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Horticultural Characters of Tomatoes

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Preface

The purpose of this bulletin is to summarize for tomato breeders and other interested people much of the information on inherited characters of tomatoes from extensive published literature and from the research records of the Tomato Disease Laboratory, Jacksonville, Texas, and the University of Toronto, Toronto, Canada.

Descriptions are given for 49 tomato characters for which gene symbols have been assigned, and for more than 60 additional characters which have not received gene designations. Many of the latter characters equal the former in horticultural importance.

Apparently, first descriptions are given for the genetic characters of bushy stems, xanthophyllic leaves, beaked fruits and macrocalyx flowers. Fuller descriptions are given for the genetic characters of broad leaves, mottled leaves, necrotic leaves and woolly leaves. The allele for lutescent leaves also causes yellowing of the stems and unripe fruits.

Table 1 lists the characters that are desired in new tomato varieties for use in East Texas. It suggests the varieties and selections from which these characters may be secured, and points out the undesirable characters that will be introduced into the crosses with these parents. The genes that control fruit colors are summarized in Table 4. Tables 2 and 3 list the inherited characters of tomatoes.

The new gene map in Figure 14 shows the groups of characters that may be linked so that the tomato breeder can anticipate his problem if he must attempt to separate desirable characters that are linked with undesirable characters in a hybrid.

The work of the tomato breeder is facilitated by recognizing as many as possible of the inherited characters of tomatoes and understanding their relationships. Thus, many of the desirable characters can be separated from the undesirable ones, and it is possible to distinguish exhibitions of unusual characters from symptoms of diseases. Knowledge of genetics usually can guide the plant breeder in making crosses and selections efficiently to improve commercial varieties of crop plants.

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Horticultural Characters of Tomatoes

P. A. Young* and J. W. MacArthur**

Crossing and selecting cultivated plants to improve varieties involves the use of genetics. Inherited characters are presumed to have a genic basis, including the polygenic characters that remain without gene identification. Inherited characters distinguish the botanical species and varieties and the horticultural varieties of tomatoes. Plant breeding and genetics are closely related, as plant breeding is a practical use of genetics. Hence, a plant breeder finds that knowledge of the inherited characters of the crop that he is trying to improve facilitates and accelerates his breeding program (91).

Tomato breeding was started at the Tomato Disease Laboratory at Jacksonville, Texas, in 1937 to develop better commercial varieties with immunity to Fusarium wilt. Hundreds of tomato crosses were made and thousands of hybrid selections and varieties were tested for their horticultural qualities and resistances to wilt, blossom-end rot and catface. These kinds of tomatoes showed both desirable and undesirable characters. Efficiency in detecting and evaluating these characters has improved with increasing knowledge of the inherited characters of tomatoes.

Study of tomato breeding preferably begins with the distinguishing characters of the botanical species, varieties, and forms of the genus, *Lycopersicon* Mill. (4, 44, 55). All of the species are diploids with 12 pairs of chromosomes (51). Mostly small differences distinguish the 350 or more horticultural varieties of tomatoes (54).

Interspecific hybrids were made to study inherited characters, and to add markers, disease resistance, ornamental value and other desirable characters to their descendants. Vigorous hybrids were secured from each of the three most distinct sections of *Lycopersicon* (51, 59, 61). These hybrids were represented by: (a) *L. esculentum* X *L. peruvianum*, (b) *L. esculentum* X *L. hirsutum* and (c) *L. peruvianum* X *L. glandulosum*. Thus, alleles from wild species of tomatoes become available for the improvement of the commercial varieties of tomatoes.

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*Plant pathologist in charge, Tomato Disease Laboratory, Jacksonville, Texas, who supplied the data from Texas and wrote the manuscript.

**Professor of Genetics, University of Toronto, Toronto, Canada, who supplied the gene map, many seed samples, some pictures, and most of the information about the recently studied genes.

Although a breeder of commercial varieties of tomatoes wishes to avoid the economically undesirable characters, many of these are likely to appear in segregating hybrids because they exist both in the commercial varieties and the wild species. Hence, work to eliminate the undesirable characters must continue through many years. The ideal variety for each region would combine all of the desirable characters (86, 101) (Table 1). Even though the varietal requirements may change before perfection is approached, the improvements in tomato varieties that are made through breeding have great commercial value.

Varieties, hybrids and selections of tomatoes can be arranged in four general groups that are valuable for: (a) commercial market and processing, (b) selections for further breeding work, (c) ornament and food production in home gardens and (d) scientific study. These four groups include 49 characters that are designated by gene symbols and more than 60 other characters without gene symbols (Tables 2, 3). These tables are a convenient index to the inherited characters of tomatoes.

Table 1. Desirable characters for new varieties of tomatoes for East Texas

Desirable characters	Source of characters	Undesirable characters introduced in crosses with these parents
Production of early fruits	Bison*	Self-topping; oblate fruits
Production of early fruits	Earliana	Prostrate stems; oblate fruits
Prolific fruiting habit	Stokesdale	Fruits may be too small
Prolific fruiting habit	Red Cloud	Small fruits without shade
Resistance to puff and catface	Stokesdale	Inadequate shade for fruits
Abundant yielding ability	Pritchard	Slightly angular fruits
Resistance to blossom-end rot	Pritchard	Susceptible to puffing
Large spherical fruits	Pan America	Late bearing habit; small upper fruits
Immunity to Fusarium wilt	Pan America	Small yield of marketable fruits
Commercial red globe fruits	Marglobe	Susceptibility to puffing
Wide corky stem-end band	Marglobe	Susceptibility to stem cracking
Upright large plants	Marglobe	Midseason production of fruits
Dark green stem end on fruits	Grothens Globe	Fruits may be too small
Very large fruits	Ponderosa	Fasciated, lobed, catface fruits
Very large fruits	Oxheart	Prostrate stems; giant plum fruits
Resistance to leaf mold	Bay State	Fruits are too small
Resistance to stem cracking	Crack Proof	Late bearing habit
Uniform ripening of fruits	Bounty	Yellow-white color in green-wrap stage
Resistance to Septoria	USDA S26-6	Clear peel; late bearing habit
Resistance to collar rot	USDA CRW-25	Catface and blossom-end rot
Tough peel	Rutgers	Susceptibility to stem cracking
Large leaves and stems	Rutgers	Blossom-end rot and puffing
Dark green leaflets	Rutgers	Catface of earliest fruits
Summer bearing habit	Summerset	Small fruits
White-flower marker	T935	Catface of earliest fruits

*Genes are listed in Table 2.

Table 2. Index to gene symbols for characters in tomatoes.

Gene symbol*	Character	Page	Gene symbol*	Character	Page
A_1	Purple stem	15	mc	Macrocalyx flowers	29
a_2	Purple stem becoming green	15	m_{1-4}	Modifies red fruit color	33
ad	Resistance to Alternaria collar rot	16	ms_{1-2}	Male sterility	31
br	Brachytic stems	11	n	Nipple-tip fruits	43
bk	Beaked fruits	42	ne	Necrotic leaves	26
bu	Bushy stems	12	o	Elongated plum fruits	42
c	Potato leaf-type	18	pr	Elongated plum fruits (duplicate symbol)	42
Cf_{p1}	Immunity to Cladosporium	23	p	Pubescent fruits	38
Cf_{p2}	Resistance to Cladosporium	26	R	Red flesh color of fruits (vs. yellow flesh, r)	33
Cf_{sc}	Resistance to Cladosporium	26	r_1	Ridged leaflets	22
D_1	Tall stems	11	rc	Rolled cotyledons	11
d_2	Extremely dwarfed stems	11	s	Compound inflorescence	27
e	Broad leaflets	18	Se	Septoria resistance	27
f	Fasciated fruits	42	sp	Self-topping, determinate stems	15
G	Inhibits modifiers making red fruits	34	st	Sterile plants	31
h	Hairy stems	12	t	Tangerine-orange flesh color of fruits	34
I	Immunity to Fusarium wilt	17	u	Uniform unripe fruit color	35
j	Jointless pedicels of fruits	28	u_2	Uniform unripe fruit color	35
K	Inhibits modifiers making orange fruits	34	v	Virescent white seedlings	10
l	Yellowing of leaflets (lutescence)	18	w	Wiry leaves	22
lf	Leafy inflorescence	28	wf	White or tan corolla	28
lc	Many locules in fruits	43	Wo	Woolly leaflets	19
m	Mottled cotyledons and leaflets	11	wt	Wilty leaflets	22
			x	Ineffective microgametes	31
			Xa	Xanthophyllic leaves	19
			Y	Yellow peel on fruits	34
			ys	Yellow seedlings	10

*Capital letters refer to dominant alleles.

The purpose of this bulletin is to describe, classify, and discuss as many as possible of the inherited characters of tomatoes to facilitate the work of tomato breeders and other interested people for whom it is hoped that this compilation of information will be useful. Further research work is expected to provide the basis for recording other inheritance ratios and gene symbols. Many of the characters that are listed in Table 3 have great horticultural importance.

Table 3. Index to polygenic and other tomato characters without gene symbols

Key to Botanical Characters of Lycopersicon

Red or yellow fruits that usually are glabrous when ripe; seeds flat, broad, usually hairy; inflorescence bractless; leaves without pseudostipules; fruits contain lycopene and carotin...........Subgenus *Eulycopersicon* (Muller).

Plants villous with 2 to many loculed fruits that are at least 1 cm. (usually 3 cm. to 10 cm.) in diameter, often lobed, oblate, or globe shaped; inflorescence is a short raceme........... *L. esculentum* Mill. (4).

Fruits nearly globe shaped, 5 to 10 cm. in diameter, preferably not lobed...........*L. e.* var. *commune* Bailey.

This botanical variety contains the horticultural varieties of tomatoes (54). The main commercial varieties were arranged in similar groups (7). The characteristics of the Glovel variety were described technically (62).

Fruits pear-shaped with constricted stem-ends; 2-loculed, not lobed........... *L. e.* var. *pyriforme* Alef. Red and yellow pear tomatoes (54).

Fruits spherical, 2-loculed, 1 to 2 cm. in diameter; plants usually with characteristically rounded lobes on leaflets; raceme is elongate........... *L. e.* var. *cerasiforme* Alef. Cherry tomatoes (55).

Fruits usually 3 to 4 cm. long with the polar diameter exceeding the equatorial diameter........... *L. e.* var. *cerasiforme* form *pruniforme*. Plum tomatoes.

Large plants with leaves like those of Irish potatoes........... *L. e.* var. *grandifolium* Bailey. The potato-leaf tomatoes.

Upright dwarfed plants that are stout, erect, and very compact; leaves crowded and curled; a cultigen........... *L. e.* var. *validum* Bailey. Upright tomatoes.

Plants not villous, leaves very small, flowers small, corolla deeply divided into attenuate lobes, fruits ½ to 1 cm. in diameter, usually red fruits, inflorescence elongate........... *L. pimpinellifolium* Mill. or *L. racemigerum* Lange. The currant tomatoes.

Fruits white, green, or yellowish, often with purple stripes, containing chlorophyll and anthocyanin pigments, often hairy when ripe; seeds thick, naked, brown; inflorescence bracted; leaves usually with pseudostipules........... Subgenus *Eriopersicon* (55).

Plants canescent with short hairs.

Plants without bracts.

Leaflets entire or sinuate-dentate........... *L. cheesmanii* Riley.

Leaflets or some of them basally divided or compound........... *L. cheesmanii* form *minor* Muller.

Plants with bracts subtending peduncles, rachises, and usually pedicels; minor leaflets usually present.

Major leaflets entire, toothed, or shallowly lobed; truncate at base, very small, subsessile; fruits often not hairy when ripe........... *L. peruvianum* (L.) Mill.

Major leaflets deeply lobed or pinnatifid (fern-like, resembling *Aspidium*), or if leaflets are subentire, then long-petioled and cordate........... *L. peruvianum* var. *dentatum* Dun. (*L. chilense* Dun. or *L. pissisi* Phil.) (44).

Stems decumbent, densely short hairy; minor leaflets usually absent; major leaflets entire, ovate-lanceolate.......... *L. peruvianum* var. *humifusum* Muller.

Plants pale green with dense long-spreading pubescence; bitter fruits containing solanin. Stems thick, erect; corolla flat, slightly divided; fruit with dense spreading hairs.

Stems and leaves hirsute..........*L. hirsutum* Humb. & Bonpl.

Stems and leaves slightly hirsute..........*L. hirsutum* form *glabratum* Muller.

Stems viny, not thick and erect; corolla limb divided half way to base; fruit slightly pubescent..........*L. glandulosum* Muller.

Description of Tomato Characters with Notes for Breeders

The genes and segregation ratios are given in all cases where they are known. The characters are arranged alphabetically in Tables 2 and 3. In this section, they are grouped on the basis of the main part of the plant that they affect.

Characters of Seeds and Seedlings

Size of seeds. Each tomato variety has a characteristic range in sizes of seeds that may differ from that of other varieties. Seeds of *L. peruvianum* are small and pass through a 16-mesh screen that retains the seeds of *L. esculentum* (55). Clark's Special B variety averaged 9,295 seeds per ounce, while the Gulf State Market variety had 10,468 seeds per ounce in counts made in 1937. Marglobe seeds are like those of Clark's Special B.

Virescent white seedlings. Allele: *v*. Seeds from a radium-induced chimera produced virescent white seedlings that were due to a recessive mutation (43). These seedlings became green and grew slowly but their tops remained white, and some leaf margins were white.

Yellow seedlings. Allele: *ys*. Yellow lethal seedlings resulted from a mutation that was induced by radium (43). Probably a similar character was found in T735* that produced a plant with about half of its leaves yellow. Seeds from this plant produced 10 yellow seedlings and 5 normal green seedlings. The yellow seedlings grew during a few weeks but died before they were 2 inches tall.

*General note: T refers to a tomato selection of the Tomato Disease Laboratory at Jacksonville, Texas. The selections so designated came from hybrids with complicated inheritance.

Rolled cotyledons. Allele: *rc*. A radium-induced mutation resulted in upward-rolled cotyledons (43). The leaflets drooped and grew slowly. The plants had a potato-type leaf that was inherited independently from the *c*-allele. The *rc*-allele affects the rate or vigor of growth, and appears to be recessive.

Mottling. Allele: *m*. This recessive allele caused prominent mottling of the cotyledons and mature leaflets. This allele appeared as an x-ray induced mutation (48, 51). Leaf mottling also is caused by mosaic virus (76).

Giant cotyledons. Cotyledons that are 3/8 inch wide and 1 to 1½ inches long characterize some of the wilt-immune (*I*-allele) hybrids such as T773 in contrast with the hundreds of other selections and varieties of tomato seedlings that have the narrower, shorter cotyledons.

Type of Stem Growth and Disease Resistance

Tall versus dwarf plants. Alleles: D_1-d_1. The F_2 segregation is 3 tall to 1 dwarf (8). Tetraploid segregation is about 22:1 (8). Most commercial varieties of tomatoes have the D_1-allele. Some selections of dwarf tomatoes have rugose leaves and this may account for the botanical variety, *L. e.* var. *validum*.

Dwarf versus extreme dwarf. Alleles: D_2-d_2. The F_2 segregation is 3 dwarf to 1 extreme dwarf (8). Plants with the d_2-allele have very short internodes (51). A cross involving the D_1 and d_2-alleles probably would show D_1 to be dominant.

Tall versus brachytic plants. Alleles: *Br*-*br*. The F_2 segregation is 3 tall to 1 brachytic (8). The dwarfed plants of T593, T605, T607 and T609 probably had the d_2 and *br*-alleles.

Midget tomato. This mutant type had many auxiliary branches, aerial roots and very small leaves and flowers (37). This witches-broom type of dwarfing was due to a simple recessive factor with low viability, so definite ratios of inheritance were not secured.

Extremely tall plants. The character for extreme tallness in the Louisiana Slicer variety is recessive to ordinary tallness in Marglobe (53). The extreme tallness is due to very long internodes and is linked with the giant-plum type of fruit.

Climbing tomatoes. Burgess Trip-L-Crop variety and T564 cherry tomato exemplify the so-called climbing tomatoes that grow outdoors with the support of strings, wires or tall stakes. Their stems usually are much longer than those of Marglobe variety.

Runty plants. A seriously large percentage of runty plants commonly occur in cold frames of tomatoes and are especially noticeable after 3 or 4 weeks of growth. The runty plants usually are distributed at random among the large plants. In addition to pathological and physiological causes of dwarfing, many of the runty plants are due to hereditary weakness that differs from the effects of the d_1, d_2, and *br*-alleles. Some tomato varieties may show as many as 14 percent of such runty "rogues" (13), while such defective plants may be rare in other varieties. Segregation shows normal, intermediate and runty plants. Such dwarfing may be due to unstable genes that mutate toward and away from normal size (15). The runty plants in cold frames have inherited dwarfing and are unproductive when transplanted into fields.

Broad petiole on lowest leaf. In a few selections of T773, some plants showed an expanded, flattened base of the petiole of the lowest leaf of each stem (Figure 1,B), while the other petioles remained normal on the same plants. In many cases, these slightly fasciated petioles were curved near the point of attachment. The abnormality of flattened petioles was observed in the descendants of such plants.

Bushy stems. Allele: *bu*. MacArthur's X-ray mutant No. 42M (T1078) produces dwarfed plants with short internodes. The branches grow very early from the nodes, giving the plants a bushy appearance in contrast with the open type of growth of ordinary commercial varieties of tomatoes in this early stage of growth (Figure 1,A). This bushy character is a simple recessive. The plants have dark green leaflets and large oblate red fruits.

Excessive branching of stems. Some of the *I*-allele hybrids developed their branches too early in the growing season, so that it was difficult to prune them to two main stems for producing green-wrap tomatoes. Marglobe variety has the usual habit of producing a branch at each node, but these branches develop slower than those of certain hybrid selections, and of the bushy tomatoes (Figure 1,A).

Hairless versus hairy stems. Alleles: *H-h*. The F_2 segregation is 1 hairless, 2 intermediate, and 1 hairy (8). Pure *L. pimpinellifolium* has glabrous stems due to the *H*-allele (Figure 9,C), while pure *L. esculentum* like Marglobe has hairy stems due to the *h*-allele (12) (Figures 5,B; 9,B). The true F_1 hybrid of *L. esculentum* X *L. pimpinellifolium* is slightly hairy on the growing tips of the stems, but the hairs disappear as the stems become mature. This explains the partial dominance of the H-allele in the 1:2:1 ratio.

Prostrate versus upright stems. Oxheart variety and selections of T585 produce long, extremely prostrate stems that lie on the ground unless they are staked to hold them upright. When the stems lie on the ground, the leaves do not shade the fruits and protect them from sunburn. Most tomato varieties have mainly prostrate stems. Farmers in East Texas ceased tying their tomato plants to stakes, so hybrids must be selected for upright stems. In contrast with the tomato varieties with prostrate stems, Rutgers and Marglobe stems grow upright and do not lie on the ground until strong wind or weight of fruit makes them do so. When the plants are only about 1 foot apart in the rows, they help to hold each other upright. Holding the fruit off the ground is a main protection against fruit-rotting parasites that live in the soil (103). Although desirable production of early fruits tends to pull the stems to the ground, Rutgers and Marglobe tomatoes commonly hold most of their fruits off the ground early in the growing season. The prostrate habit of stem growth appears to be partially dominant in a cross of Oxheart X T667, as in T878. It is very difficult to select green-wrap tomatoes for upright habit of stem growth.

Thick, strong stems. The Buckeye State variety and T698 have very thick strong stems that hold their fruits off the soil, but they lack other necessary qualities. Marglobe and Rutgers varieties have thick stems and are preferable to T623 and T738 that have slender weak stems.

Shady plants. Plants that shade their fruits well and prevent sunburning are needed for growing green-wrap tomatoes in the southern part of the United States (103). Upright habit of growth, thick strong stems, indeterminate growth, abundance of large dark green leaves and large plants are desirable characteristics for this purpose. These partly intergrading qualities probably are polygenic with quantitative inheritance. Rutgers variety is excellent in shading its fruits and, with luxuriant growth, the shade is extreme. The unripe fruits are nearly white in the very dimly lighted center of dense plants where there is not enough light for normal development of chlorophyll. In northern regions with short growing seasons, determinate-growth varieties like Bison are preferred, because their fruits are exposed to sunshine for early ripening. Farther south, hot drouths end the growing season of the spring crop of tomatoes.

Three leaves between flower trusses. Pritchard variety usually has 2 or 3 leaves between flower trusses and usually has an adequate ratio of leaves to fruits so that it bears large yields of early, well-shaded fruits. Marglobe and Rutgers varieties have 3 to 5 leaves between trusses and must produce longer stems than Pritchard for

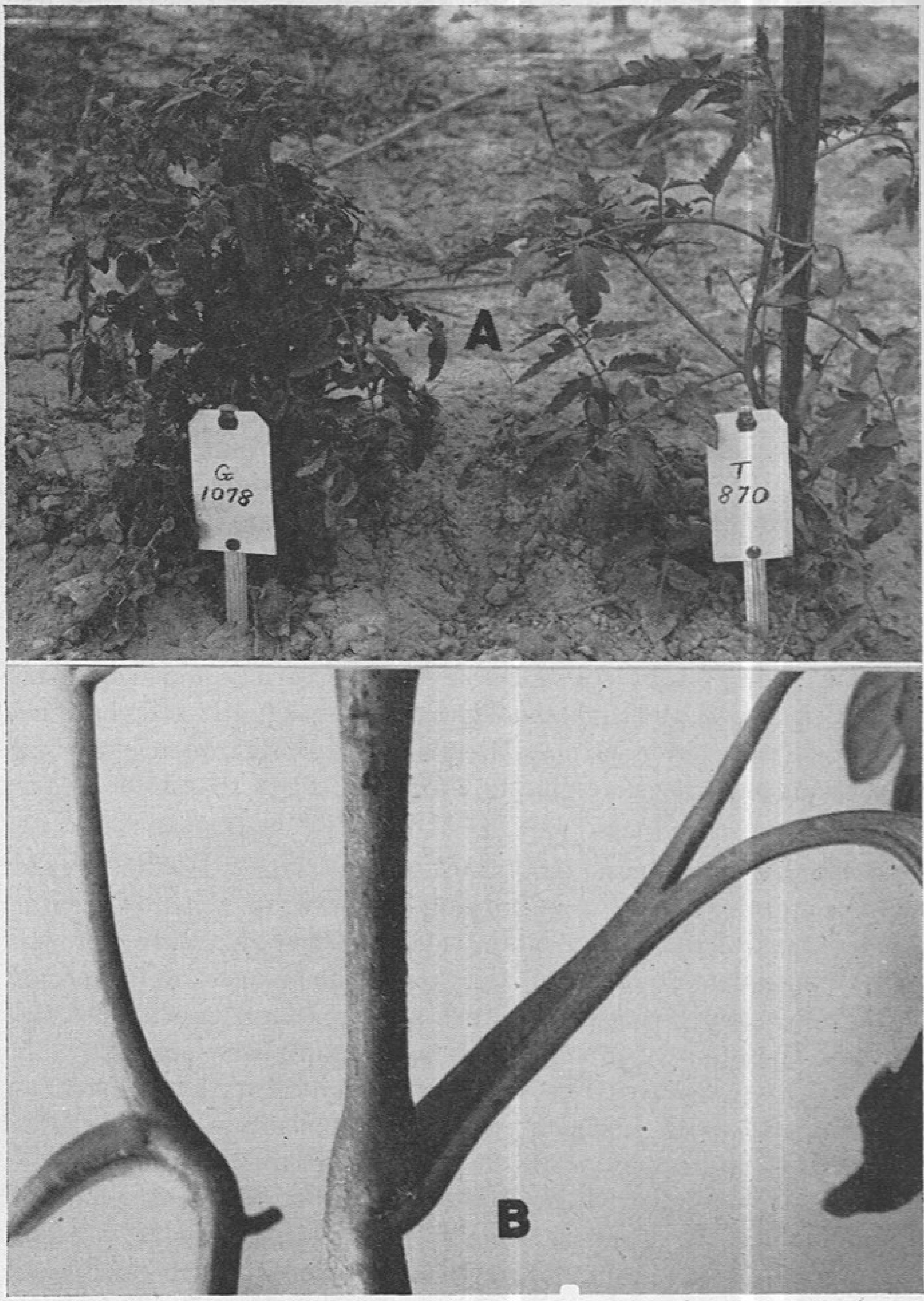

Figure 1. A: Tomato plant, G1078, is bushy due to the *bu*-allele and is densely compact in habit of growth in this pre-bloom stage when commercial tomatoes (as exemplified by T870) have long stems and petioles but relatively few leaves. B: Broadened (slightly fasciated) petioles of lowest leaves partly clasp stems of these plants of T773V. Stem may be curved at place of attachment of petiole.

equal crops of fruits. Hybrids with Bison parentage have 0, 1, 2 or 3 leaves between flower trusses and may not have enough leaves for shade.

Indeterminate versus self-topping stems. Alleles: *Sp*- *sp*. The F_2 segregation is 3 indeterminate to 1 self-topping (8, 46). Marglobe is indeterminate while Pritchard variety is partly determinate (probably due to a modifier of the *sp*-allele), but new branches continue the growth of the stems so that the fruits are well shaded. In contrast, Bison variety is self-topping as the main stems end in flower trusses that expose the fruits to maximum sunshine. Some plants have the determinate habit of growth so extremely that they are almost leafless (Figure 2,C,D).

Running flower trusses. Gulf State Market and some other varieties often have long leafy stems growing from the first and sometimes other flower trusses, making a combination of flower truss and branch (Figure 2,C). A flower truss is a specialized branch one part of which may bear a leafy stem as an inherited character. Running flower trusses are undesirable.

Very hairy stems. T328 tomato stems are very hairy, which character segregated with sticky peel and light green leaves, indicating linkage of these characters. The key to tomato species records species with hairy stems. Capitately stellate hairs occurred on stems of *L. p.* var. *dentatum* (40).

Purple stems. Allele: A_1. The F_2 segregation is 3 purple to 1 green. Well illuminated seedling stems of Marglobe and similar varieties show prominent purpling of the stems below the leaves, especially when they are only 1 to 6 inches tall (Figure 3,E). The upper parts of the stems also become purple when the plants suffer from drouth. The mature stems are mostly green but usually have some purple color. Plants with the a_1-allele are always green (Figures 2,B; 3,D).

Purple stems becoming green. Allele: a_2. F_2 segregation is 3 purple to 1 purple becoming green (12). Ordinary tomato varieties (such as Marglobe) have the A_1 and the A_2-alleles.

Purple stems of large plants. T772-56 segregated so that 70 percent of the 44 plants had purple epidermis on the upper parts of the stems (and many of the upper leaflets were purplish-green), while 30 percent of the plants had ordinary green mature stems. When the leaflets and stems of the purple-stem plants became old, the purple color disappeared, but the new upper stems and leaflets were purple. T773-63 was selected from one of these purple-stem

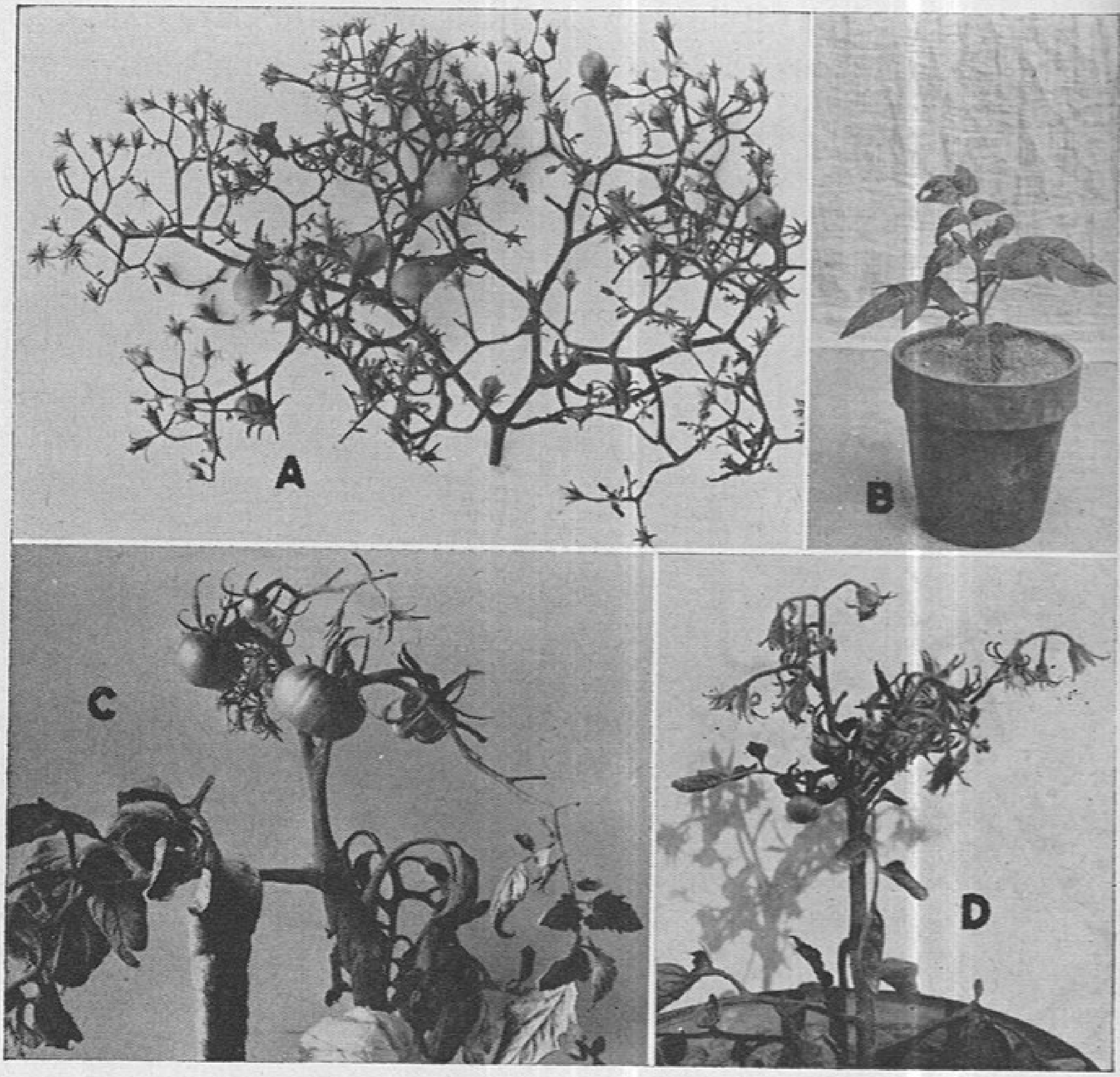

Figure 2. A: Extremely compound flower truss (due to *e*-allele) of T1079 beaked yellow pear tomato. This truss bore more than 300 flowers and buds. B: Tomato plant showing dwarfing (due to *d*-allele), potato leaf (due to *c*-allele), and green stem (due to a_1-allele). C: Extremely determinate tomato plant with a flower top (due to *sp*-allele). This plant was 1 foot tall with only 4 compound leaves. It had a running flower truss because a compound leaf grew from it. The plant grew in a commercial field. D: An extremely determinate tomato (T630C) due to *sp*-allele with only 4 compound leaves and a flower top.

plants and it produced only plants with purple stems. These purple stems showed a broad green streak of epidermis below each flower truss, suggesting a chimera. This appears to be a new character. At Toronto, crosses with Florida Purple variety did not show clear segregation for purple stems. Thus, there is complicated inheritance of stem colors.

Collar-rot resistance. Allele: *ad*. Resistance to collar rot (caused by *Alternaria solani*) is a valuable character to have in commercial varieties. The *Ad*-allele for susceptibility is incompletely dominant (68). T978 to T995 with resistance to collar rot were tested for horticultural qualities. Their resistance to collar rot due to the *ad*-allele came from their Norduke and Devon Surprise parents (68).

Fusarium-wilt immunity. Allele: *I.* Immunity to Physiologic Race No. 1 of *Fusarium oxysporum* f. *lycopersici* (77) is due to the dominant *I*-allele that came from one selection of *L. pimpinellifolium* (5). Pan America variety has the *I*-allele (60). The immunity of Pan America is localized in the roots (24). Most tomato varieties are susceptible or moderately resistant to Fusarium wilt. Different races of *F. o. lycopersici* differ in virulence (85), and 3 races cause wilting of some tomato plants that have the *I*-allele (1). The main project of the Tomato Disease Laboratory is to transfer the *I*-allele to selections of tomatoes with excellent horticultural qualities (103). More than 200 hybrids are tested for these qualities each year, and some of them are commercially promising (101).

Fusarium-wilt resistance. The Louisiana Red and Marglobe varieties exemplify the many commercial varieties that have mod-

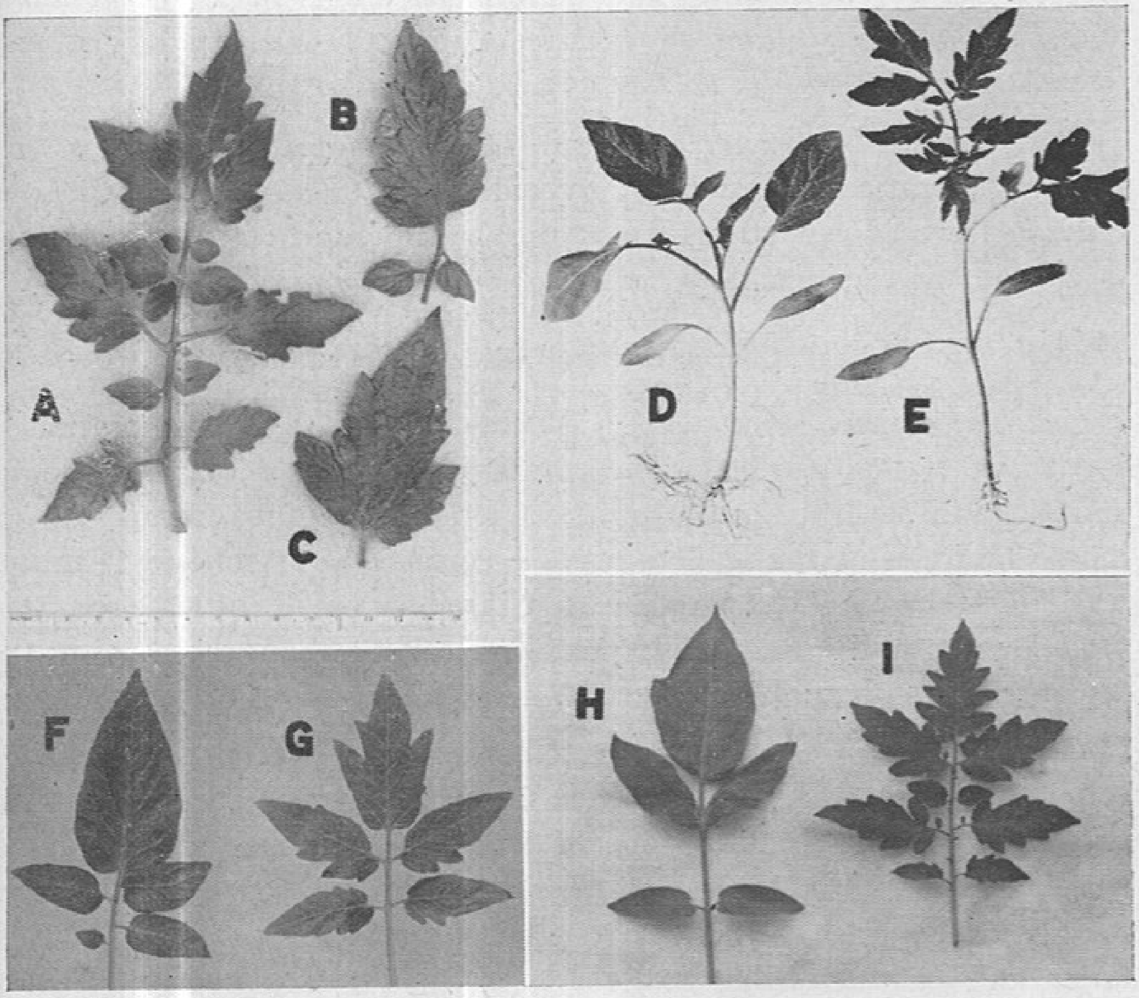

Figure 3. A: Very small light green compound leaf of T1072, macrocalyx tomato. B,C: Two terminal leaflets of T1069 (*I*-allele tomato) showing the comparative size of ordinary tomato leaflets; A to C are all mature leaflets. D: Tomato seedling showing potato-leaf type due to *c*-allele, green stem due to *a*-allele, and lutescence due to *l*-allele. E: Ordinary tomato seedling with cut leaflets due to *C*-allele, purple stem due to *A*-allele, and green leaf-color due to *L*-allele. F,H: Potato-leaf tomatoes due to *c*-allele. G,I: Cut tomato leaves due to *C*-allele.

erate (probably polygenic) resistance to Fusarium wilt (77, 94). When growing in infested soil, such varieties usually resist wilt long enough to produce about half of a crop of fruit, but their resistance is decreased by root-knot nematodes. The Stone variety lacks wilt resistance. Tomato wilt may also be caused by *Fusarium retusum* (84), and this complicates the problem of breeding tomatoes for wilt resistance (1).

Verticillium-wilt resistance. The Riverside and Essar varieties of tomatoes are resistant to wilt that is caused by *Verticillium albo-atrum* (73, 74). Inheritance of this resistance probably is quantitative. Neither of these varieties has the horticultural qualities that are necessary for green-wrap tomatoes in East Texas. *L. hirsutum* is tolerant to Verticillium wilt and tobacco mosaic (40a).

Resistance to southern blight. One plant of the Red Rock commercial variety of tomato, and certain selections of *L. peruvianum* and *L. pimpinellifolium* showed resistance to southern blight that is caused by *Sclerotium rolfsii* (53a).

Resistance to root-knot. Certain selections of *L. peruvianum* and fourth-generation selections of hybrids of *L. esculentum* X *L. peruvianum* have shown strong resistance or tolerance to root-knot that is caused by the nematode, *Heterodera marioni* (53a).

Leaf Characters and Disease Resistance

Cut leaf versus potato leaf. Alleles: *C-c*. The F_2 segregation is 3 cut leaf to 1 potato leaf. The potato-leaf type is *L. e.* var. *grandifolium* with several horticultural varieties including Alpha (8, 47, 54). The bases of the leaflets may be equilateral or oblique (Figures 3,D,F,H; 2,B). The potato-leaf character in T1071 segregated with less angular and lighter green leaflets than those with the broad-leaf character (Figure 4,A).

Broad leaflets. Allele: *e*. A tomato selection from F. W. Sansome has the recessive *e*-allele that is manifested as broad and nearly entire leaflets some of which have a few sharp-pointed basal lobes (Figure 4,A). In T1077, the leaflets are dark green, rugose, and many of them have very oblique bases. The plants are large and bear globular red fruits 2 inches in diameter (Figure 12,H,I).

Yellowing of leaflets. Allele: *l*. The F_2 segregation is 3 green to 1 becoming yellow or lutescent (21). The Honor Bright variety has the lutescent character that affects the leaflets and fruits (54). In T1071 and T1077, 3 plants became yellow with the lutescent character after they had been green during 3 months (Figures

5,D,E,F; 11,F). The lower leaflets became yellow or light green and the green fruits that were larger than 1 inch in diameter became yellow to white and remained very firm before they began to turn pink or red. MacArthur's Linkage Tester No. 902 (T1073) produced extremely dwarfed plants with rugose leaflets of the potato-leaf type which showed some yellowing after they became large seedlings. The stems of these plants became whitish yellow during 3 months and bore lutescent fruits. This is an emended description of the lutescence character. It may not be delayed in exhibiting its symptoms (12). A radium-induced mutation produced plants with the recessive lutescent character due to the *l*-allele (8, 43).

Chlorotic leaves. Apparently a recessive gene caused one-fourth of the plants to be chlorotic in segregates of a cross of *L. esculentum* X *L. p.* var. *dentatum*. The petioles and basal parts of the young leaves were yellowish (40a).

Xanthophyllic leaves. Allele: *Xa*. MacArthur's natural Mutant No. 3401 (T1074), that he selected from a field, manifested the xanthophyllic character as bright yellow leaflets and stems (Figure 4,B). The heterozygous plants developed enough chlorophyll in their lower leaflets to keep the plants alive while the top leaves remained yellow. They bore pinkish yellow fruits ¾ to 1½ inches in diameter. The homozygous yellow dominant plants did not become green, usually were sterile, and died much sooner than the normal segregates did. T1074 produced 39 yellow seedlings and 13 green seedlings as a perfect example of 3:1 segregation. The yellow seedlings grew slowly and finally produced very brittle plants only 6 to 12 inches tall in 4 months, while the green seedlings grew to be 3 feet tall with pinkish-yellow fruits ¾ to 1½ inches in diameter. Xanthophyllic tomatoes would make attractive ornamental plants in flower pots or beds.

Woolly leaves. Allele: *Wo*. Seeds of T1075 from J. W. MacArthur produced 11 plants with ordinary pubescent leaflets and 9 plants with canescent leaflets, the lower sides of which were almost tomentose (Figures 5,A; 9,A). The woolly plants looked gray. Magnifying the leaflets 50 times showed that they had the usual pubescence of short 1-to-few-celled hairs that were almost hidden by the abundant long hairs on the woolly leaflets. The 11 ordinary plants showed the short-hair pubescence with relatively few long hairs (Figures 5,B; 9,B). This T1075 produced 4-locule red globe, very late fruits. This selection came originally from W. S. Porte of the U. S. Department of Agriculture who called it "Angora."

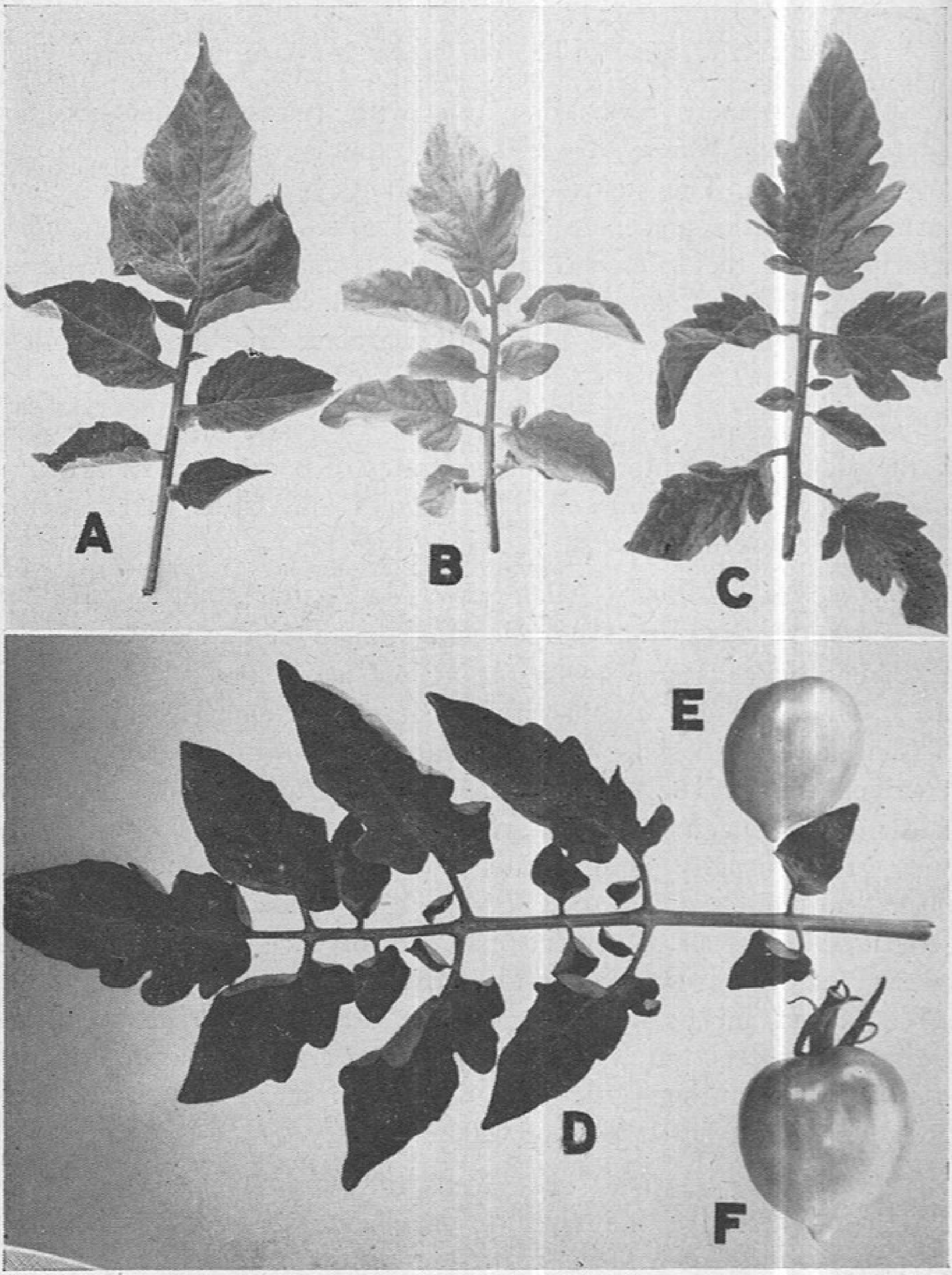

Figure 4. A: Broad tomato leaflets due to the *e*-allele; leaflets are rugose and dark green with oblique bases. B: Yellow leaflets resulting from presence of the *Xa*-allele. C: Ordinary dark green cut leaflets due to *E* and *xa*-alleles. D,E,F: Associated characters of T667V showing the characteristic unwrinkled leaflets with slightly upturned margins and the nipple-tip fruits (due to *n*-allele).

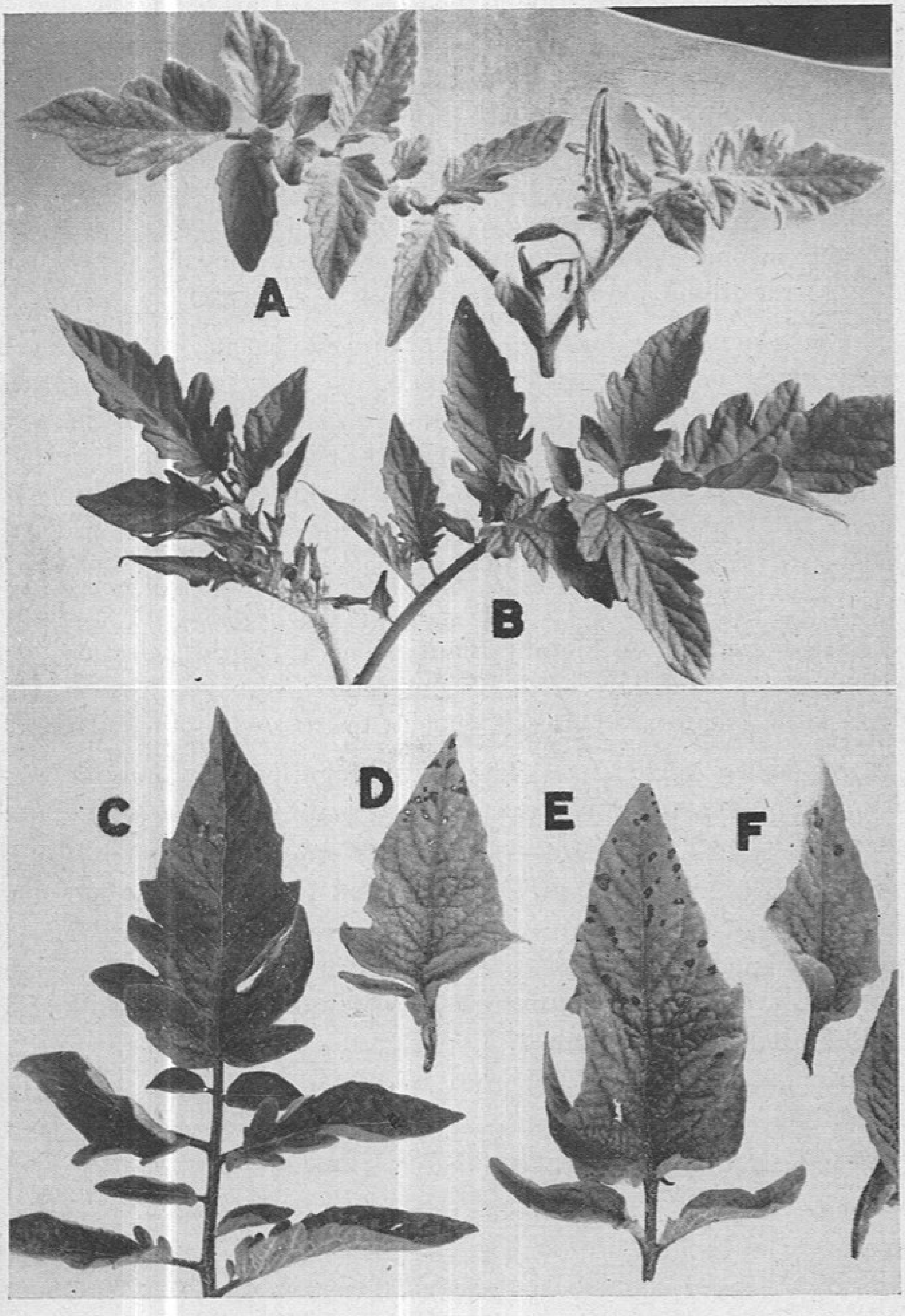

Figure 5. A: Woolly (hirsute or angora) leaflets of T1075 due to the *Wo*-allele. B: Ordinary slightly pubescent and glandular leaflets. C: Large ordinary dark green cut compound leaf of T1071 (*L*-allele segregate). D,E,F: Lutescent leaflets with yellow ends (and some remaining green veins) due to the *l*-allele in T1071; leaflets have Septoria spots.

The *Wo*-allele is typically dominant and is lethal in homozygous condition so that segregation is near a 2:1 ratio, based on studies at Toronto. A dominant allele that is lethal when it is homozygous may be explained as being due to a missing segment in a chromosome. The complete chromosome is necessary for life. In a heterozygous diploid plant, the normal recessive allele supplies the segment of chromosome that is missing in both parts of a diploid chromosome with the homozygous dominant alleles. The plants with the incomplete chromosomes die without showing leaf characters so the living plants segregate with a 2:1 ratio.

Yellow margins on leaflets. The margins become yellow or yellowish green on many of the leaflets of T162 at fruiting time (Figure 6) (97). This x-ray mutant character appeared in only about one-fourth of the leaflets of each plant, and was inherited through several generations. T497B was the first generation of a cross of T333 (*wf*-allele tomato) X T162. All of its progeny had normal leaves indicating that the character for yellow margins is recessive.

Twisted leaves. A mutant plant from a hybrid selection had twisted leaves and few seeds. Some fruits were seedless in this Oligosperm tomato (21). It was difficult to cross with other tomatoes.

Wiry leaves. Allele: *w*. The F_2 segregation is 3 normal to 1 wiry. The plants with this abnormality were dwarfed and slender and had strap-like leaves that resembled those of plants with fern-leaf disease which is caused by Cucumis Virus 1 (35, 76, 103).

Ridged leaflets. Allele: r_1. This recessive mutation after radium treatment appeared as irregular ridges in the epidermis of the leaflets (43, 8). The leaflets grew slowly and remained small. The r_1 and *c*-alleles may be linked.

Wilty leaflets. Allele: *wt*. The F_2 segregation is 3 normal to 1 wilty (12). The Stemless Pennred variety has wilty leaflets (56). T738 has slightly wilty leaflets.

Slender leaflets. The leaflets are broad and blunt-tipped in most tomato varieties (Figure 15,E). In contrast, the leaflets of T738 are long, slender and sharp pointed (Figure 15,F). The plants are prostrate with *u*-allele fruits (Figure 12,C). These characters have been inherited together through several generations.

Curled margins. T667V has characteristically upturned margins on the leaflets (Figure 4,D). The margins were slightly wilty.

Light green leaflets. Commercial varieties of tomatoes have characteristic colors of leaflets that are exemplified by the light green of Globe, T328 and T736; the medium green color of Gulf State Market and T738; and the dark green color of Marglobe and Rutgers leaves (54). The light-green character appeared to be recessive in segregating progeny of T328 X Marglobe. The characters of light green leaflets, hirsute stems and sticky fruits always segregated together, indicating linkage. The other segregates of this cross were medium green, instead of dark green like the Marglobe parent, so complex inheritance of leaf color is suspected.

Albino leaves. A bud mutation resulted in a white branch with striped fruits. Seeds from them produced white seedlings that died early (45) as a result of this lethal mutation. T244 and Rutgers variety each produced a plant with epiphyllous gray to white leaf spots. None of the progeny of T244 showed any albinism, so, apparently, the change was only somatic in the original plant.

Dwarfed leaflets. T1072 had the smallest mature leaflets of any of the nearly 2,000 varieties and hybrid selections of tomatoes that were tested at the Tomato Disease Laboratory (Figure 3,A). This small-leaf character was associated with macrocalyx, 2-locule fruits and single-fruit trusses.

Leaf roll. When Blair Forcing variety of greenhouse tomato was grown in fields for a few seasons, it reacted to hot, dry weather by upward rolling of its upper leaflets that thereafter remained rolled (103). T550 also had this rolling of its upper leaflets. It transmitted this character to its T740 progeny in crosses with Pan America variety that shows no rolling of its upper leaflets. Selections through 3 generations eliminated this susceptibility to physiologic leaf roll in the golden globe tomato (T841). The Lloyd Forcing variety also is predisposed to leaf roll (16, 27).

Leaf size. With favorable growing conditions, each tomato variety has a characteristic range in sizes of its leaves. Rutgers has large leaflets, T738 has medium-sized leaflets, and T1072 has small leaflets (Figures 3,A; 15,E,F). The leaf type of *L. pimpinellifolium* (very small) was dominant over that of *L. esculentum* (Figure 9,C) (29, 64).

Immunity to Cladosporium fulvum. Allele: Cf_{p1}. This allele gives tomatoes immunity to Physiologic Races No. 1 to 4 of *C. fulvum* (30, 103). Because it does not give resistance to Race No. 5, the Vetomold variety is susceptible to this race. Races No. 1 to 3 of *C. fulvum* on completely susceptible varieties entirely suppress Race 5 (3). Vetomold also is susceptible to Races No. 6, 7 and 8 of *C. fulvum* (Report for 1945-1946 of Hort. Exp. Sta., Vineland Station, Ontario).

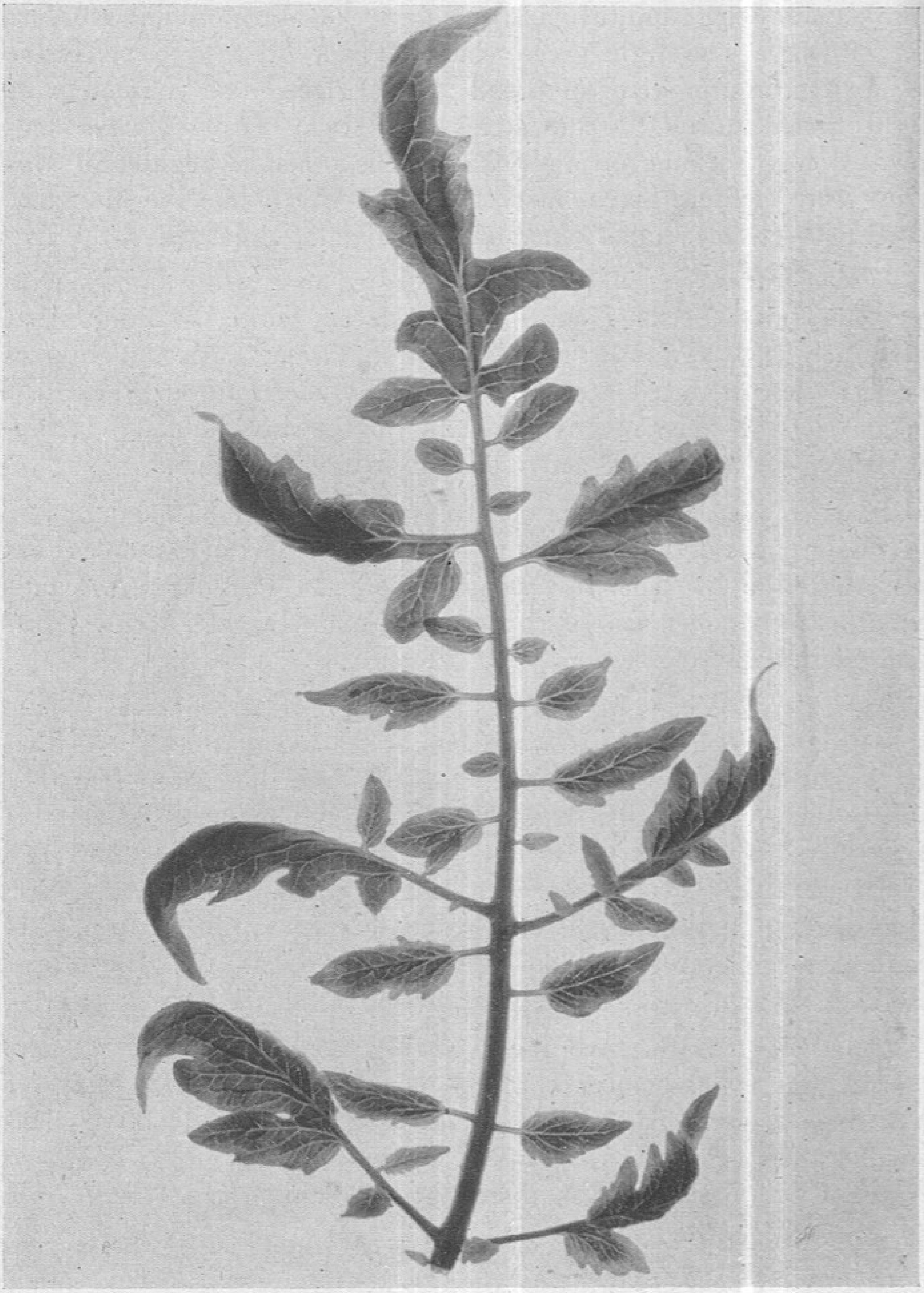

Figure 6. Yellowish-green margins on the green leaflets of the original plant of T162 which is the X-ray mutant for the character of yellow margins on leaflets.

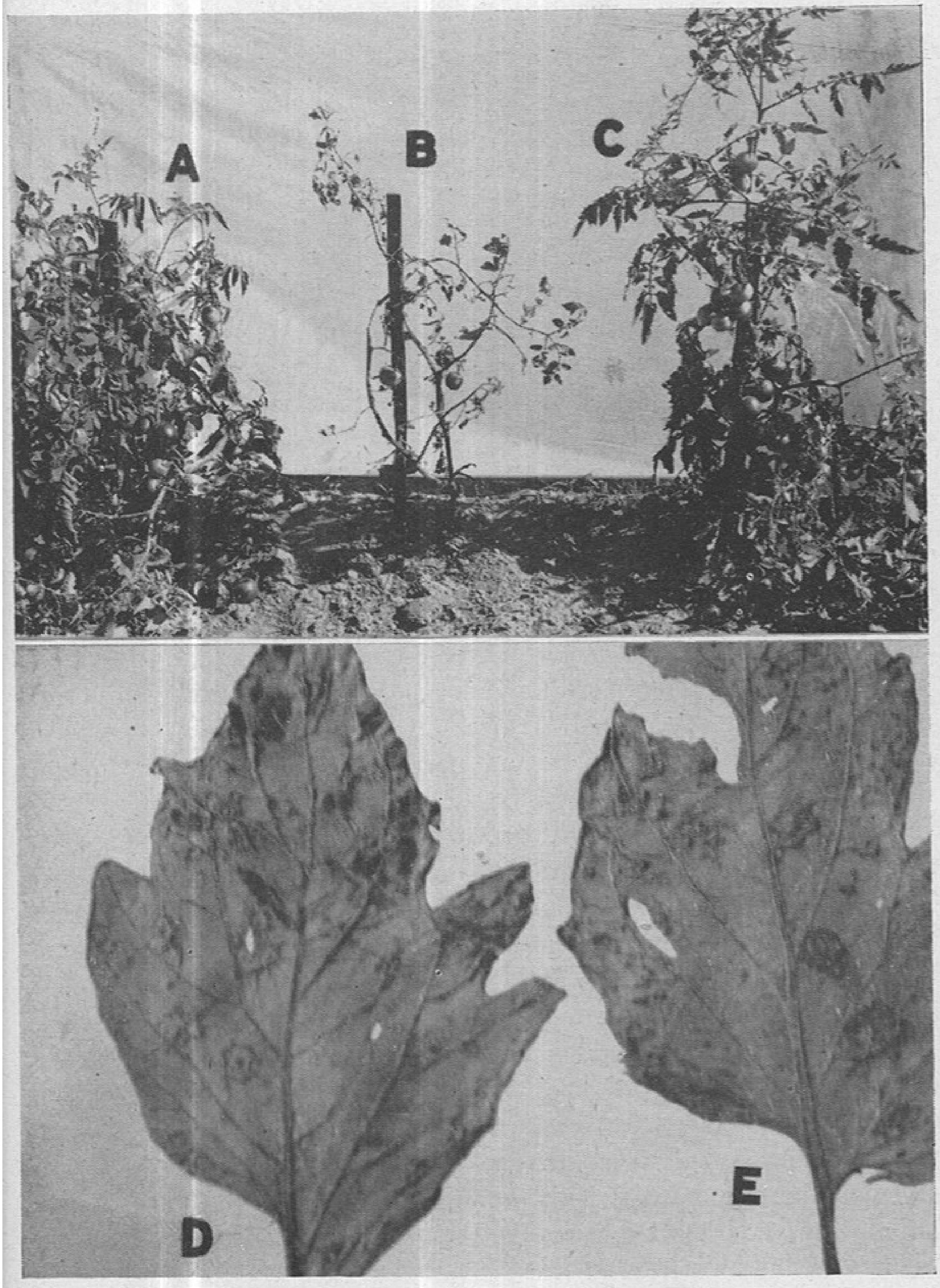

Figure 7. A,B,C: Three tomato plants of T585 segregating for the inherited leaf-spotting abnormality. A and C are normal, but B shows dwarfing and defoliation. D,E: Tomato leaflets with ring-shaped purple-brown spots due to inherited leaf spots.

Resistance to 4 races of C. fulvum. Allele: Cf_{P2}. This allele gives tomato leaflets resistante to Physiologic Races No. 1 to 4 of *C. fulvum* (30).

Resistance to 2 races of C. fulvum. Allele: Cf_{sc}. This allele gives tomato resistance to Physiologic Races No. 1 and 3 of *C. fulvum* that causes tomato leaf mold (30). The alleles: Cf_{P1}, Cf_{P2}, and Cf_{sc} are all dominant.

Necrotic leaves. Allele: *ne*. This recessive character manifests itself as a severe progressive necrosis of the leaves (31). The Vetomold variety has 2 genes that it received from *L. pimpinellifolium*: Cf_{P1} that gives immunity to *Cladosporium fulvum*, and *Ne* that conditions the compatibility with the chromosome complex of *L. esculentum*. Vetomold is homozygous for Cf_{P1}/Cf_{P1}; *Ne/Ne*. In contrast, pure varieties of *L. esculentum* such as Marglobe are homozygous recessives: cf_{P1}/cf_{P1}; *ne/ne*. When Vetomold (or maybe some selections of Bay State and Globelle varieties) are crossed with Marglobe, necrosis results from incompatibility only in the segregating genotype with the Cf_{P1}/Cf_{P1}; *ne/ne*-alleles in association with the *L. esculentum*- chromosomes (31, 31A, 103A). In T1080, that segregated for this genotype, the plants remained normal until they developed small fruits. Of the 24 plants, 8 remained normal while the other 16 became necrotic. First, the lower sides of the tips of the leaflets (especially the terminal leaflets) showed interveinal, slightly sunken, light brown or purplish shiny spots. These necrotic areas enlarged until they occupied the interveinal spaces. The leaflets died, dried, and became ragged. Both the leaflets and the rachis of the compound leaves curled downward with prominent epinasty (Figure 15,A). Some of the spots showed a characteristic greenish yellow color on the upper sides of the leaflets. When the plants were 4½ months old, they had living leaves only on their tops. The epidermis of the stems showed general blackening or browning with some black or brown streaks, suggesting the symptoms of a virus disease (76). This abnormality may be serious where tomatoes with immunity to leaf mold are grown, unless the seed stocks have the homozygous dominant *Ne*-allele, as in Vetomold variety.

Inherited spotting of leaflets. T585G produced slender stems on which the leaflets soon developed characteristic yellow spots, beginning in the lowest leaflets. The spots became brown or purplish brown and some of them formed rings (Figure 7,D,E). The leaf spots had a peculiar yellow-green color on the upper sides and were purple or black on the lower sides of the leaflets (98). The rachises were curled downward. Many leaves died without prominent spotting. On all affected plants, the leaves died progressively until only a few leaves remained alive on the tops, and the plants were dwarfed (Figure 7,B). The stems usually were very brittle. As the leaves died, the epidermis became brown to black on the stems and flower trusses. Sunken brown or white spots appeared in the epidermis of old stems. These inherited symptoms may be due to the *ne*-allele that could be in T585. It came from a cross of T532 X T543 which latter is the F_1 of Burpee's cross of Marglobe X Farthest North variety. This Farthest North variety came from a cross of Bison X Red Currant (*L. pimpinellifolium*) (91). The 51 plants of T585A in the F_2 generation produced 45 percent of the segregates with normal leaves and 55 percent with necrotic leaves. This indicates a nearly typical 1:1 backcross segregation.

Resistance to Septoria lycopersici. Allele: *Se.* The F_2 segregation is 3 resistant to 1 susceptible (2). The resistant plants showed restricted leaf spots. Selections T997 to T1007 with the *Se*-allele resisted Septoria leaf spot in a severe test in a field. As plants with the *Se*-allele are only resistant and not immune to Septoria blight, they yield best when they are protected from infection. The *Se*-allele plants accordingly should be isolated from the ordinary susceptible varieties (Figure 5,D,E,F).

Unusual susceptibility to Alternaria solani. Most tomato varieties are susceptible to early blight that is caused by *Alternaria solani* (103). Hybrid T874 and certain selections of T870 were defoliated by early blight sooner and more severely than Marglobe, indicating unusual susceptibility to early blight in these segregates of *I*-allele hybrids. Plant breeders should guard themselves against the constant hazard of losing some valuable qualities in their segregating hybrids.

Curly-top resistance. *L.p.* var. *peruvianum* was resistant to the curly-top virus disease (25, 82, 103).

Mosaic resistance. *L. hirsutum* tolerates the virus, and *L.p.* var. *dentatum* escapes the tobacco-mosaic virus (25, 40a).

Flower Characters and Fruitfulness

Compound inflorescence. Allele: *s.* The F_2 segregation is 3 simple to 1 compound. The tetraploid segregation is about 22:1 (8). The Marglobe variety has the *S*-allele with 3 to 7 flowers per truss. MacArthur's beaked pear tomato (T1079) has extremely compound hirsute trusses on plants that are otherwise only slightly pubescent (Figure 2,A).

One flower per truss. The Stemless Pennred variety (56) and macrocalyx selections T1072 and T1071 usually have only one flower and fruit per truss. The macrocalyx and the 1-flower-per-truss characters segregated together in T1071, suggesting linkage of these characters, but their genes are not located on the chromosome map (Figure 14).

Leafy inflorescence. Allele: *lf*. F_2 segregation is 3 ordinary to 1 leafy (12). Commercial varieties do not have leafy inflorescence. *L. peruvianum, L. hirsutum* and *L. glandulosum* have foliar bracts on their flower trusses (55).

Giant terminal flowers. The Early All Red variety and T519 exhibited extremely determinate growth that approached the kinds shown in Figure 2,C,D, except that the plants had more leaves. Each compound flower truss of these selections bore a giant terminal flower with a prominent brown joint in its pedicel, and most of such flowers fell off without making fruits (98). Possibly the effect of the *J*-allele for abscission was modified in such cases.

Jointless flower pedicels. Allele: *j*. The F_2 segregation is 3 jointed to 1 jointless. The pedicel joints are abscission layers. The Stemless Pennred variety has jointless flower and fruit pedicels which facilitates removing the green calyx when the fruit is picked (56). The fruits of this variety are globe shaped with some distinct ridges.

Flower size. *L. pimpinellifolium* and *L. peruvianum* typically have small simple flowers with 5 petals and 5 sepals (51, 55). The petals of the latter are united except for their points in some selections (T1059, Figure 15,G). The common large-fruited varieties of *L. esculentum* have large flowers with 5 to 8 petals each. The Ponderosa variety has very large fasciated flowers, many of which have flat styles.

White or tan flowers. Allele: *wf*. The F_2 segregation is 3 yellow to 1 white (93, 95). T935 has the *I*-allele for wilt immunity and the *wf*-allele as a marker that aids in maintaining pure seed. Data secured in 1947, show that the *r*-allele and the *wf*-allele are linked. In crosses of *RR/wf wf* X *r r/Wf Wf*, 3 crossovers in the 545 plants gave a new genotype: *r r/wf wf* with yellow fruits and white flowers (T1106). The *wf*-allele makes the petals pure white or slightly yellowish tan colored so that they are easily distinguished from the dark yellow flowers of most tomato varieties. Some selections of yellow-fruited tomatoes may have some very pale yellow flowers, especially flowers that are 2 days old that have been bleached by rain and sunshine.

Pistil length and quality. Each tomato variety has a characteristic range in length of pistils that greatly influences its adaptability. The long exserted pistils of the Magnus, Ponderosa and Earliana varieties facilitate cross-pollination, but also increase the damage by dry wind, hot sunshine and storms (34). Tomatoes with exserted stigmas showed 4.9 percent cross-pollination, while tomatoes with included stigmas showed only 0.59 percent cross-pollination. Hot weather tends to stimulate tomato flowers to protrude their stigmas beyond the stamen cone (Figure 15,H,J,K), which is a factor in causing non-receptiveness of stigmas that is followed by flower shedding from common varieties during hot dry weeather (76a). Under favorable conditions, the Marglobe, Dwarf Champion and Break O'Day varieties have their stigmas inclosed by the stamen cones (26). The Bonny Best variety developed very long pistils with an 8-hour photoperiod, whereas its pistils were inclosed by the stamen cones with a 16-hour photoperiod (9). A hybrid with the Princess of Wales variety showed trangressive segregation for shortness of pistils that facilitated self-pollination in winter (9). Pistils are thick and strong in the Ponderosa variety. Flat styles indicate fasciated ovaries or fruits that will have an oval outline in equatorial section. Hence, such flowers should be avoided in hand-pollination of flowers. The Marglobe variety has moderately strong styles with good capitate stigmas. The styles are slender and weak in T615. The style and staminal cone usually are much bent in *L. p.* var. *dentatum* (40). The pistils are long in some green-fruited species of *Lycopersicon* that are mostly cross-pollinated (44). Lobed ovaries are likely to produce lobed fruits (91).

Capitate stigmas. The Marglobe variety has capitate stigmas on strong styles and medium-sized ovaries. The Ponderosa variety has non-capitate, often elongated and lobed stigmas and lobed ovaries. Some flowers show compound styles with about 5 adhering parts and 5 stigma lobes. Capitate stigmas apparently are advantageous for pollination. Each variety is likely to have a characteristic type of stigma.

Macrocalyx. Allele: *mc.* This name was given by MacArthur to J. W. Sansome's mutant plant in the Best of All variety (T1072). The recessive *mc*-allele manifests itself as very large sepals many of which have inflated calyx-bases and broad lobes that show prominent veins (Figure 8,B). The corolla is inconspicuous in the bottom of the calyx tube of many flowers while other flowers have a wide-spreading calyx that exposes the corolla. The sepals are ¼ to ⅜ inch wide and 1 to 2¼ inches long. They grow with the fruits and may become partly separated (Figure 8,F). The fruits of

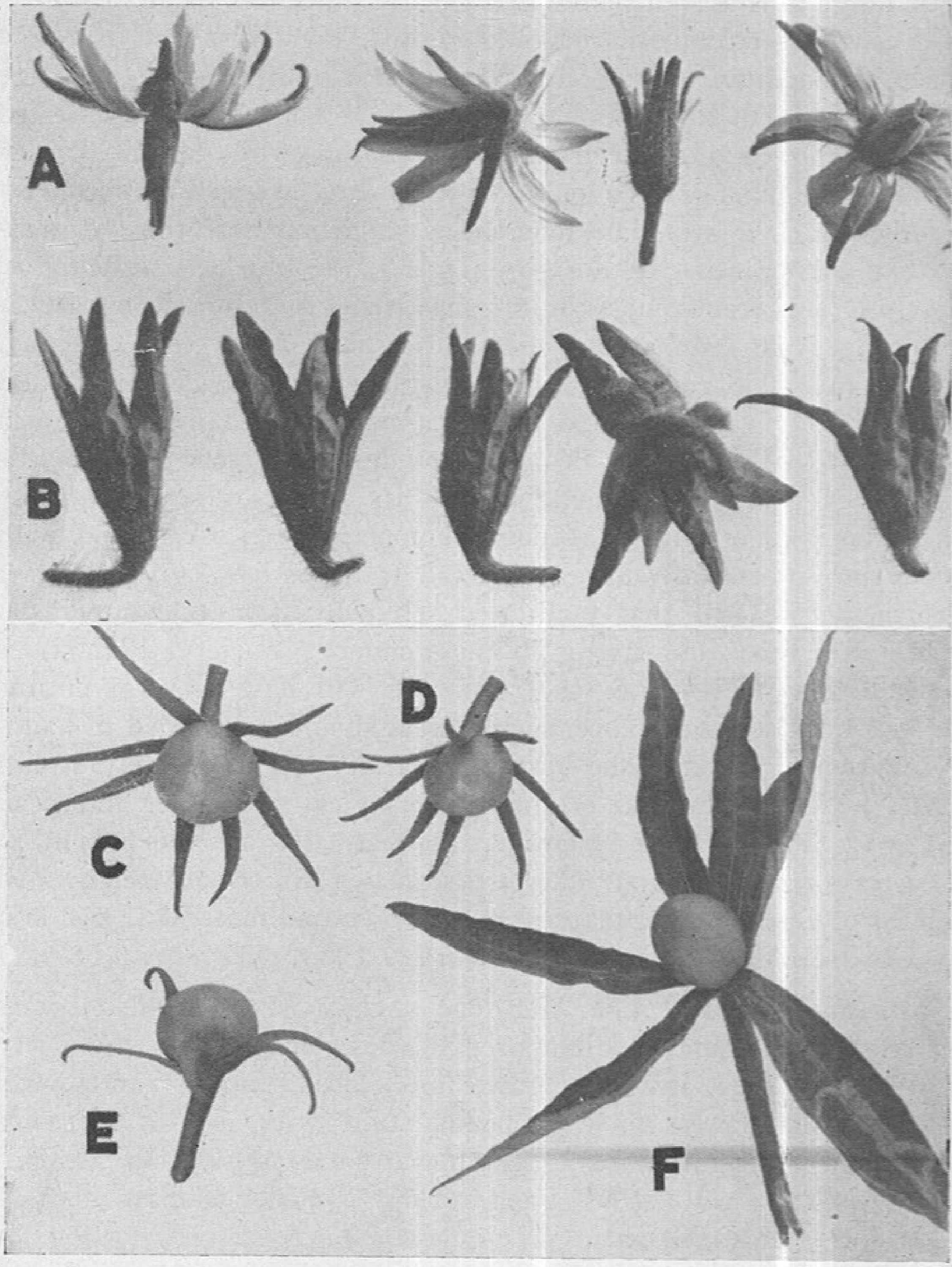

Figure 8. A: Top row shows ordinary tomato flowers with small awl-shaped sepals that are separate due to the *Mc*-allele. B: Second row shows flowers of T1072, macrocalyx tomato, with large inflated tube of calyx, prominent veins and broad sepals due to the *mc*-allele. C,D,E: Ordinary little green tomato fruits with small sepals due to the *Mc*-allele. F: Similar little green tomato fruit with calyx 3¾ inches wide due to the *mc*-allele. The irregular white area in one sepal was due to a leaf miner worm.

T1072 are 2-loculed, red, plum-shaped and 1½ inches in diameter. MacArthur's selection No. 4004 (T1071) segregated into 10 plants with macrocalyx and 22 plants with ordinary calyx (Figure 8,A,C,D). The macrocalyx character will be a good marker when it is separated from the one-fruit-per-truss character and the late habit of fruiting of its T1072 ancestor.

Competitive microgametes. Alleles: *X-x.* (5). "The symbol, *X*, is arbitrarily selected to indicate a genetic factor favorable to effectiveness of microgametes bearing it; the symbol, *x*, indicates the allele which tends to prevent fertilization by gametes bearing it in competition with gametes bearing *X*. Since plants homozygous for *x* set fruits readily, the factor *x* does not prevent fertilization by microgametes bearing it if these are not competing with *X*-bearing gametes; it is not a lethal factor." (5). The factors, *X* and *I*, are linked. The *I*-allele parent should be the female in back crosses in order to get a typical 1:1 back-cross segregation of wilt-immune and susceptible progeny.

Fruitfulness. Many genes probably determine fruitfulness in tomatoes. Inheritance of physiological behavior is the basis for the following classification (81): The Bison variety is very fruitful but weakly vegetative; Pritchard and Bonny Best are fruitful and moderately vegetative; Marglobe is fruitful and strongly vegetative; and Rutgers is more or less unfruitful and very strongly vegetative. The varieties in these different classes have different responses to temperatures and times of fertilizer applications (19). Pritchard is a low-metabolism variety and Rutgers is a high-metabolism variety. Factors that affect the efficiency of the flowers and growth of the plants also affect fruitfulness.

Sterile plants. Allele: *st.* This was observed as a recessive, radium-induced mutation in *L. pimpinellifolium*. The plants with the *st*-allele were sterile (43).

Male sterility. Two recessive genes, ms_1 and ms_2, acted together to cause male sterility, with the possibility of a third dominant allele from male fertile plants. The unfruitful plants came from a simple trisomic F_2 plant with an extra H (IV) chromosome (38). Commercial fields may have unfruitful plants from this cause. Photoperiodism may influence blooming and fruitfulness of *L. hirsutum* (40a). In commercial varieties, the pollen may mature imperfectly in hot dry weather. Segregates of *L. esculentum* X *L.p. var. dentatum* produced many diploid gametes, and most plants were unfruitful (40a).

Sticky-chromosome tomato. Dr. F. O. Holmes sent to the senior author, 3 rooted cuttings of the hybrid, *L. esculentum* X *L. chilense* (25). These plants of T448 grew luxuriantly, bloomed profusely, but did not set any fruits as they appeared to be self-sterile. However, the pollen of T448 was used in back-crosses on the Marglobe, Century and Tennessee Red varieties and produced the hybrids, T509, T512 and T513. Their progeny segregated into many kinds of intermediate plants ranging from those with finely dissected leaflets like the *L. chilense*-grandparent (all of which were sterile) to fertile plants that had cut leaves like *L. esculentum*. Many of the latter plants bore fruits that were red, pink, orange or dark yellow on different plants. The sterility and complicated inheritance probably were due partly to the sticky chromosomes from the *L. chilense*-parent that affected the behavior of the chromosomes (40).

Seedless fruits. Flowers of the large-fruited varieties of *L. esculentum* lack the ability to develop normal seedy fruits in hot dry weather probably because the ovules and pollen do not mature normally, and also because the styles become exserted and the pollen may fail to reach the stigmas or die on them (76a). Subnormal development of a triploid endosperm may prevent maturity of the embryo (11, 40). Chromosome deficiency may result in seedless fruits (21, 61, 36, 39). Sterile ovules have resulted from collapsed tissues or from undifferentiated megaspore mother cells (71). Genetically male sterile tomato plants in fields may be useful in producing F_1 tomato seed (70). The Summerset variety develops mostly seedless fruits in hot, dry weather (22, 87) due to parthenocarpic growth. Rutgers plants developed about one parthenocarpic fruit per plant in the summer of 1947. Flowers that are treated with certain hormones may develop seedless fruits in greenhouses. The high-altitude species (*L. hirsutum* and *L. glandulosum* from the Andes Mountain Range) apparently developed imperfect female flower parts due mainly to the different amounts of light in Ontario, although the pollen was fertile (51). Crosses of *L. esculentum* X *L. peruvianum* produced large red fruits with very small abortive seeds in 1940.

Flower shedding. The various inherited causes of sterility and unfruitfulness mentioned above, in addition to many pathological and physiological causes, may result in flower shedding.

Summer fruiting ability. A hybrid from a cross of (Bonny Best X Red Cherry) X Bonny Best produced a segregate that was developed into the Summerset variety (87). It produces red globe fruits 1 to 2 inches in diameter in both hot and cool weather. Summer Prolific variety also sets fruits in hot weather (15a).

Fruit Characters

Seed catalogues classify red tomatoes into two main groups: Red varieties (Marglobe, Rutgers and Louisiana Red as examples) and pink-purple varieties (Louisiana Pink, Gulf State Market and Glovel as examples) (62). The different colors and shades of the fruits are due to different combinations of gene alleles and modifiers, or accessory genes (Table 4). Thus, red tomatoes have red flesh under yellow peel; pink tomatoes have red flesh under colorless peel (such varieties often are purplish-red when very ripe); dark yellow tomatoes have yellow flesh under yellow peel; pale yellow or lemon tomatoes have yellow flesh under colorless peel; so-called white tomatoes have very pale yellow flesh under a colorless peel, probably with an undiscovered modifier of the *r*-allele, and pink blossom-ends in yellow tomatoes probably are due to a gene for pink flesh color that is different from the *R*-allele. The cause of the yellow color in the sticky-chromosome tomato (T509) differs from the *r*-allele (40). Accessory genes, $m_{1\text{-}4}$, may modify the shade or brightness of the red color in the red and orange fruits (34).

Table 4. Genetic basis of different colors of tomato fruits

Fruit color	Variety or selection	Allele affecting: Flesh color	Allele affecting: Peel color	Modifier genes
Red	Marglobe	*R* or *T*	*Y*	G, $m_{1\text{-}4}$: (34, 18).*
Pink-purple	Gulf State Market	*R*	*y*	
Dark yellow	Golden Queen	*r*	*Y*	
Light yellow	T910, lemon	*r*	*y*	
White	Snowball	*r*	*y*	Probably
Yellow with pink end	Yellow Ponderosa	*r*	*Y*	Probably
Orange (tangerine)	Jubilee	*t*	*y*	K, $m_{1\text{-}4}$: (18).

*In crosses with *L. esculentum*, *L. hirsutum* gave evidence of 3 different fruit-color genes that are partially dominant and cumulative. Segregations showed new color-types of tomatoes. *L.p.* var. *dentatum* has color factors like those of *L. hirsutum*, (40a).

Red versus yellow flesh color. Alleles: *R-r*. The F_2 segregation is 3 red to 1 yellow (8, 41). Tetraploid segregation was between 22:1 and 35:1 (8). Red fruits usually are preferred for canned and green-wrap tomatoes, but yellow tomatoes are better for preserves. *R* is the major gene for lycopene formation (40, 40a). The new wilt-immune golden globe tomato has very fleshy fruits (Figure 13,A). Fruits of an F_1 hybrid of *L. esculentum* X *L. p.* var. *dentatum* had ochraceous buff to apricot buff flesh color that was intermediate between the flesh colors of its parents (40). Apparently the wild species contributed a gene (or genes) that is not present in *L. esculentum* and that is allelic and dominant to *R*, or non-allelic and suppressing its action (40). Intermediate fruit colors were found in T509 that had this parentage. The fruits of T1074 were yellowish-pink plum tomatoes.

Red versus orange flesh color. Alleles: *T-t*. The F_2 segregation is 3 red to 1 tangerine orange (8). The factor, *G*, inhibits the action of the modifiers in producing synthetic red fruits, while the factor, *K*, has a similar action on yellow fruits in preventing the production of synthetic orange color (18). Prolycopene occurs in the Tangerine variety of tomato (105). Red flesh color may be due to the *R*-allele, the *T*-allele, or possibly both of them (40a).

Yellow versus colorless peel color. Alleles: *Y-y*. The F_2 segregation is 3 yellow to 1 colorless (8, 20). Tetraploid segregation was about 35:1 (8). The *Y*-allele causes the development of 10 times more alkali-soluble yellow pigment in the epidermis than the *y*-allele, so this genetic factor seems to be manifested mainly as a chemical effect (33). Fruits of an F_1 hybrid of *L. esculentum* X *L. p.* var. *dentatum* showed pale yellow peel color that was intermediate between the parental colors. Evidently the wild parent contains a gene or genes for non-yellow peel color other than *y*, which latter is recessive to *Y* in *L. esculentum* (40, 40a).

White fruits. Frew's Snowball, Crystal White and White Beauty varieties of tomatoes have so-called white fruits due to the very pale yellow flesh under a colorless peel. These 3 varieties (T434, T1010 and T1060) were indistinguishable in a field test. They had large prostrate stems with large oblate, lobed, catfaced fruits (Figure 12,A). The Snowball variety was crossed with the Riverside and Michigan State varieties (T484, T496). All 35 plants of the F_1 progenies had red fruits, indicating that the genes causing the nearly white flesh are recessive. The flesh color of the Snowball variety is paler than that of the T910 or T908 lemon-colored tomatoes. The flesh color of *L. p.* var. *dentatum* and *L. hirsutum* is greenish-white (40, 40a). The peel color of *L. hirsutum* is almost colorless (40a). The greenish-white flesh color of *L. peruvianum* is partially dominant.

Radiating green stripes in green peel. Many unripe fruits of the white tomatoes and of the bushy tomatoes (T1078) had prominent dark green stripes radiating from the blossom-end toward the stem end (Figure 12,A,B). The stripes apparently were over the locule walls. Fruits of the Earliana variety also show such stripes and they are likely to appear in some descendants of Earliana hybrids.

Pink color in yellow fruit. Especially in hot summer weather, flesh tissues near the blossom end may be pink and show through the peel of fruits of Golden Queen, Yellow Ponderosa, Crystal White and the lemon tomato, T910. The Oligosperm yellow tomato had a pink blossom end due to red flesh showing through the peel (21). This indicates that there is a gene for pink flesh color that differs from the *R*-allele for red flesh color. Such a new gene is inherited independently from *R*, but a visible character is expressed only when this gene is in combination with the *r*-allele for yellow flesh color in hot weather.

Stripes and pits in peel. Dark green short stripes with or without corky brown pits in the peel characterized about one-tenth of the fruits of T560 (100), (Figure 10,c,d). This character was inherited through several generations. It is found in occasional Marglobe tomato fruits and differs in degree from tomato pox (103).

Dark green stem ends versus uniform unripe fruit color. Alleles: *U-u*. The F_2 segregation is 3 dark green stem end to 1 uniform unripe fruit color (47) (Figures 10,A; 11,K). Tetraploid segregation was about 22:1 (8). Certain varieties of tomatoes such as Black Queen and Kilgore Special have very dark green peel which indicates that there may be a modifier of the *U*-allele. Uniform ripening tomatoes have the *u*-allele. The uniform green unripe fruits of the Red Cloud variety bleach to white or light yellow in the hot sunshine, making the fruits unmarketable for green-wrap tomatoes (Figure 11,K). However, such fruits show some resistance to sunburning. Green-wrap tomato varieties such as Marglobe have the *U*-allele so that the stem ends of the fruits are darker green than the sides and blossom ends of the unripe fruits (Figure 11,E,H,J). Fruits with the *u*-allele resisted cuticle cracking (102). Dark green stem ends ripen last, especially in July, which decreases the value of *U*-allele fruits for canneries. In T1112 and T1119, the uniform unripe apple-green color of fruits may be due to a separate gene.

Peel uniform green on unripe fruits. Allele: u_2. The F_2 segregation is 3 dark green stem ends to 1 uniform green unripe fruit color (6). The Uniform Globe variety has the u_2-allele.

Light green blossom ends. Unripe fruits of the Gulf State Market and Break O'Day varieties have dark green stem ends and pale green or white blossom ends when they are 2 to 4 inches in diameter, which distinguish them from the darker green blossom ends of Marglobe and Rutgers fruits. Usually only fruits of the same color are packed in a car.

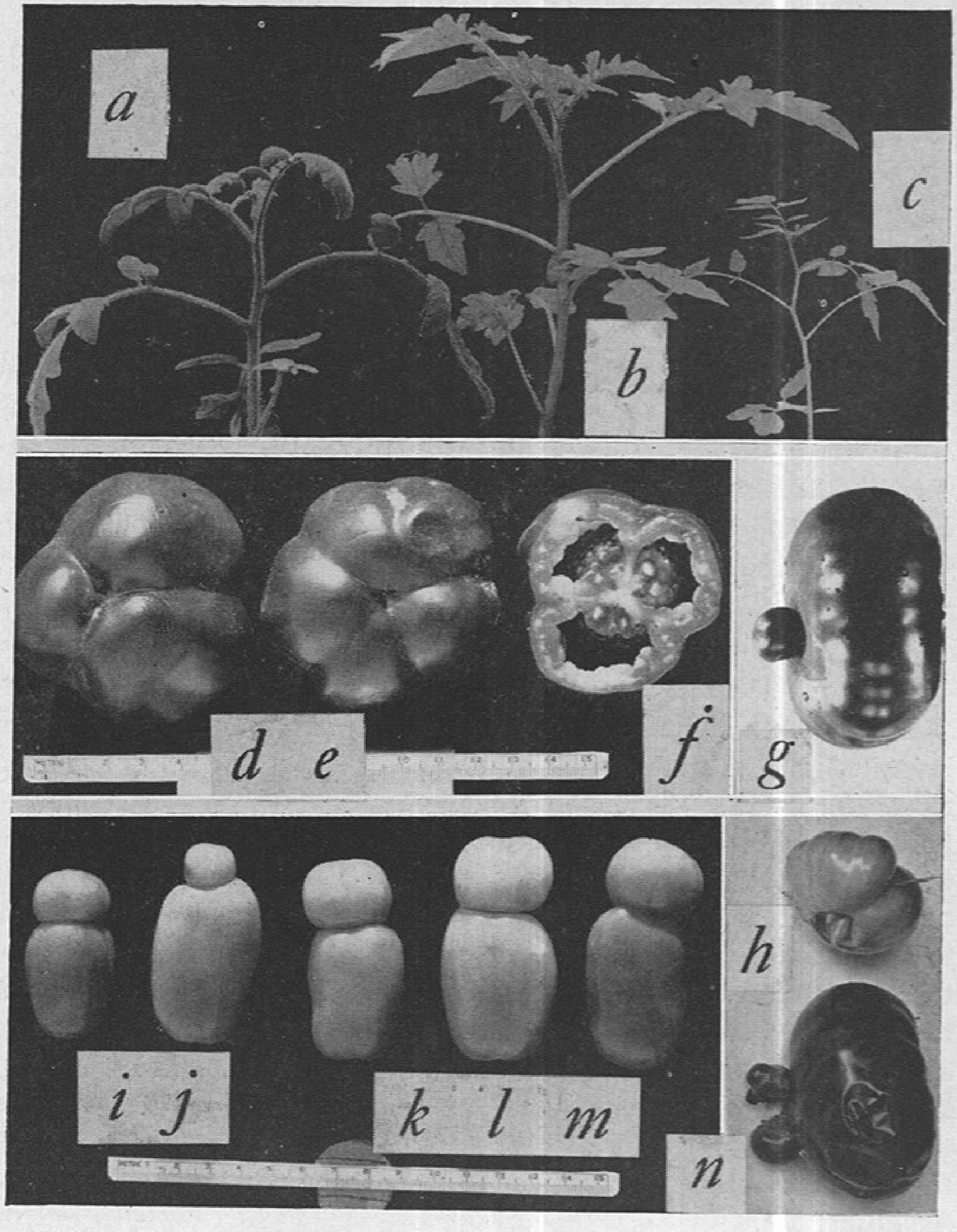

Figure 9. a: Woolly tomato plant with hirsute leaflets and stems due to the *Wo*-allele. b: Ordinary tomato plant with moderately pubescent leaflets due to the *wo*-allele, and pubescent stems. c: *Lycopersicon pimpinellifolium* showing hairless stem. d,e,f: Large superpuff tomato fruits that resemble bell peppers (T480). g: A teratological knob on blossom-end of tomato fruit. h: Teratological spurs in hole-type catface in a tomato fruit. i,j,k,l,m: Knob tomato fruits of T19 that is predisposed to corolla constriction. n: Two teratological knobs on the blossom-end of a very ripe red tomato.

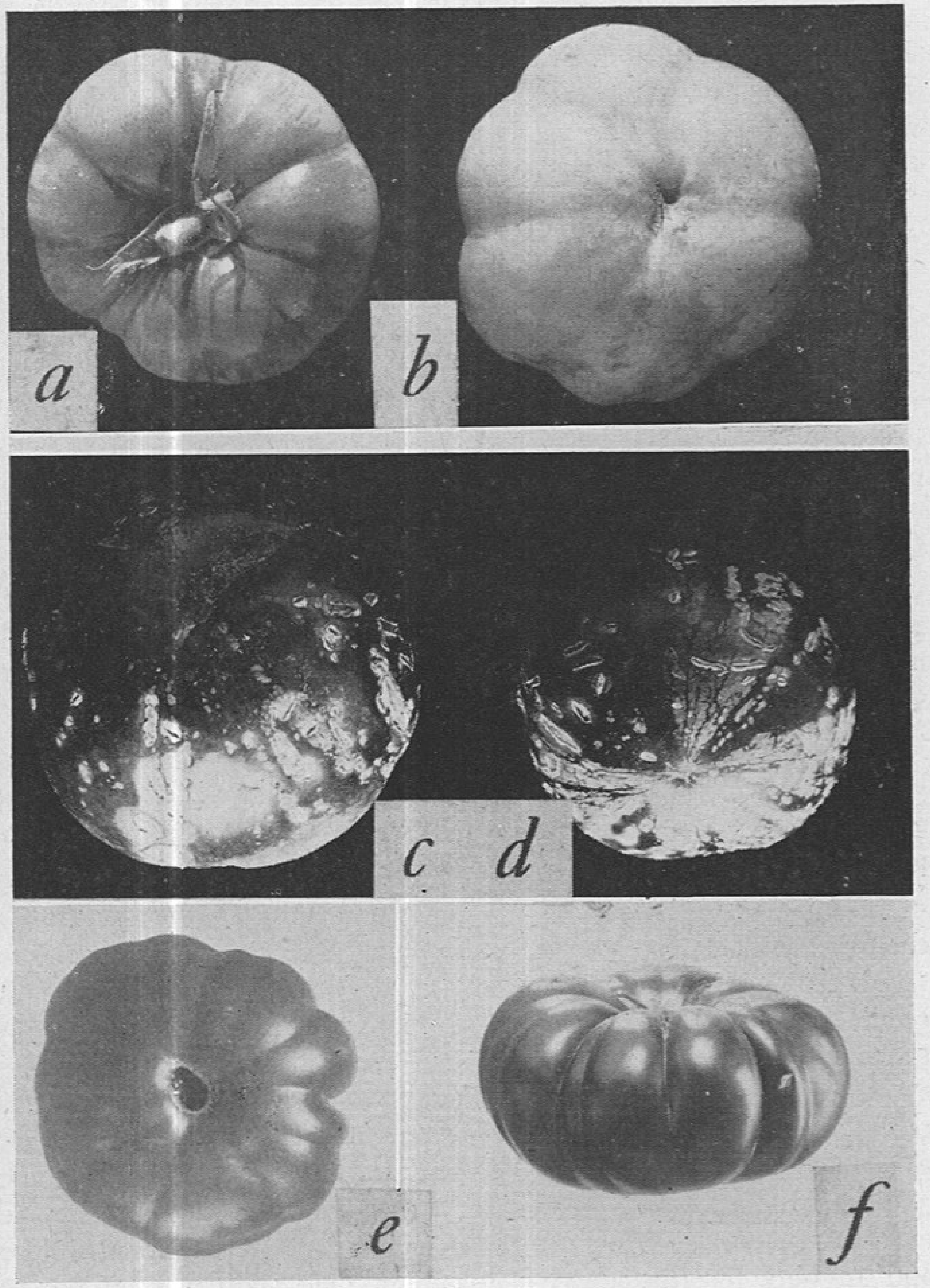

Figure 10. a,b: Sticky-peel tomato fruits of T328 probably due to poorly cutinized epidermis. "a" shows dark green top due to the dominant allele of the *U*-gene. c,d: Hereditary stripes and corky brown pits in peel of tomato fruits; pictures were published first in Phytopathology (100). e: Hole-type of catface in a fasciated tomato fruit. f: Oblate, lobed, fasciated tomato fruit with 1:2 ratio of polar to equatorial diameters.

Tough peel. Toughness of the fruit peel determines much of the resistance of a tomato to injury in shipping and marketing. The Rutgers and Marglobe varieties are favored for their fine shipping quality, while the Gulf State Market is much less durable in transit and also deteriorates faster in rainy weather in fields. San Marzano and Porter varieties have very tough peels.

Pubescent peel. Allele: *p*. The F_2 segregation is 3 glabrous to 1 pubescent (12). The Pink Peach and Yellow Peach varieties have the *p*-allele (Figures 11,L,M,N; 15,C.D.). The fruits of the Pink Peach variety were 1 to 2 inches in diameter with 3 kinds of epidermal hairs: (a) A small percentage of the hairs were 700 to 1,000 microns long; (b) the abundant hairs that made the fruits look dull or fuzzy by reflected light were 180 to 360 microns long, pointed, septate and hyaline (some of the hairs had brown basal cells); (c) four-celled brown capitate glandular hairs 15 to 30 microns in diameter with short hyaline basal cells. Green-wrap tomato varieties with the *P*-allele have fruits that are glandular-pubescent while they are ¼ to 1½ inches in diameter, but which become glabrous and shiny as they attain maximum size and ripen (Figure 15,B).

Hairy peel. *L. hirsutum* and certain varieties of *L. peruvianum* have fruits with hairy peel (55). Immature fruits of *L. cheesmanii* are slightly pubescent, and those of *L. glandulosum* are pilose to pubescent (55). This character may be identified with the *p*-allele.

Sticky peel. The peel of the mutant tomato T328 is peculiarly cutinized and almost hairless so that it feels sticky (97) (Figure 10,a,b). The fruits are large, oblate, smooth, and have very dark green peel near the stem end. The plants have the inherited light green leaflets and very hairy stems. The F_2 segregates of a cross of Marglobe X T328 showed that the sticky-peel character was recessive and was always associated with the characters for light green leaves and very hairy stems, indicating linkage of these 3 characters, none of which have been located on the chromosome map (Figure 14). Of these 67 F_2-plants, 55 were like Marglobe and 12 were like the sticky-peel parent. One plant showed rugose leaves and leafy flower trusses, the latter character being rare in *L. esculentum*. The fruits of T328 were very dark red due to bundles of long red crystals in the epidermal cells in addition to the red chromoplasts in the flesh-parenchyma (20).

Ascorbic acid. The concentration of vitamin C (ascorbic acid) in tomato species is inherited, but the range in concentrations for each variety may vary with differences in growing conditions,

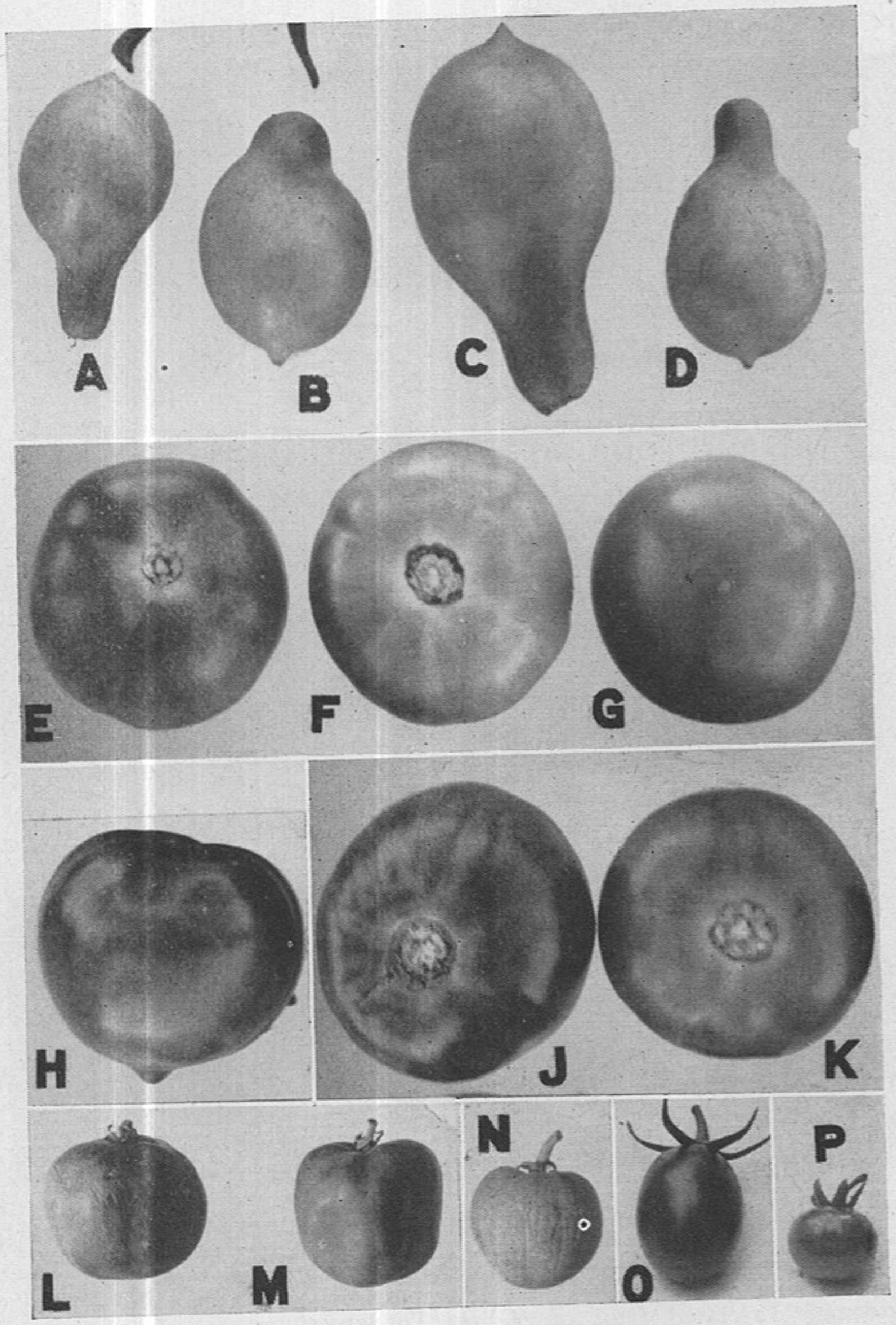

Figure 11. A,B,C,D: Yellow pear tomatoes with beaks due to the *bk*-allele (T1079). E: Unripe tomato fruit with dark green top due to the *U*-allele. F: Yellow-white firm unripe fruit of T1071 due to the *l*-allele. G: Ripe yellow fruit of T841 due to the *r*/*Y*-alleles. H: Nipple-tip fruit due to *n*-allele with dark green stem end due to *U*-allele. J: Unripe tomato fruit with dark green stem end due to *U*-allele. K: Uniformly colored light green unripe fruit of Burgess Crack Proof variety, due to *u*-allele. L,M,N: Pubescent-peel tomato fruits due to *p*-allele. O: Plum-shaped fruit of Wonder of Italy variety due to *o*-allele. P: Cherry tomato fruit of *L. esculentum* var. *cerasiforme.*

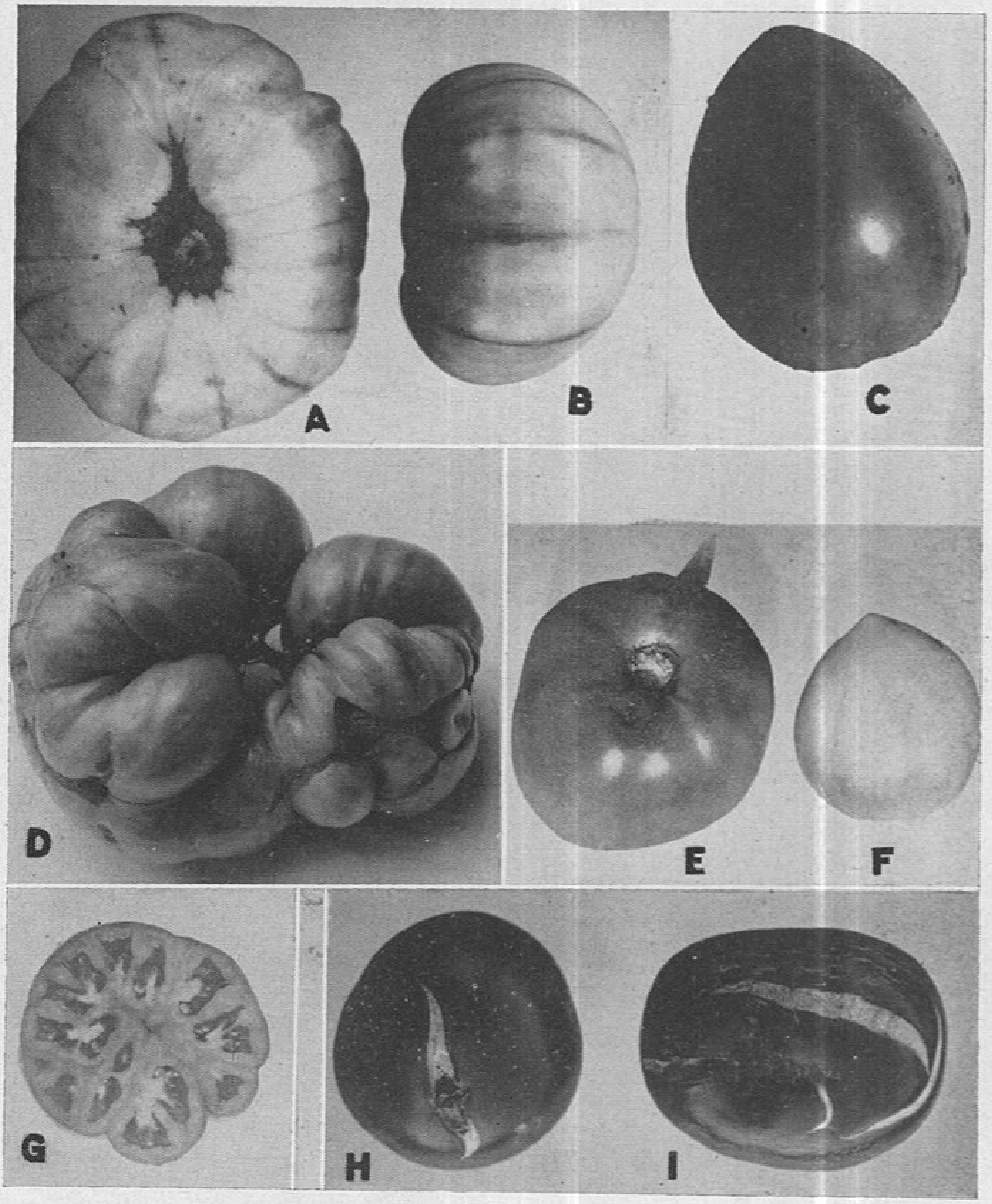

Figure 12. A,B: Dark green stripes radiate from the blossom end toward the stem end in the greenish-white peel of unripe fruit of Henderson's Crystal White tomatoes. C: Giant red plum tomato (T590) 3 inches long and 2½ inches in diameter (drops of water on peel). D: Extremely fasciated fruit of Yellow Ponderosa tomato with natural hole through the center due to the *f*-allele. E: A teratological spur on fruit. F: A mild type of nipple-tip (due to *n*-allele) in T667. G: Section of a tomato that was fasciated by the *f*-allele. H,I: Blossom-end cracking in fruits of broad-leaf tomato, T1077.

especially exposure to sunlight (52). The concentration of vitamin C per 100 g. of fruit ranged from 48 to 78 mg. in *L. peruvianum* and 35 to 73 mg. in *L. pimpinellifolium* that have fruits ¼ to ½ inch in diameter. The concentration of vitamin C ranged from 11 mg. per 100 g. in Bonny Best to 18 mg. in Rutgers varieties (67). A pear tomato averaged 50 mg. and Summerset variety averaged 22 mg. of ascorbic acid as representatives of small-fruited varieties of *L. esculentum*. Thus, the concentration of vitamin C was higher in small-fruited varieties than in large ones. High concentration of vitamin C is desirable. According to one theory, inheritance of concentration of ascorbic acid may be correlated with fruit sizes as they affect the ratio of surface area to volume of fruit (Table 5). Thus, the smaller the fruit, the more sunshine that it receives per unit of volume and the more ascorbic acid it develops. However, the amount of sunshine that each fruit receives is influenced by its degree of shading, and by the number of hours of sunshine per day that, in summer, increases with decreasing distance from the poles of the earth.

Table 5. Ratio of surface area to volume of fruit, considered as perfect spheres

Tomato variety	Radius of fruit cm.	Area of fruit sq. cm.	Volume of fruit c.c.	Approximate ratio*	
				Surface area	Volume
Cherry	1	12.57	4.19	3	1
Summerset	2	50.28	33.52	3	2
Marglobe	4	201.12	268.16	4	5
Ponderosa	6	452.52	905.04	1	2

*Increasing the radius of a sphere decreases the ratio of surface area to volume, and this decreases the relative amount of sunshine that can be received on the fruit.

Prominent core in fruit. The core is very large and prominent in the Pearson S variety. This is an undesirable character for a canning variety.

Mottled green fruits. Large green fruits of the Pearson, Pearson S and Santa Clara Canner (T435) varieties showed light green mottling of the peel that might be objectionable in marketing green-wrap fruits. However, this mottling disappeared as the fruits became red.

Yellow stem end. Prominent yellow color developed in the dark green stem end of ripening fruits of the Garriprihe, Porter, Oxheart and New Porter varieties, and also in some segregates of crosses that had Louisiana Red as one parent (T466). The epidermis was red on the other parts of these fruits. Some of the hard yellow tops were separated by distinct ridges from the other parts of the fruit peel.

Corky brown stem-end ring. A corky brown ring ¼ to ⅜ inch wide characteristically surrounds the abscission spot of mature green-wrap fruits of Rutgers, Marglobe and similar varieties of tomatoes. Hence, pickers and graders of these tomatoes usually use this character to determine the green-wrap maturity of the green fruits. A corky brown ring that is only ⅛ inch wide indicates a fruit that is so immature that the seeds are not mature sized with gelatinous material around them. Therefore, it is desirable for new varieties of green-wrap tomatoes to have the inherited character of broad corky brown ring around the abscission spot. The nearer that the fruit approaches ripening, the broader the brown ring becomes. Other varieties of tomatoes such as Louisiana Red develop brown stem-end rings that are only ⅛ inch wide around the abscission spot. There is the probability that graders might guess such fruits to be immature and discard them as culls even when such fruits are nearly ripe enough to become pink (Figures 11,E,F,J,K; 12,E).

Globe versus pear shape. Globe shape tends to be dominant in ratios that approximate 3:1 in crosses of globe X pear-shaped tomatoes (8, 64) (Figure 11,A,D). The mature shape of a fruit may be foretold by examining the ovaries of the flowers (91). Small or irregular ovaries are likely to produce small or irregular fruits.

Elongated versus short fruits. Alleles: *O* or *Pr* versus *o* or *pr*. The F_2 segregation is 3 short to 1 elongated. Short probably refers to oblate or flattened shape (42) (Figures 11,O; 12,C). *O* and *Pr* are 2 symbols for the same gene. One of the most difficult problems in tomato breeding is attaining large globe-shaped fruits, as oblate shape appears to be partially dominant over globe shape.

Fasciated fruits. Allele: *f*. The F_2 segregation is 3 normal to 1 fasciated (8). The fasciated fruits usually have 7 or more locules per fruit, and most of such fruits are oblate, lobed and catfaced (Figure 12,A,B,D,G). The largest tomatoes usually are fasciated as exemplified by the Ponderosa variety. An unusual kind of fasciation is shown in Figure 13,B.

Beaked tomatoes. Allele: *bk*. The beaked-fruit character is recessive and is manifested as a sharp beak on the blossom end of fruits (Figure 11,A-D). The *bk*-allele is in MacArthur's selection No. 706 (T1079) that also has the alleles: *d,p,o,s,r,* and *y*.

The extremely compound flower trusses (Figure 2,A) were hirsute and bore 100 to 300 flowers and buds each, but the stems and leaves were only pubescent. T1079 has ornamental value.

Nipple-tip tomatoes. Allele: *n*. The F_2 segregation is 3 normal to 1 nipple-tip (8) (Figure 11,H). Most of the fruits on an *n*-allele plant may have prominent nipple tips as in T661, or only a small percentage of the fruits may have nipple tips as in T667V in which it was decreased by selection (Figure 4,E,F). After selection through 9 generations, T937 has relatively few nipple-tip fruits and these usually are only mildly affected (Figure 12,F). Figure 9,g,h,n shows blossom-end protuberances that probably are teratological and are not due to the *n*-allele or *bk*-allele. As many as 1 percent of the fruits of Marglobe tomatoes may have nipple tips on the third and later trusses. These are probably due to an undescribed gene that differs from the *n*-allele. Some nipple tips were also found on fruits on late trusses of the Pritchard variety.

Two or many locules. Alleles: *Lc-lc*. The F_2 segregation is about 3 plants with 2 or 3 locules per fruit to 1 plant with 5 or more locules per fruit on the 3 earliest trusses (8). Inheritance of the tendency for 3½ or 4 locules per fruit is the same as that for 5 locules, but it is very difficult to select a variety of tomato with 5-locule fruits from parents that have only 3 or 4 locules per fruit. Early generations of crosses of *L. esculentum* X *L. pimpinellifolium* had only 2 or 3 locules per fruit, and many back crosses with commercial varieties and numerous selections were required to secure segregates with 5-locule fruits (T511). Each fruit of a commercial variety should have 5 or more locules. Usually there are more locules in fruits on the earlier trusses than on later trusses on the same plants. Most fruits with 2 to 4 locules are only ½ to 2 inches in diameter. Tomatoes usually have 2 to 16 locules each, but a few fruits had 215 locules each (104). The first fruit that forms on the first truss may have more locules than the later fruits. Fruits with 7 to 16 locules each may or may not show fasciation. Fruits with 10 or more locules each may have all of the locules surrounding the central core, or some of the locules may be in the core. In selecting *I*-allele hybrids for commercial use, large red-globe fruits with 5 to 8 locules each are chosen.

Shape of fruit. Fruit shape is controlled mainly by the interaction of two different pairs of genes *o* and *lc*. The combination of *O* and *Lc* result in globular or round fruits, *o* and *Lc* result in oval (plum-shaped) fruits, and *O* and *lc* result in oblate or flat fruits (90) (Figures 11,l,o,p; 12,B,C). The uncommon combination of *o* and *lc* probably occurs in the giant plum fruits of T738. It is usually difficult to attain ratios of 1:1 (spherical) or 4:5 for polar to equatorial diameters of the large hybrid tomato fruits, especially if an ancestor had oblate or fasciated fruits. For example, some selections of T935 have fruits with a ratio of 2:3; fruits of T841 have a 1:1 ratio like the Pan America variety; fruits of T738 and T590 have a 3:2 ratio; and Figure 10,F shows a fruit with a 1:2 ratio. Changes in chromosome numbers influence the shape of tomato fruits and leaves according to a study of haploid, diploid, triploid and tetraploid tomatoes (70, 39).

Size of fruit. Fruit sizes depend on 3 to 5 pairs of major genes affecting locule numbers, and twice as many genes affecting mature locule sizes (10, 49). Size of fruit is determined by complicated inheritance of quantitative factors (50, 63). There is intermediate segregation for fruit size in the F_1 generation, and all gradations in the F_2 generation (8). Two or 3-locule fruits are mostly ¼ to 2 inches in diameter, but the largest fruits with 3 or 4 locules each may be 3 to 4 inches in diameter. Fruits with 5 to 14 locules each usually are 3 to 5 inches in diameter when growing conditions are favorable. In fields, the Gulf State Market and Pan America varieties usually produce fruits of marketable size only on the first 3 or 4 trusses.

Earliness of fruit maturity. Earliness is quantitative in inheritance with all gradations in segregations following crosses (8, 14). Unfortunately, in commercial varieties, very early fruits 3 to 4 inches in diameter have been almost inseparably associated with prostrate stems and foliage that is inadequate to shade the fruits, as exemplified by Earliana and Bison. The genes for these characters are not located on the chromosome map (Figure 14), and the linkage is suspected but not proved. The combination of the characters of earliness, large fruits and adequate foliage has not been accomplished yet. T543, with fruits averaging 1½ inch in diameter, is very early while the Crack Proof variety is very late in maturing fruits. The Danish Export variety, that is homozygous for the alleles *D,P,O,S,* was earlier than plants that are homozygous for the alleles *d,p,o,s* (14) (Figure 14). Plants that bloom early usually produce early fruits (91). Early fruit production is so profitable that tomato breeders strive to attain it in their selections.

Oxheart shape of fruit. The Oxheart variety has many inverted pear-shaped fruits that are 3 to 4 inches in diameter near the stem ends and taper to narrow blossom ends. The fruits are pink, soft, and grow on long prostrate stems. The ripe pink fruits have

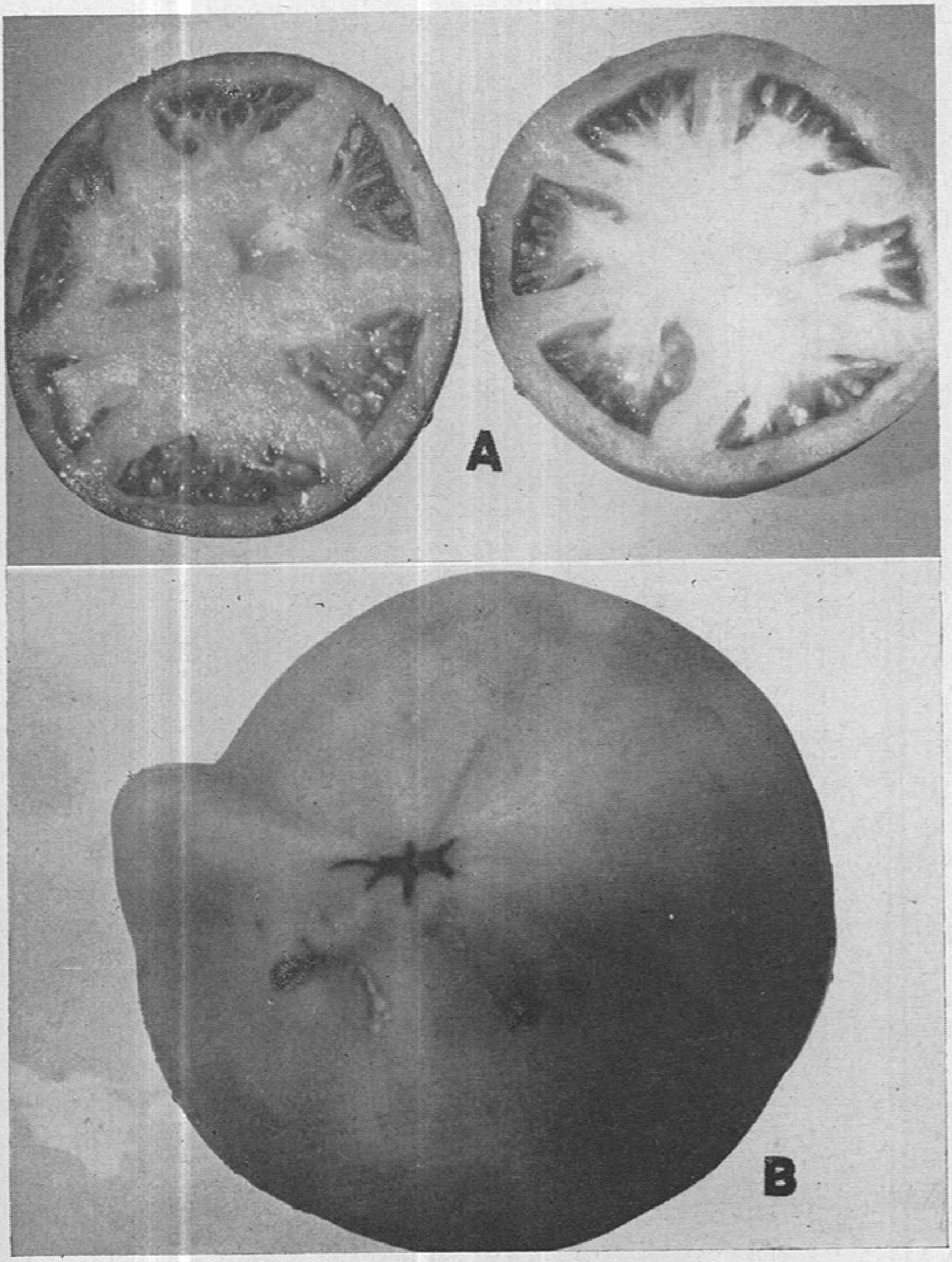

Figure 13. A: Very thick locule walls and cores in 2 fruits of T841, the golden globe tomato. The larger fruit is 3¾ inches in diameter. B: Extra-locule lobe on side of a Rutgers tomato; the lobe had a seedless cavity.

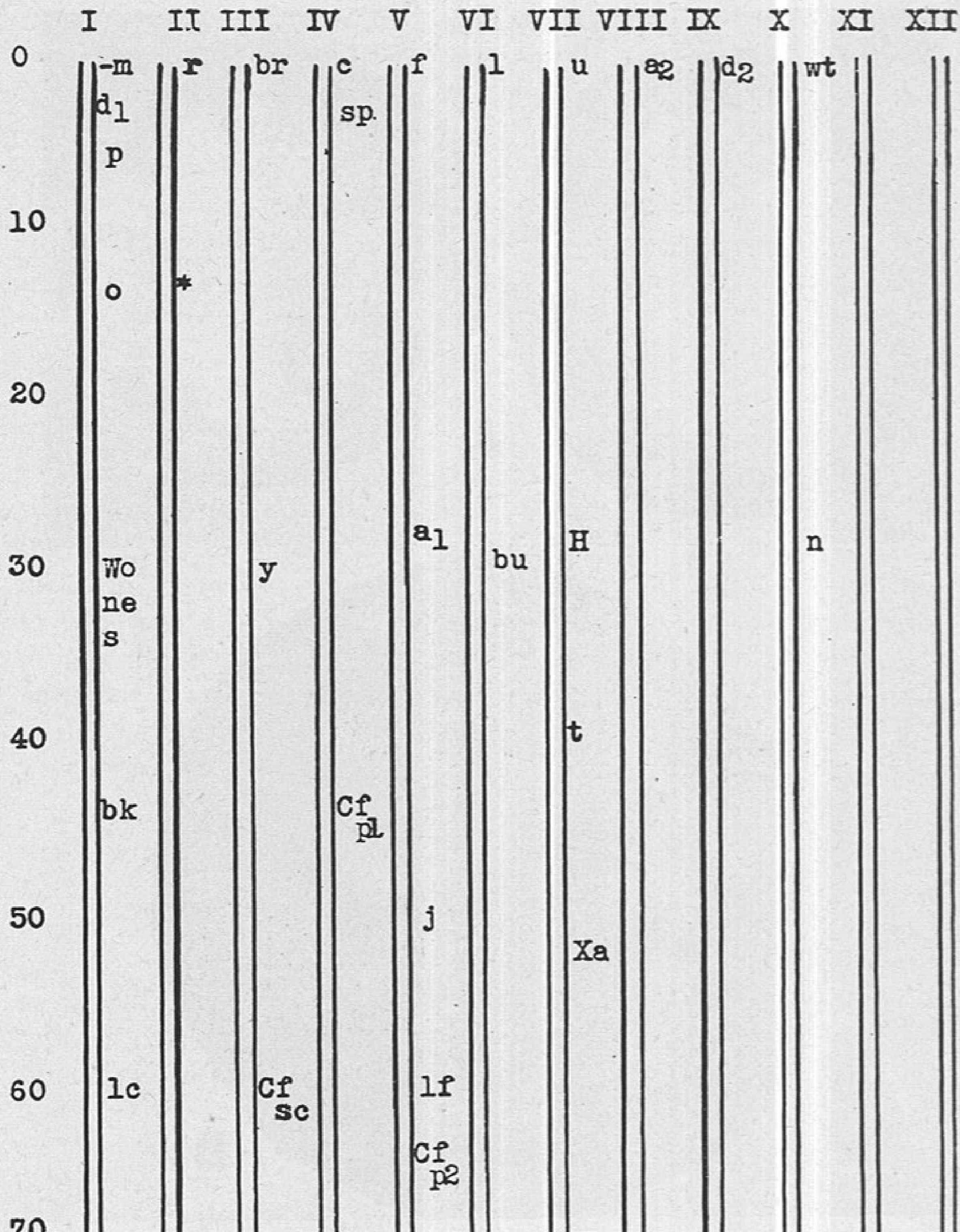

Figure 14. Chromosome map of the tomato showing the approximate locations of 31 genes in 10 of the 12 pairs of chromosomes as determined by the linkage method. (After J. W. MacArthur.) Gene-symbols are written on the right-hand sides of their chromosomes. *The *wf*-gene is in Chromosome II.

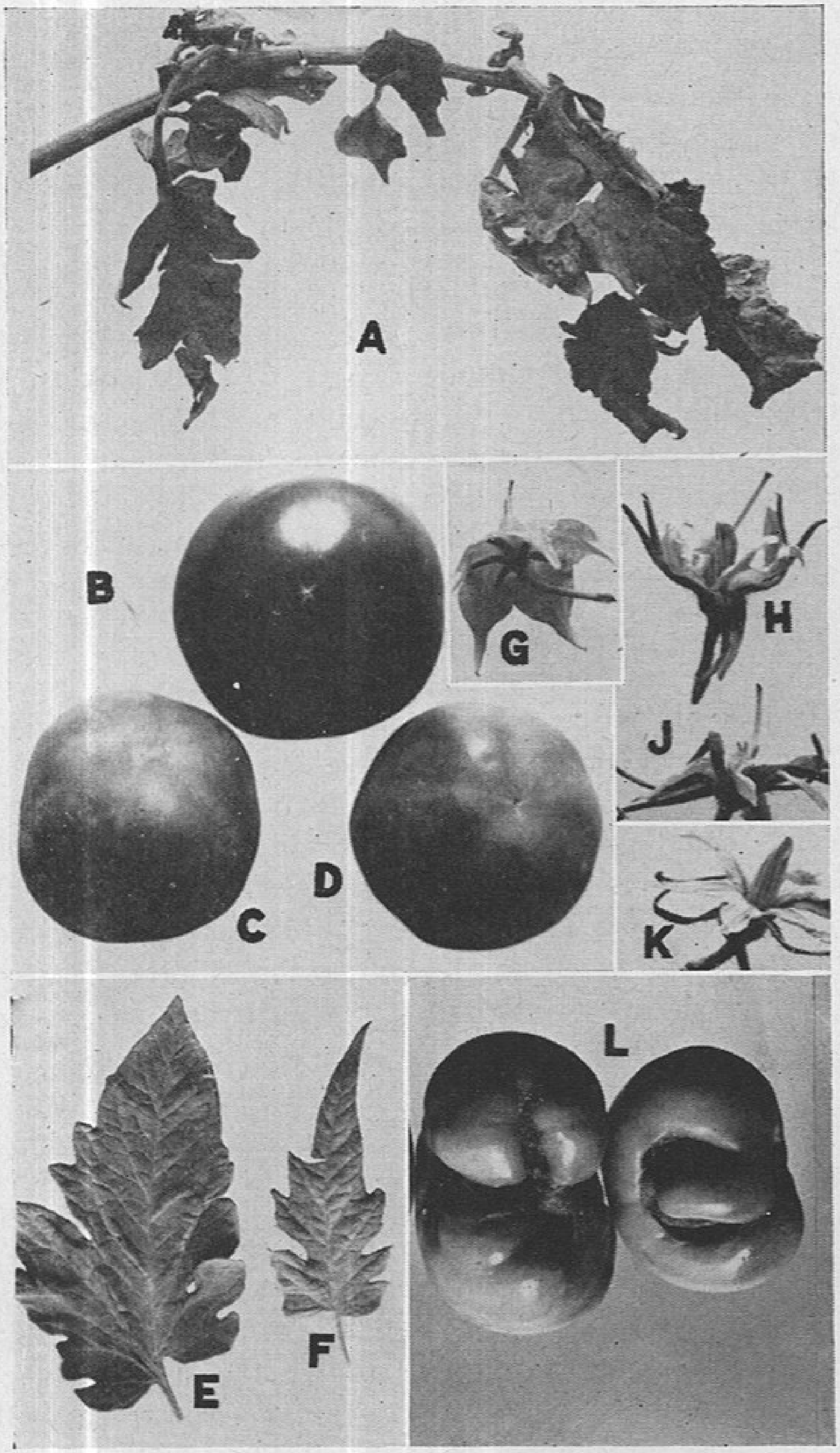

Figure 15. A: Tomato leaf showing downward curling of the rachis and drying and breaking of the leaflets due to the *ne*-allele. B: Glabrous, shiny peel of tomato fruit due to *P*-allele. C,D: Dull reflection of sunlight by pubescent peel of Pink Peach tomatoes due to *p*-allele. E: Broad dark green terminal leaflet of Rutgers tomato. F: Slender, sharp-pointed, medium green terminal leaflet of T738K. G: T1059 flower of the type of *L. peruvianum* with exserted pistil. H,J: Rutgers tomato flowers with exserted pistils and browned stigmas due to hot weather. K: Rutgers flower with included pistil. L: Catface abnormality in sides of 2 tomato fruits.

yellow stem ends. When tomatoes with the *I*-allele were crossed with Oxheart (T844, T850, T857), the F_1 hybrids had prostrate stems like their Oxheart parent but the fruits did not show the Oxheart shape, some having the giant plum shape. This indicates that the habit of prostrate growth may be dominant while the Oxheart shape of fruit may be recessive.

Knob fruits. Blossom-end knobs, or double fruits, may be due to corolla-tube constriction (90). This abnormality was found only in T19 and the Tomato Grande variety (T131) that are 2-locule, paste-type, plum tomatoes (Figure 9,I-M). These selections had an inherited predisposition for this abnormality. Tomato Grande was selected through three generations by saving seeds only from the fruits with knobs, but this selecting did not increase the percentage of knob fruits to more than 5 percent of the fruits on the plants.

Paste-type tomatoes. The San Marzano, Tomato Grande and Garriprihe varieties have 2 to 3 locule fruits (54). These Italian-paste varieties are unlike other tomatoes in several ways. They have long, slightly pear-shaped fruits with depressions over the locule walls of the 2-locule fruits. They are used by the canning industry for special tomato-paste products and for processing whole fruits. In a few generations, the Garriprihe variety had hollow fruits like those of bell peppers. This tendency for puffing appeared to be partially dominant in crosses of Garriprihe X Marglobe as the F_1 fruits were all puffed (93, 96, 98).

Superpuff fruits. The hollow-locule fruits of T480 had 3 to 5 locules each and resembled bell peppers (Figure 9,d,e,f) (96). They were 1½ to 2 inches in diameter and were not paste-type nor small like those of the San Marzano variety.

Puffing of fruits. Puffed tomatoes have air spaces in locules that are incompletely filled with seeds (103). Air spaces also may occur in other tissues (88). Some locules are seedless. Puffed fruits are subnormal in weight and are soft so they are excluded from lugs of green-wrap fruits. Excessive rain that decreases pollination is a main cause of puffing of fruits because each seed requires a pollen grain. During rainy weather, only enough fertilization takes place to stimulate fruit formation. The Marglobe variety is very susceptible to puffing while the Red Cherry and Stokesdale varieties are resistant (19). Susceptibility to puffing is inherited and tends to be recessive (88). The smaller the number of locules in a fruit, the more conspicuous puffing becomes. Hence, in selecting *I*-allele tomatoes for commercial use, attractive red globe fruits are rejected when they have only 3 or 4 locules each.

Cracking of fruits. Most commercial varieties of tomatoes crack so badly that they become low in quality or unmarketable when they mature to the green-wrap stage or ripen in rainy weather (103). Under such conditions, Marglobe has deep cracks that radiate from the stems, while Louisiana Red has concentric cracks (16). The Trip-L-Crop variety and T1077 usually had blossom-end cracks (Figure 12,H,I). Blossom-end cracks were common in Rutgers tomatoes in 1947. A few fruits of a hybrid selection cracked so extremely that the outer fruit wall rolled backward over the side of the fruit. In contrast, the Crack Proof variety resisted the formation of deep cracks or cuticle cracks (102).

Thick placental walls. The placental walls in tomato fruits range from ½ inch thick in T841, Pan America and Break O'Day to only 1/16 inch thick in most other varieties (Figure 13,A). The thick-walled large fruits usually have central cores 1 to 2 inches in diameter and the locules usually are small with relatively few seeds (T914). Thick locule walls are preferred in commercial tomatoes.

Concave blossom ends. A sunken blossom end, commonly with a small hole near the center, characterized many of the fruits of T692 through several generations. In 6 crosses of T692 with varieties lacking concave blossom ends, most of the F_1 plants showed some fruits with concave blossom ends, indicating partial dominance of this trait.

Catface fruits. Catface fruits have corky brown to black lines, holes, and rough areas ⅛ to 1½ inches wide at the blossom end in contrast with the very small spot of the stylar scar on fruits that do not show this defect (Figures 10,E; 12,A,D). Unusual fruits have catface in the sides (Figure 15,L). Catface apparently is due to the accumulation of multiple factors and is often associated with fasciation (16). The Rutgers and Gulf State Market varieties commonly have their first-truss fruits damaged by catface, especially when the young fruits develop in cool windy weather (86). Selections of *I*-allele hybrids are usually discarded when they show many catface fruits. Graders discard catface fruits at tomato-buying sheds, especially when the blemishes are large or deep. The Ponderosa variety usually has catface fruits and their development can be foretold by examining the ovaries of the flowers. The catface symptom is often associated with adhering corollas on green fruits while they are only ¼ to ½ inch in diameter. The Stokesdale variety is resistant to catface.

Blossom-end rot. The Pritchard and Marglobe varieties resist blossom-end rot while the Buckeye State, Louisiana Red and San

Marzano varieties are very susceptible to this physiological abnormality (99). Susceptibility to blossom-end rot in the Rutgers variety is an inherited weakness that probably is polygenic. Development of blossom-end rot is affected by calcium and phosphate fertilizers, and by amounts and distribution of rains (103). An excess ratio of leaves to fruits may be conducive to blossom-end rot.

Giant plum tomato. The fruits of T590 and T738 were commonly 3 inches long and 1½ to 2 inches in diameter (Figure 12,C). Selection through several generations did not produce any plants with all of its fruits of this giant-plum type, but most of the fruits of T738J had the giant-plum shape. The plants had the *u*-allele, long prostrate stems, and slender, sharp-pointed, slightly wilty leaflets (Figure 15,F). The Louisiana Slicer variety has the giant-plum type of fruit (53).

Other genetic characters resulting from X-ray treatment. X-ray treatment of tomato seeds resulted in 43 mutants, some of which were like characters that have been described, but others were different (48). The new ones are listed together pending additional descriptions. The different mutants displayed the following characters: long cotyledons, curly leaves, ultra dwarfs, lethal and yellow-green types, and leaflets and cotyledons with white dots, variegation, gray edges, stripes and brown speckles. Plants that contain dominant lethal genes are likely to die without having their characters recognized.

Interspecific Crosses

L. esculentum has been crossed with other species of tomatoes to add genes that give the hybrids resistance to diseases or distinguishing characters, or to add other desirable qualities to them. Several characters of hybrid origin were described in the preceding section. Study of the interspecific hybrids adds much to the knowledge of tomato characters.

Sterile-seed tomatoes. Collapsed sterile seeds in red globe fruits of T660 resulted from crossing Marglobe as a female parent with a variety of *L. peruvianum* (T478, P.I. 39138) that has glabrous green fruits (36, 51, 96). None of the seeds of T660 produced plants. Some fertile seeds were secured when an Italian-paste variety of tomato was crossed with *L. peruvianum* with the stimulus of hormones on the pistils (61). Most of the resulting F_1 fruits were seedless but some fertile seeds produced viable F_2 plants with red or yellow fruits. Embryos were cultured from a tomato species hybrid to study the plants (75a).

Triple-cross tomato. J. S. McFarlane of the University of Hawaii sent seeds of a triple cross: (*L. hirsutum* X *L. esculentum*) X (*L. peruvianum* var. *humifusum*) (T1058, T1059). They produced luxuriant, drouth-resistant plants that bloomed profusely throughout the summer and fall seasons. They resembled their *L. peruvianum*-ancestor in appearance and characteristic non-tomato odor. The different plants had either green or yellow fruits that were 1/3 to 3/4 inch in diameter. These tomatoes have much ornamental value in addition to their potential use as breeding stock. The F_1 hybrids of (*L. esculentum* X *L. pimpinellifolium*) X *L. p.* var. *dentatum* produced fruits with the least red color of the 7 types that were classified (40a).

One-way compatibility. Pollen of *L. esculentum* did not fertilize the flowers of *L. hirsutum* but the reciprocal cross was fertile (59). *L. hirsutum* was female-sterile even with its own pollen under abnormal conditions for it, although its pollen caused seed formation in red-fruited tomatoes (51). A hybrid of *L. chilense* X *L. esculentum* was self-sterile but its pollen fertilized *L. esculentum* (T509, T512, T513). Night temperatures and photoperiodism may influence unfruitfulness in *L. hirsutum* and *L. peruvianum* (40a).

Crossability. Crossability may be increased by providing the natural conditions that facilitate female fertility in the introduced species so that reciprocal crosses may produce viable seeds (51). Superior crossability was shown in Earliana X Valiant variety crosses that gave excellent F_1 hybrids with earliness and high yields (55a).

Recessive genes remained recessive in interspecific crosses. Sixteen distinctive recessive characters from *L. esculentum* were also recessive in the hybrids from *L. esculentum* X *L. hirsutum*. Thus, *L. hirsutum* evidently supplied a homologous dominant allele for each of these 16 recessive alleles in the other parent of the crosses (51). There was intermediate inheritance of leaf type and flower size in these interspecific crosses.

Partially dominant genes. The F_1 plants from a cross of *L. esculentum* X *L. p.* var. *dentatum* showed partial dominance of canescence, leaf shape, pseudostipules, bracts and pubescence on the fruits as inherited from the wild parent (40). No dark green or purple sectors were seen in the F_1 fruits, and the density of glandular hairs on the inflorescence and leaves also resembled those of the *L. esculentum*-parent (40).

Triploid tomato. A cross of *L. esculentum* X *L. p.* var. *dentatum* resulted in 45 triploid seedlings (40).

Genes, Chromosomes and Environment

All of the known species of *Lycopersicon* are diploids with 12 pairs of chromosomes (51). Tomato chromosomes have been illustrated, showing differences in haploid, diploid and tetraploid cells (29, 36, 51, 57). Study of chromosomes facilitates understanding of polyploidy and the possibilities of interspecific crosses.

A gene is the unit of inheritance that is located in a chromosome and controls the development of a character in interaction with other genes and the environment (23). This is the basis of plant breeding. Forty-nine tomato genes have been designated by symbols (Table 2) and most of these have been designated as allelic pairs with 3:1 Mendelian ratio of inheritance. Many of these genes are used fairly easily in tomato breeding.

Many of the most valuable qualities of tomatoes do not have gene symbols assigned to them. These include size, earliness and yielding ability that appear to have a complex mode of inheritance. These are probably quantitative, polygenic characters. It has been estimated that a quantitative character may be controlled by 5 to 100 genes, many of which may be small and similar in their effects, non-dominant and cumulative (75).

Genetic characters are expressed normally only when the growing conditions are favorable for each species or variety because environmental influences and physiological processes modify the expression of hereditary factors (63). This is exemplified by earliness of fruit maturity. A tomato flower may develop into ripe fruit in 40 days at 85° F. but may require 70 days for such development at 65° F.

Genes that occur in the same chromosome form a linkage group (Figure 14). The genes that occur close together in a chromosome are rarely separated by crossing-over. Independently inherited genes affecting the season of maturity occur in Chromosome I (14). Large oblong (giant-plum) fruits and extremely tall stems are linked characters (53).

No genes have been located in Chromosomes XI and XII (Figure 14). In the other 10 chromosomes, 31 of the 49 genes with designated symbols have been located. More than 60 other tomato characters (of which many probably are polygenic) are described in this bulletin. Some chromosomes and chromosomal regions may have few if any genes in them, but continued research is likely to locate genes in Chromosomes XI and XII. Some genes are unstable and may cause frequent variations in tomato characters (13, 15).

Inherited changes usually are characteristic for a species and tend to recur, the frequency depending on the stability of the genes. Any character that occurs in the genus, *Lycopersicon,* might appear in commercial varieties of tomatoes.

Mutations and Polyploidy

Tomato seeds were treated with radium (8, 43) and with X-rays (48, 80, 95) to induce mutations resulting in new characters of tomatoes. Seeds and growing plants have been treated with colchicine to induce polyploidy (57). Colchicine was used to secure tetraploids of the hybrid (*L. esculentum* X *L. hirsutum*) which resulted in decreased pollen fertility (51). Autotetraploids can be advantageous in plant breeding (58).

Mutation often initiated defective characters many of which were recessive. This indicates that some good quality was lost through the occurrence of the defective allele. However, recessive characters are not necessarily abnormal, as red or yellow fruits, hairy or hairless stems, few or many locules, and the *U* or *u*-alleles for unripe fruit colors are equally normal (12, 39, 40). Both dominant and recessive characters have been found to originate by mutation, so all recessive characters are not assumed to be mutant in origin.

Hybrid Vigor

Hybrid vigor is now used to aid the tomato industry. First-generation hybrids with trade names (such as Burpee Hybrid, Fordhook Hybrid and Clinton Hybrid) are sold to commercialize heterosis in tomatoes (32). Extensive reviews of literature contain different theories to explain hybrid vigor (17, 65, 69, 75, 83). The following theory appears to be a good explanation of hybrid vigor in tomatoes: Heterosis results in the suppression of unfavorable recessive characters by the favorable action of dominant genes. Hybrid vigor and dominance thus may be related (63). Practically pure-variety parents are selected with a maximum number of desirable characters and a minimum number of undesirable characters. Many of the desirable characters are quantitative and act together (75). When these selected parents are crossed, the F_1 progeny show greater vigor and yielding power than either of their parents. The hybrids show increased speed or efficiency in their metabolism (17, 69). However, in the F_2 and later generations, the desirable characters segregate and thus decrease their total effectiveness while the undesirable recessive characters appear.

Hence, seed is not saved from the first-generation hybrid tomatoes to produce later generations of marketable tomatoes. Instead, new crosses are made to get more first-generation seed. Increased root growth was found to be one expression of hybrid vigor (72).

According to another theory of hybrid vigor, high yields were explained by prominent hybridity due to crossing very dissimilar parents (17, 28). Thus, hybrid vigor resulted from great heterozygosity. This theory helps to explain heterosis where desirable characters are not dominant. This theory does not apply well to tomatoes because all of the varieties of green-wrap tomatoes are quite similar, and crossing very dissimilar parents would result in some very undesirable characters in the first generation. Many of the genes that cause wide diversity in tomato selections are non-commercial in quality.

Besides their desirable characters and relative freedom from undesirable characters, the parents for crop-production hybrids should have useful combining power (crossability) (23, 55a). This crossability results in the exhibition of desired kinds of hybrid vigor. Genetically male-sterile tomato plants may be used to facilitate crossing for production of hybrid tomato seed (70). A desirable male-sterile parent with exserted stigmas would make possible the mass production of F_1 hybrid seed.

Present methods of hand-pollination of tomatoes are tedious and slow, and many fruits are required to produce an ounce of seed (about 500 pounds of fruits for one pound of seed). The high cost of labor now makes hybrid tomato seed too expensive for large fields. However, hybrid tomatoes are very useful in home gardens where abundant production is very profitable for food and satisfaction despite the usual high cost of gardening.

Breeding Tomatoes for Resistance to Diseases

Many of the parasites that cause tomato diseases exist as physiologic races and their continuous mutations produce new ones (78, 103). Different degrees of resistance of tomato varieties to the parasites identify the physiologic races (66). Such races have been identified for the fungi that cause leaf mold and Fusarium wilt (1, 30, 103). Facultative parasites that have been economically unimportant may become very destructive (92). Moderately destructive parasites may become increasingly virulent or attack new hosts. Newly introduced varieties of tomatoes may be found to be extremely susceptible to certain parasites. The inherited changes in parasitic bacteria, fungi and viruses complicate the difficulties in breeding and maintaining resistant varieties of field crops (79). Hence, there is continuous need for breeding to protect and improve varieties by increasing their resistance to diseases (78).

Method of Crossing Tomatoes

A previous method of crossing tomatoes (89) was modified as follows: For female parents, flowers with whitish-green anthers were selected one or two days before their blossoming time. With straight small forceps, the anthers were caught by their bases and removed without injuring the female parts. This was done early in the forenoon as this is the best time to secure adequate amounts of pollen. Ripe yellow anthers were removed from the open flowers of the male parent. One to three anthers were held by their tops between the thumb and the side of a finger. A small sharp pointed scalpel was used to scrape pollen from the anthers onto a finger. The tip of the stigma of an emasculated flower was touched to the specks of white pollen on the finger. This method did not bruise the stitgma as a scalpel might have done, and used pollen economically. Some anthers suddenly discharged white clouds of pollen into the air when the stamens were touched, and left a layer of pollen on the style, so the stigmas were touched to this layer of pollen. For self-pollinating flowers that had inclosed stigmas, it was satisfactory to use flowers with yellow anthers on their opening day. Two-day-old flowers often were partly closed and were emasculated easily by pulling on the corolla. All hand-pollinated flowers were tagged and all other flowers, buds and fruits were cut from their trusses. To avoid undesired pollen and to protect the developing fruit until it ripened, each truss was covered with a brown Kraft-paper grocery sack (1-pound size) the top of which was cut to fit around the stem where it was held with 2 paper clips. The glued seam of the sack was placed downward to minimize opening by rain.

Crossing tomatoes in winter in a greenhouse is advantageous because there is less hazard from accidental crossing, an extra season's work can be gained, the work is convenient, and field crops compete less for the worker's time. Because ripe anthers commonly explode and scatter their pollen grains into the air, hand-pollinated flowers should be bagged for protection in both greenhouses and fields. For increasing seed, tomato plants in greenhouses should be shaken every day for natural pollination.

Summary

Descriptions are given for 49 tomato characters with named genes, and more than 60 other tomato characters without identified genes,

as listed in Tables 2 and 3. Many of these latter characters apparently are complex, polygenic and show quantitative inheritance. Their horticultural importance equals that of the named genes. Such quantitative characters are earliness, fruit size and yielding ability. Thirty-one of the named genes are located on the chromosome map (Figure 14) that shows the linkage groups. A key to tomato species is given.

Apparently, first descriptions are given for the recently discovered alleles *bu, Xa, bk,* and *mc.* Fuller descriptions are given for the recently studied alleles *e, m, ne,* and *Wo.* Additional description is given for the *l*-allele. The genes with designated symbols are listed alphabetically in Table 2, which will help the tomato breeders in selecting letter combinations for newly discovered genes.

New descriptions are assembled for many of the tomato characters with unnamed genes. The brief discussions on chromosomes, genes, interspecific crosses, mutations, polyploidy, hybrid vigor and disease resistance are essential to an understanding of tomato breeding. A convenient method of crossing tomatoes is described.

Table 1 lists the inherited characters that are especially desirable in new varieties of green-wrap tomatoes in East Texas. It lists the parents from which the desired characters may be secured in crosses, and also the undesirable characters that will enter the hybrids with these parents. Tomato hybrids, especially those from dissimilar varieties or species, commonly show some undesirable characters. For example, selections from thousands of plants of T935 through 8 generations have not eliminated its predisposition to catface that it inherited from its Ponderosa ancestor even after 16 generations.

Work of the tomato breeder is facilitated by recognizing all of the good, mediocre and undesirable characters so that the good ones can be separated from the poor ones efficiently, and certain characters may be distinguished from the parasitic and physiological diseases. Thus, additional crosses and selections can be made efficiently in attaining improved commercial varieties.

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