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

J.H.M. Barten¹ and J.W. Scott
Gulf Coast Research and Education Center, Institute of Food and Agricultural Sciences, University of Florida, 5007 60th Street East, Bradenton, FL 34203

R.G. Gardner
Mountain Horticultural Crops Research and Extension Center, North Carolina State University, 206 Fanning Bridge Road, Fletcher, NC 28732

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 F₁ and F₂ 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. F₁ complementation tests were difficult to interpret. Wild types segregated in F₂ of all complementation crosses, except for LA 986 x 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.

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 gene was controlled by three 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.

Received for publication 27 Aug. 1993. Accepted for publication 31 Jan. 1994. Florida Agricultural Experiment Station Journal series no. R-02109. This research was supported in part by grant no. US-993-85 from the U.S.-Israel Binational Agricultural Research and Development Fund. We gratefully acknowledge the assistance of K. Köntst during the Fall 1990 season. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

¹Current address: De Ruiter Zonen, P.O. Box 4, 2665 ZG Bleiswijk, The Netherlands.
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 F₁ 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, F₁s, and F₂s were grown in Spring and Fall 1990. Generally, the results agreed between seasons, and two crosses for which F₂ 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 F₁s and F₂s 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 F₁s and in single 30-plant plots for F₂s. 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, F₁s, and F₂s 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 F₁s, data were averaged over 10 plants. F₂ 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).](image)

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

| Accession | Source | Blossom-end morphology gene | Average leaf curl | Fruit shape | Other mutant genes |
|-----------|--------|-----------------------------|------------------|-------------|--------------------|
| LA 2-5    | TGSC   | Persistent style (pst)      | 1.0              | Ovate       | d, s, sp⁺         |
| LA 986    | TGSC   | Beaky (bk)                  | 1.0              | Pear        | d, p, s, r, Y/y, sp⁺|
| LA 1787   | TGSC   | Beaky-2 (bk-2)              | 1.7              | Ovate       | en, sp             |
| LA 2353   | TGSC   | Nipple tip (n)              | 1.4              | Ovate-round | y, sp⁰             |
| NC 140    | NCSU   | ?                           | 1.2              | Round       | sp⁺               |
| Fla 890559-24 | UF | ? | 1.1 | Round | sp⁰ | |
| Fla 894413-1 | UF | ? | 2.3 | Round | sp | |
| Valerie   | RNK    | ?                           | 4.5              | Round       | sp | |

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

Ten 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.

+ = 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).

J. AMER. SOC. HORT. SCI. 119(4):798–803. 1994.
identify mutant F1 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 F2 generation allelism tests, the presence of wild types would indicate complementation between two different genes. Plants were counted as wild type when they had ≤15% pointedness in round or oblate fruit and ≤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 ×25. Flowers of parental and F1 generations were investigated and, subsequently, the association of observed characteristics with mutant genes was evaluated in segregating F2 generations.

**Results**

*Inheritance of blossom-end morphology genes.* All blossom-end morphology genes inherited as single recessives as indicated by F2 segregation ratios, yet various degrees of pointedness were observed in F1s (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 u-type blossom-end morphology had various levels of expression in heterozygous condition (Table 2). The F2s 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, F2 segregation ratios generally agreed between seasons and did not significantly deviate from 3 normal : 1 mutant. One exception was the F2 segregation of “Florida MH-30” × 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 F2 with ‘Horizon’ segregated in a clear-cut 3 normal : 1 mutant ratio (Table 2). This agreed with observations on the F2 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.

F2 segregations generally deviated significantly ($\alpha = 0.01$) from 15 normal : 1 mutant ($\chi^2$ values not shown), rejecting digenic

| Cross (P1 x P2) | Season* | Pointed fruit (%) | Threshold† | F2 segregation |
|-----------------|---------|------------------|------------|----------------|
|                |         | P1 | P2 | F1 (T, %) | + : m | ($<T : >T$) | $\chi^2_{(3:1)}$ | P |
| Fla MH-30 x LA 2-5 (pst) | S90 | 3 | 100(p) | 21(u) | 100(p) | 26: 3 | 3.32 | 0.068 |
| Fla MH-30 x LA 2-5 (pst) | F90 | 20 | 100(p) | 17(u) | 100(p) | 26: 4 | 2.18 | 0.140 |
| Fla MH-30 x LA 986 (bk) | S90 | 3 | 99(p) | 84(u) | 92(p) | 23: 6 | 0.29 | 0.590 |
| Fla MH-30 x LA 986 (bk) | F90 | 20 | 100(p) | 74(u) | 100(p) | 25: 4 | 1.94 | 0.164 |
| Fla MH-30 x LA 1787 (Bk-2) | S90 | 3 | 63(u) | 13(u) | 50 | 19: 8 | 0.31 | 0.578 |
| Fla MH-30 x LA 1787 (Bk-2) | F90 | 20 | 70(u) | 39(u) | 55 | 21: 9 | 0.40 | 0.527 |
| Fla 890559-1 x LA 1787 (Bk-2) | S90 | 4 | 63(u) | 19(u) | 50 | 20: 9 | 0.56 | 0.454 |
| Fla 890559-1 x LA 1787 (Bk-2) | F90 | 15 | 70(u) | 11(u) | 55 | 24: 6 | 0.40 | 0.527 |
| Fla MH-30 x LA 2353 (n) | S90 | 3 | 88(u) | 6(u) | 67 | 19: 8 | 0.31 | 0.578 |
| Fla MH-30 x LA 2353 (n) | F90 | 20 | 77(u) | 21(u) | 65 | 20:10 | 1.11 | 0.292 |
| Fla 894413-1 x LA 2353 (n) | S90 | 4 | 88(u) | 6(u) | 67 | 22: 6 | 0.19 | 0.663 |

*Based 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.

†Minimum percentage of pointed fruit per plant in mutant parent. F2 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.

‡The notation does not always indicate the actual direction of the cross.

*S90 = Spring 1990, F90 = Fall 1990, S91 = Spring 1991.

The F1 generation was grown in Fall 1990 and the F2 generation was grown in Spring 1991. Parents were grown in both seasons.
models. Exceptions were ‘Florida MH-30’ × 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’ × LA 986 (bk) with $\chi^2_{(15:1)} = 2.82$ ($P = 0.093$) in Fall 1990. When data for ‘Florida MH-30’ × 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’ × 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) × LA 2-5 (pst), each plant in the parental, F1, and F2 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 F2 of LA 986 × 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 F1 of ‘Florida MH-30’ × LA 986 than in the F1 of ‘Florida MH-30’ × 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 F1.

In other complementation crosses involving bk, differences in the type of blossom-end morphology between parents suggested the presence of different alleles (Table 3). F2s of complementation crosses other than LA 986 × LA 2-5 had a high expression of u-type pointedness (Table 3) compared to the expression in F2s of corresponding wild type crosses in Table 2. This can be explained by the fact that the F2s in Table 3 had ovate fruit, whereas the F2s of wild type crosses in Table 2 had round fruit. High expression of u-type pointedness made F2 complementation tests difficult to interpret. However, the expression of pointedness in F2 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 F2s of all complementation crosses except LA 986 × 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 F2 plants was expected to have a wild type genotype. Significant deviation from a 15 pointed : 1 wild type ratio in F2s of LA 1787 (bk-2) × LA 2-5 (bk) and LA 2353 (n) × 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 × Fla 890559-24 (Table 4). In the F2 of NC 140 × 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 F2 complementation data, differences in expression between parents and expression of pointedness in F2s lower than in their most pointed parent indicated that different genes were involved. In all crosses, including those in which parents and F2s were similar in expression [e.g., all crosses involving LA 1787 (bk-2) and Fla 890559-24 × Fla 894413-1], enough wild types segregated in F2 allelism tests to be certain of complementation between two different genes (Table 4).

CROSSES WITH LA 986 generally had higher expression of pointedness in F2s and fewer wild types segregating in F2s 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 F2, except for NC 140 × LA 986 and NC 140 × LA 1787. Crosses with a high expression of pointedness in the double heterozygotes generally had fewer wild types segregating in the F2s (Table 4). Besides segregation of wild types in F2s,
Table 4. F₁ and F₂ 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 (P₁ x P₂)w | Season† | P₁ | P₂ | F₁ | Threshold‡ | Total | Wild type§ |
|------------------|---------|----|----|----|------------|-------|------------|
| NC 140 x LA 2-5 (bk) | F90 | 20(u) | 100(p) | 14(–) | 17 | 27 | 16 |
| NC 140 x LA 986 (bk) | F90 | 20(u) | 100(p) | 57(u) | 17 | 26 | 2 |
| Fla 890559-24 x LA 2-5 (bk) | S91 | 50(u) | 100(p) | 57(u) | --- | --- | --- |
| Fla 890559-24 x LA 986 (bk) | F90 | 47(u) | 100(p) | 83(u) | 35 | 27 | 4 |
| Fla 894413-1 x LA 2-5 (bk) | S91 | 49(u) | 100(p) | 40(u) | --- | --- | --- |
| Fla 894413-1 x LA 986 (bk) | F91 | ---a | 100(p) | 49(u) | 40 | 31 | 7 |
| Fla 894413-1 x LA 986 (bk) | S91 | 49(u) | 98(p) | 74(u) | --- | --- | --- |
| NC 140 x LA 1787 (bk-2) | F90 | 20(u) | 70(u) | 41(u) | 17 | 30 | 2 |
| Fla 890559-24 x LA 1787 (bk-2) | S90 | 52(u) | 63(u) | 63(u) | 40 | 27 | 8 |
| Fla 890559-24 x LA 1787 (bk-2) | F90 | 47(u) | 70(u) | 51(u) | 35 | 30 | 5 |
| Fla 894413-1 x LA 1787 (bk-2) | F90/S91 | 60(u) | 70(u) | 46(u) | 40 | 30 | 10 |
| NC 140 x LA 2353 (n) | F90/S91 | 20(u) | 77(u) | 12(–) | 17 | 28 | 18 |
| Fla 890559-24 x LA 2353 (n) | S90 | 52(u) | 88(u) | 31(u) | 40 | 29 | 7 |
| Fla 890559-24 x LA 2353 (n) | F90 | 47(u) | 77(u) | 34(u) | 35 | 29 | 8 |
| Fla 894413-1 x LA 2353 (n) | 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‡ |
| 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 |

*Based 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.
†Minimum percentage of pointed fruit in least pointed parent.
‡Plants with ≤5% pointed fruit in round and ≤35% pointed fruit in ovate or pear-shaped fruit are considered wild types.
§Notation does not always indicate the actual direction of the cross.

na = Spring 1990, F90 = Fall 1990, S91 = Spring 1991, F91 = Fall 1991.
Table 5. Percentage of pointed mature fruit in parents (diagonal) and F₂s of crosses involving six blossom-end morphology genes (Fall 1990).

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

*Data 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.

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). F₁ 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 F₂ 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 involving 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 morphologically associated with mutant genes. Observations on the density and position of trichomes on the style indicated quantitative inheritance, and, in F₂ generations, no association was observed between pointed blossom-end morphology and trichome density or position of trichomes on the style.
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, F₁, and F₂ generations of LA 2-5 x LA 986. In F₂, generations involving LA 2-5 or LA 986 as one of the parents, bk plants were easily identified at anthesis. In some of these F₂s, 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 F₂ 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 F₂ generations. It was hard to distinguish morphology associated with n in F₂ 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, F₁ and F₂, 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.

Literature Cited

Barten, J.H.M., J.W. Scott, N. Kedar, and Y. Elkind. 1992. Low temperatures induce rough blossom-end scarring of tomato during early flower development. J. Amer. Soc. Hortic. Sci. 117:298–303.

Barten, J.H.M., Y. Elkind, J.W. Scott, S. Vidavski, and N. Kedar. 1993. Diallel analysis over two environments for blossom-end scar size in tomato. Euphytica 65:229–237.

Bouwkamp, J.C. and S. Honma. 1970. The inheritance of five morphological characters in the tomato. J. Hered. 61:19–21.

Gardner, R.G. 1990. ‘Mountain Delight’ tomato; NC 8288 tomato breeding line. HortScience 25:989–990.

Gardner, R.G. 1992. ‘Mountain Spring’ tomato; NC 8276 and NC 84173 tomato breeding lines. HortScience 27:1233–1234.

Gardner, R.G. and A.F. Nash. 1987. Observations on the nipple (n) trait and associated characteristics. Rpt. Tomato Genet. Coop. 37:45.

MacArthur, J.W. 1934. Linkage groups in the tomato. J. Genet. 29:123–133.

Mutschler, M.A., S.D. Tanksley, and C.M. Rick. 1987. 1987 Linkage maps of the tomato (Lycopersicon esculentum). Rpt. Tomato Genet. Coop. 37:5–34.

Nash, A.F. and R.G. Gardner. 1988. Heritability of tomato early blight resistance derived from Lycopersicon hirsutum P.I. 126445. J. Amer. Soc. Hortic. Sci. 113:264–268.

Rick, C.M. 1945. A survey of cytogenetic causes of unfruitfulness in the tomato. Genetics 30:347–362.

Rick, C.M. 1966. Inheritance and linkage relations of fy, mnt, Pn, and pst. Rpt. Tomato Genet. Coop. 16:27–29.

Rick, C.M. and L. Butler. 1956. Cytogenetics of the tomato. Adv. Genet. 8:267–382.

Tikoo, S.K. and N. Anand. 1984. Expressivity and inheritance of the nipple tip trait in tomato. Rpt. Tomato Genet. Coop. 34:19–20.

Tomato Genetics Cooperative. 1990. TGSC stock list. Rpt. Tomato Genet. Coop. 40:44–64.

Young, P.A. and J.W. MacArthur. 1947. Horticultural characters of tomatoes. Texas Agr. Expt. Sta. Bul. 698.