991.

^uThe F_1 generation was grown in Fall 1990 and the F_2 generation was grown in Spring 1991. Parents were grown in both seasons.

^sSeparation of wild types is based on expression of pointedness and size and shape of blossom-end scar.

transgression over the highest level of pointedness in the parents was remarkable in several crosses involving Fla 890559-24 and Fla 894413-1 (data not shown). Blossom-end morphology genes in Fla 890559-24 and Fla 894413-1 apparently add to the effect of other blossom-end morphology genes in duplicate recessive condition, in some cases leading to pronounced, p-type blossom-ends, especially in ovate-shaped fruit.

The data in Table 4 indicated that the blossom-end morphology genes in the three breeding lines were different from the previously reported ones and that they were different from each other. Since the phenotypes of these mutants closely resembled the *n* gene described by Young and MacArthur (1947), the proposed gene symbols are *n-2*, *n-3*, and *n-4* for nipple tip in NC 140, Fla 890559-24, and Fla 894413-1, respectively.

Usefulness of mutant genes for breeding toward smooth blossom-end scars. Since pointedness is only objectionable when persistent on mature fruit, hybrid combinations were evaluated by calculating the percentage of pointed mature fruit (Table 5). F_1 hybrids, heterozygous for two different blossom-end morphology genes, generally had less pointed mature fruit than their homozygous parents, except for crosses involving LA 986 (*bk*). Thus, parents with different blossom-end morphology genes may be intercrossed to obtain smooth F_1 hybrids with few undesirable pointed blossom-ends in mature fruit. Genetic background plays a major role in expression of pointedness, as indicated by the differences between hybrid combinations involving LA 2-5 vs. LA 986 (Table 5). NC 140 (*n-2*) and hybrid combinations involv-

Table 5. Percentage of pointed mature fruit in parents (diagonal) and F_1 s of crosses involving six blossom-end morphology genes (Fall 1990).

	<i>n</i>	<i>n-2</i>	<i>n-3</i>	<i>n-4</i>	<i>bk</i>	<i>bk</i>	<i>bk-2</i>
LA 2353 (<i>n</i>)	62	3	8	20	51	54	16
NC 140 (<i>n-2</i>)	---	7	1 ^z	4	1	15	14
Fla 890559-24 (<i>n-3</i>)	---	---	22	25	27 ^z	67	23
Fla 894413-1 (<i>n-4</i>)	---	---	---	34	14 ^z	53 ^z	25
LA 2-5 (<i>bk</i>)	---	---	---	---	100	100	18
LA 986 (<i>bk</i>)	---	---	---	---	---	100	59
LA 1787 (<i>bk-2</i>)	---	---	---	---	---	---	47

^zData from Spring 1991; values for NC 140, Fla 890559-24, Fla 894413-1, LA 2-5, and LA 986 were 3, 20, 19, 96, and 100, respectively.

ing NC 140 had relatively low percentages of pointed mature fruit (Table 5). Combinations of NC 140 (*n-2*) with LA 2353 (*n*), Fla 890559-24 (*n-3*), Fla 894413-1 (*n-4*), and LA 2-5 (*bk*) resulted in acceptable hybrids ($<5\%$ pointed mature fruit) (Table 5). However, incorporating various blossom-end morphology genes into different genetic backgrounds could result in other acceptable hybrid combinations.

Early identification of mutants. Pistils of flowers at anthesis were observed under a binocular microscope to identify morphology associated with mutant genes. Observations on the density and position of trichomes on the style indicated quantitative inheritance, and, in F_2 generations, no association was observed between pointed blossom-end morphology and trichome density or posi-

tion. The position of the separation between style and ovary was not helpful either, whereas the shape of the stylar base was more helpful in classifying mutants. Pistils of plants with *bk* were characterized by a tapered stylar base extending up to about one-third of the length of the style, a slight bend in the style at the end of the tapering, and an angular transition between style and ovary. This morphology was observed in parental, F_1 , and F_2 generations of LA 2-5 x LA 986. In F_2 generations involving LA 2-5 or LA 986 as one of the parents, *bk* plants were easily identified at anthesis. In some of these F_2 s, all fruitless and less vigorous plants had a pistil morphology characteristic for *bk*, suggesting the association of *bk* with unfavorable genes and explaining the deficiency of mutants in the F_2 of 'Florida MH-30' x LA 2-5 (Table 2). LA 2353 had a rounded stylar base with a short zone of tapering and gradual transition between style and ovary. However, only plants with ovate fruit and *n* had the appearance of LA 2353 in segregating F_2 generations. It was hard to distinguish morphology associated with *n* in F_2 generations in which pointedness and fruit shape segregated, rendering classification of *n* mutants at anthesis unreliable. It should be noted that the genotypes in this experiment were different from the ones reported by Gardner and Nash (1987).

Discussion

Probably due to problems with variable expressivity and the influence of genetic background, the terminology surrounding blossom-end morphology has been unclear. Frequently, pointedness has been referred to as nipple tip without establishing allelism with the *n* gene described by MacArthur (1934). This experiment attempted to organize the fragmentary information currently available on blossom-end morphology genes. Bouwkamp and Honma (1970) reported *bk-2* to be dominant; however, in the present experiment, recessive gene action was observed. Allelism of *bk-2* with other blossom-end morphology genes had not been established previously. Data from Table 2 indicated that *bk-2* was not allelic with *bk* or *n*. The blossom-end morphology gene in LA 2-5 was reported to be *pst* (Tomato Genetics Cooperative, 1990); however, in this experiment, F_1 and F_2 allelism tests indicated that *bk* in LA 986 was allelic with *pst* in LA 2-5. Although the original *pst* gene described by Rick (1966) still may be available somewhere, intermediate expression in the heterozygotes was reported (Rick, 1966); thus, *pst* may not be suitable for breeding purposes.

The presence of three additional nipple-tip genes was established (*n-2*, *n-3*, *n-4*). The *n-4* gene, derived from NC 8276, has been used in several breeding programs. Although NC 8276 has relatively strong expression of leaf curl, Fla 894413-1 generally has less leaf curl. This illustrates the effect of modifier genes from different genetic backgrounds on leaf curl expression. Moreover, it has now been demonstrated that the nipple gene from NC 8276 is not the same as the *n* gene from the Tomato Genetics Stock Center accession LA 2353. Although no definite conclusions could be made on the identity of the leaf curl associated pointedness in 'Valerie' (data not shown), it seemed unlikely that it was allelic with *n*, since LA 2353 did not have leaf curl and the v-type blossom-end morphology in 'Valerie' was distinctly different from the u-type morphology in LA 2353. Leaf curl associated with pointedness in many breeding lines has been a drawback to the use of this pointed blossom-end characteristic in breeding smooth blossom-end scars for humid regions. The breeding lines with *n-2* or *n-3* but without leaf curl have now been identified and are a potentially useful addition to the breeding material currently available.

In a diallel study on inheritance of blossom-end scar size, two parents with a pointed blossom-end morphology, NC 8276 and NC 140, and their hybrid had remarkably smooth blossom-end scars in two very different climates (Barten et al., 1993). Thus, to obtain optimal smoothness in hybrid fruit, two parents with a pointed blossom-end morphology may be intercrossed. To prevent problems with pointed mature fruit in the hybrid, it is useful to distinguish complementing blossom-end morphology genes. In the present study, good complementation was reported when *n-2* was crossed with *n*, *n-3*, or *n-4* and when *n* was crossed with *n-3* (Table 5). Furthermore, the sources with *n*, *n-2*, and *n-3* do not have leaf curl and they can be combined with parents that have leaf curl-associated pointedness to obtain hybrids with smooth blossom-end scars and good foliage, since leaf curl is recessive (Nash and Gardner, 1988). Hybrids between advanced lines derived from NC 140 and pointed blossom-end types with leaf curl generally have excellent smoothness without pointed mature fruit or leaf curl. The diallel study also indicated predominantly additive inheritance of blossom-end scar size, and hybrids of pointed with nonpointed parents had a scar size intermediate between the parents (Barten et al., 1993). Thus, breeding lines with one of the nipple-tip genes or *bk-2* can be crossed with nonpointed but reasonably smooth-fruited parents with other desirable characteristics to obtain smooth-fruited hybrids.

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