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## TASSEL MODIFICATIONS IN *ZEA MAYS*<sup>1</sup>

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*Zea Mays* L., in addition to its great economic importance, is preeminent among plants as a tool in the study of heredity. However, even though our knowledge of maize genetics has made rapid and often spectacular advances, certain problems involving basic morphology of the plant have been left unanswered. Foremost among these is that of the pistillate inflorescence, or ear, the structure of which has been discussed elsewhere (Nickerson, 1954). Another equally basic problem involves the staminate inflorescence, or tassel. Anderson (1951) briefly summarized botanical knowledge dealing with this inflorescence, and Alava (1952) showed how certain maize races could be characterized on the basis of information obtained from their tassels.

Preliminary studies on tassel morphology by the senior author indicate that the somewhat stereotyped and simple construction of tassels is misleading; certain parts apparently have been subjected to reductions even greater than those affecting corresponding ear parts. Morphological analysis of the tassel as it occurs atop a typical maize plant is even more difficult than morphological analysis of the ear.

One source of information on ear morphology was through studies of certain genetic forms in which particular parts were present in an accentuated form. It was felt that the same technique might profitably be applied to the tassel, since variation in maize tassels is, as in other parts of this specialized grass, variation on a theme. Specimen tassels from the collection of sixteen tassel mutants assembled by the junior author were therefore examined. They contained a wealth of material;

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a search of the literature revealed that, in addition to the fact that several of them had not been described, many of the known forms had very meager descriptions. Since knowledge of the tassel mutants in themselves will serve both as a preliminary step in analysis of tassel morphology and as a basis for their employment in studies involving gene interaction, fuller descriptions of these anomalous forms are given.

We have attempted to give below a careful description of how each mutant type affects structures present in tassels and ears of North American corn-belt maize. Plants of each mutant have been bred to various combinations of two widely known corn-belt inbreds, CC5 and L317, sufficiently often to allow meaningful comparisons to be made between them. It must be remembered, however, that the standard stock is largely responsible for these particular manifestations, and that the background here employed was one found to be well adapted to growing conditions in southern California. Certain forms which might logically be included in this discussion, such as Corn-grass, Teopod, Silky-1 and Silky-2, were not studied. Silkless, a well-known ear anomaly, also was not included, because in our stocks Silkless tassels are indistinguishable from those of Standard plants.

It is possible to construct a key by which these tassel mutants may be separated. However, since even in relatively homogeneous stocks, an example of one mutant may sometimes match the description of another, such an artificial device cannot be too heavily relied upon. A key is here intended only to show certain general trends among the sixteen forms; it may or may not indicate underlying genetic and physiological similarities. The several descriptions given later are arranged in the numerical order indicated in the key.

#### KEY TO CERTAIN TASSEL MUTANTS

- A. Tassel of normal (Standard) or nearly normal proportions
  - B. Tassel with silks
    - C. Pollen shed; fruits formed
      - D. Fruits on proximal branch areas from imperfect florets..... *Ts<sub>5</sub>* — 6
      - D. All fruits from perfect florets..... *ts<sub>7</sub>* — 8
      - C. No pollen shed; no fruits formed..... *ts<sub>8</sub>* — 9
    - B. Tassel without silks
      - C. Glumes undeveloped ..... *Vg* — 13
      - C. Glumes well developed
        - D. Glumes long (average 11.5 mm.) ..... *Tu* — 14
        - D. Glumes near normal length (average 8–10 mm.)
          - E. No pollen shed ..... *ms<sub>1</sub>* — 10
          - E. Pollen shed
            - F. Up to  $\frac{1}{4}$  or  $\frac{1}{3}$  of branch tips sterile; pedicellate spikelets often with several sets of florets ..... *bd* — 11
            - F. Branch tips never sterile; pedicellate spikelets not branched..... *Club* — 12
  - A. Tassel of abnormal proportions
    - B. Tassel with silks
      - C. Half or more of tassels pistillate; staminate spikelets confined to middle areas or outer halves of branches; spikelets with no more than two florets each
        - D. Branches indeterminate, mostly ending in immature pistillate structures..... *Ts<sub>3</sub>* — 3
        - D. Branches otherwise
          - E. Spikelets loosely spaced on branches..... *ts<sub>2</sub>* — 2
          - E. Spikelets crowded on branches..... *ts<sub>1</sub>* — 1
      - C. Tassels either staminate, pistillate, or mixed; if mixed, staminate spikelets often with more than two florets



- D. Extra florets developed on both sessile and pedicellate spikelets; average peduncle length 10 cm. or less..... $Ts_8$  — 7
- D. Extra florets developed on pedicellate spikelets only; average peduncle length more than 10 cm.
- E. Seed set very sparsely if at all; average glume length 6 mm..... $ts_4$  — 4
- E. Seed set in noticeable quantities; average glume length 8.5 mm..... $ts_4^a$  — 5
- B. Tassel without silks
- C. Branches horizontal or slightly lax with reference to central culm..... $ra_1$  — 15
- C. Branches upright, close to central culm..... $ra_2$  — 16

Certain measurements have been made on at least fifteen and often twenty-five plants of each mutant form, and averages of these data are given in Table I. *Peduncle length* is the distance from the uppermost leaf-bearing node to the node at which the lowermost tassel branch arises. *Tassel length* refers to distance from the node at which the lowermost tassel branch arises to the tip of the central culm. *Branching area* is that distance along the central culm from the lowermost branch node below the central spike; it is included within the tassel length. *Primary branches* are axes of the second order, when the main culm of the plant is considered to be an axis of the first order. The percentage values for peduncles and branching areas were obtained by dividing these respective lengths by the sum of peduncle and tassel lengths.

These same data are presented graphically in fig. 1 by means of a pictorialized scatter diagram (Anderson, 1949). The diagram is meant only to indicate the average extent to which each of the mutants departs from average measurements of Standards. Limits were chosen so that Standard averages would always be char-

TABLE I  
AVERAGE MEASUREMENTS OF CERTAIN MORPHOLOGICAL FEATURES  
IN TASSELS OF NORMAL AND MUTANT MAIZE FORMS

Form	Peduncle length in cm.	Tassel length in cm.	Branching area in cm.	Number of primary branches	% peduncle of whole tassel	% branching area of whole tassel
Standard	17.1	35.0	10.4	14	33	20
(1) Tassel-seed 1 ( $ts_1$ )	6.3	23.4	8.5	16	21	29
(2) Tassel-seed 2 ( $ts_2$ )	4.9	26.4	9.7	21	16	31
(3) Tassel-seed 3 ( $ts_3$ )	3.9	22.5	9.0	26	15	34
(4) Tassel-seed 4 ( $ts_4$ )	16.2	25.2	19.1	34	39	46
(5) Tassel-seed 4 <sup>a</sup> ( $ts_4^a$ )	14.4	24.8	16.3	43	37	42
(6) Tassel-seed 5 ( $ts_5$ )	13.0	33.5	12.4	24	28	27
(7) Tassel-seed 6 ( $ts_6$ )	10.0	18.5	12.0	36	35	42
(8) Tassel-seed 7 ( $ts_7$ )	17.9	33.1	15.0	23	35	29
(9) Tassel-seed 8 ( $ts_8$ )	18.0	31.9	8.8	14	36	18
(10) Male-sterile 1 ( $ms_1$ )	19.0	33.3	10.8	18	36	21
(11) Branched-silkless ( $bd$ )	15.1	34.4	10.7	18	31	22
(12) Club ( $club$ )	13.9	30.3	10.8	20	31	24
(13) Vestigial glume ( $Vg$ )	14.9	35.3	11.7	20	30	23
(14) Tunicate ( $Tu$ )	13.7	33.3	12.1	22	29	26
(15) Ramosa 1 ( $ra_1$ )	14.6	33.8	28.0	72	30	58
(16) Ramosa 2 ( $ra_2$ )	12.0	27.7	21.7	67	30	55



acterized by long flags. Thus, similarity to Standard in both graph position and flag lengths means that a particular mutant departs relatively slightly from a normal form. The converse is also true; the farther away in position and the greater the flag deviations from Standard, the more a given mutant differs in form.

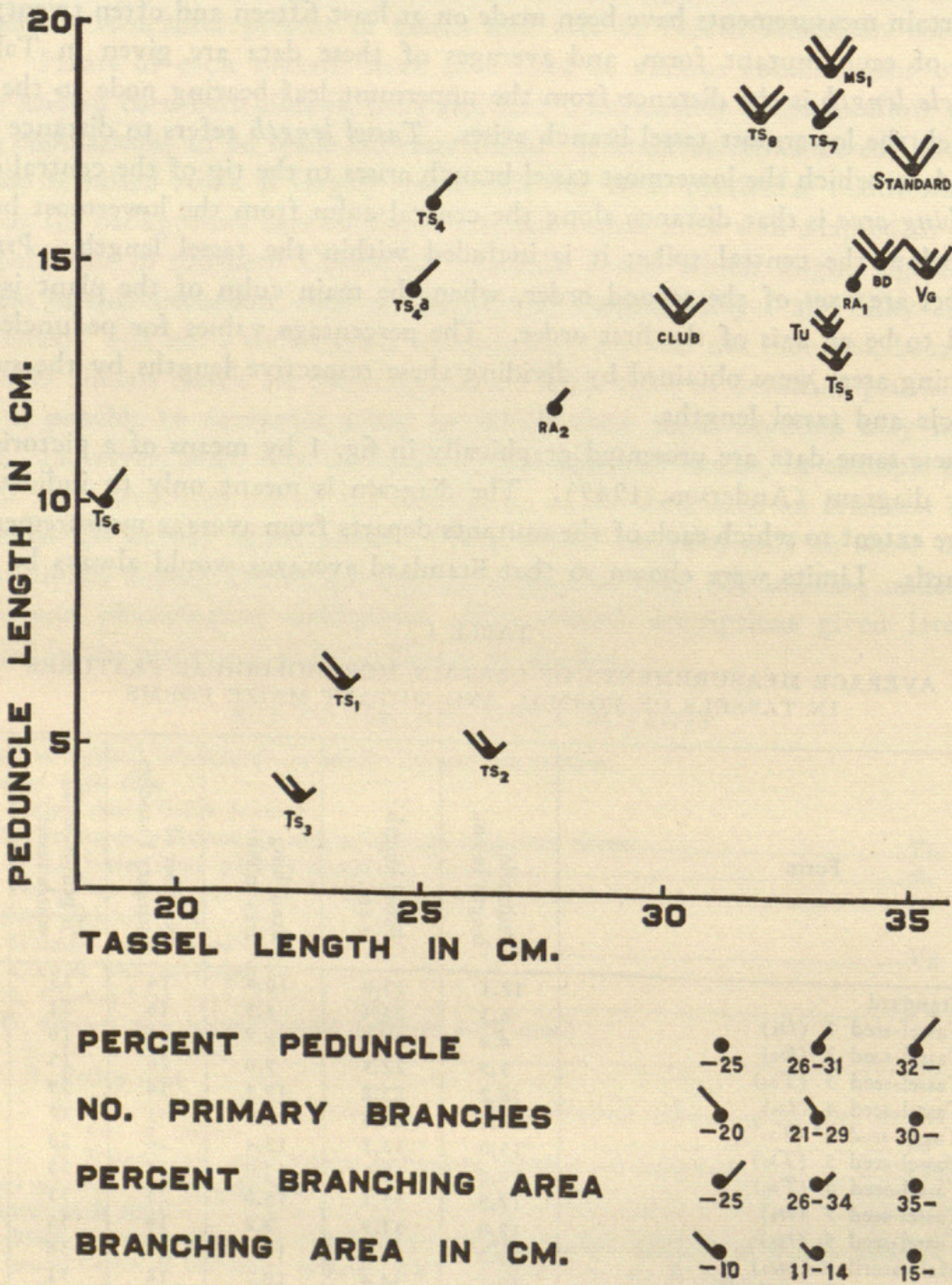


Fig. 1. Pictorialized scatter diagram of information contained in Table I, showing relationships between certain measurable features in tassels of normal and mutant forms of maize. Further explanation in the text.



## DESCRIPTIONS

*Standards, L317 and CC5* (pl. 22, fig. 1).—

Various mixtures of these two corn-belt inbreds were used. The history of Lancaster Surecropper, from which M. T. Jenkins developed L317, has been reviewed by Anderson (1944b). Wisconsin Inbred CC5 has an ancestry in the open-pollinated maize which was common to that section. Anderson and Brown (1952a, 1952b) showed that these corn-belt forms were various mixtures of Northern Flint and Southern Dent races. Nickerson further pointed out (1953) that these two races had previously been mixed in some degree, and that the excellent hybrid vigor manifest in present-day crosses, such as those between these two standards, is based on rather small differences. Ears are 14- to 18-rowed, 8 to 10 inches long, and bear bright yellow, dented kernels.

1. *Tassel-seed 1* ( $ts_1$ ) (pl. 23, fig. 1).—

First described as "tassel-ear" by Emerson (1920), this mutant was classified as Tassel-seed 1 by Emerson *et al* (1935), and assigned by them to Chromosome 2. Emerson originally described the inflorescence as being completely pistillate, compact and distinctly ear-like, with "glumes and palae short, broad and rounded, in all respects much like those of true ears." He noted that these characters could be observed in both mature and immature tassels as well as in poorly pollinated mature ones. It may be added that each pair of pistillate spikelets is associated with a well-developed cupule (Nickerson, 1954). The branches are thickened so that they appear as wide green bands in adaxial view. In our cultures, as in Emerson's, seed set was good and very often both florets of a spikelet develop a caryopsis. This development obscures any evidence of regular rowing in the central spike.

Emerson noted the general plant weakness in comparison to sibs, profuse silk production in the tassel, a general lack of elongation in upper internodes, and early assumption of a pendant position by the tassel. In our stock, this pendant position is due to bending of the culm; in Tassel-seed 2, likewise a pendant form, it is attributable mostly to bending of the tassel proper. These differences are manifestations of the degree of condensation (Anderson, 1944a), at least in part. Spikelet pairs of Tassel-seed 1 are generally closely spaced, resulting in rigid branches, while those of Tassel-seed 2 are more widely spaced, resulting in lax branches. Emerson mentioned these relative spikelet-pair densities, but he did not call attention to their differing effects on the area of bending. However, his figures 10 and 11 show each form quite well.

In our stocks, branch tips most commonly end in sterile zones characterized by closely overlapping glumes. Occasionally at the very tip, these glumes simulate those of male spikelets; they sometimes even contain stamens, but no pollen shedding has been observed.



The ear of Tassel-seed 1 is slow to develop, and, as in Emerson's strains, fails to set fruit unless the tassel is either removed or poorly pollinated. It is normal except that, just as in the tassel, both florets of each spikelet often develop, obscuring evidence of regular rowing.

2. *Tassel-seed 2* ( $ts_2$ ) (pl. 23, fig. 2).—

Emerson (1920) originally described this mutant, located on Chromosome 1 (Emerson *et al*, 1935), as "tassel-seed," and noted that the tassels were loose, like those of normal plants, with individual spikelets more or less separated. Our material never showed individual spikelets, but always paired spikelets. In Emerson's specimens, spikelet pairs sometimes occurred more densely, "but not ear-like in any way." Although it rarely occurred, he noted that staminate flowers might develop with pistillate ones throughout the entire tassel, but he did not determine whether these male florets were functional. He also observed that glumes and "palae" (paleas and lemmas) of such male spikelets were long, narrow, and pointed, as in normal tassels, while in female spikelets these parts were shorter, broader, and more rounded.

In our material, spikelets were either female or perfect, no male spikelets having been observed. On perfect spikelets, glumes were elongate and near normal. Also, each spikelet pair was associated with a cupule which was often elongated above spikelet pairs located on central spike tips. Kernels developed on nearly all spikelets; in many, as with Tassel-seed 1, both florets were functional and two kernels were formed.

Each tassel branch is thin, with spikelet pairs more widely spaced in its distal portion, but the base may be as thickly set as any found in Tassel-seed 1. Tassels of this mutant are pendant, but differ from those of Tassel-seed 1 plants in that the bending is mostly accomplished in the tassel rather than in the supporting culm. This point is discussed further with regard to Tassel-seed 1 above.

Ears of Tassel-seed 2 develop to a degree depending on the fate of the tassel. If little or no successful pollination takes place, ears are developed rapidly, but always later than on normal sibs. If tassels are removed soon after their appearance, ears are formed about the same time as in normals. These results are in accord with the findings of Emerson. Like most other tassel-seeded forms, second florets in many spikelets set fruit, after the manner characteristic of Country Gentleman sweet corn (Weatherwax, 1916), so that regular rowing may be obscured. When ears develop, they are of normal size.

3. *Tassel-seed 3* ( $Ts_3$ ) (pl. 24, fig. 1).—

The first published mention of this dominant mutant was made by Phipps (1928), who stated that "a third type of tassel seed designated as Tassel-seed 3 has been studied by Emerson, but the data have not as yet been published." Emerson *et al* (1935) also listed Tassel-seed 3 as being an unpublished discovery of Emerson's. They noted that this form was similar to Tassel-seeds 1 and 2, except that the inflorescence was generally mixed pistillate and staminate, and that usually pollen could be obtained. The gene is located on Chromosome 1.



Tassel-seed 3 tassels are easily recognizable, but, like other forms, they are variable in appearance. Branches bearing distichously arranged pistillate spikelets resemble flat green ribbons on their adaxial surfaces; both branches and central spikes most often end in tapering sterile rudimentary pistillate spikelets. Often, these sterile spikelets have an appearance of being whorled rather than distichously arranged. About three-fourths of our specimens produced some spikelets from which the florets shed pollen. These staminate spikelets are imperfect, most commonly produced on proximal portions of branches and central spikes and sometimes separated by sterile zones from pistillate regions. An occasional branch is entirely staminate and ends with a zig-zag axis, but most branches which bear staminate spikelets end in the characteristic pistillate tips described above. Tassels also are lacking in stiffness, thus becoming pendant as soon as they are exerted. The upper three to five internodes of Tassel-seed 3 plants do not elongate to the degree common in Standards, and as a result a rather tight collar of leaf sheaths is formed covering the lower sixth of each tassel. One tassel in our culture was infected with smut (*Ustilago zaeae*), a probable reflection of the extreme growth and lasting succulence of tassel parts. Emerson (1920) observed, and Dr. E. G. Anderson agreed, that Tassel-seeds 1 and 2 were highly susceptible to smut, but this year we noted no infections in any of our stocks except Tassel-seed 3.

There were often instances in which a spikelet pair consisted of one staminate and one pistillate spikelet; in these mixed pairs, the staminate one is always pedicellate. No perfect florets were observed, and only one floret in any particular pistillate spikelet would form a caryopsis. Cupules are well-developed adaxial to both pistillate and mixed spikelet pairs.

The ear of Tassel-seed 3 shows very few secondary florets, although Emerson *et al* (1935) mentioned that such florets do develop. In other respects, the ear resembles that of a Standard plant.

#### 4. *Tassel-seed 4* ( $ts_4$ ) (pl. 24, fig. 2).—

First reported by Phipps (1928), and also as Sorghum Tassel (Hayes and Brewbaker (1928),  $ts_4$  was assigned by Emerson *et al* (1935) to Chromosome 3. Phipps described the tassel as being tassel-like in structure but predominantly pistillate-flowered, and stated that when it emerged it was a mass of silks. Our material showed tassels much shorter than normal, with an abnormal number of weak branches held upright by a tangled growth of silks. In Phipps' stock, mature tassels were studded with kernels, usually densely packed together, especially on the central axis of the tassel, and not arranged in regular rows. Our specimens varied from setting fruit to this extent to setting no fruit at all. Phipps interpreted this irregular rowing as a result of development of a second floret in each spikelet; with this finding we are in agreement. In both his material and in ours, tassel branches were short and had distichously arranged spikelets, the spikelets on the proximal branch and the lower central spike producing stamens which contained functional pollen. Tassel glumes were short and papery, but we cannot agree with



Phipps that they were similar to glumes of a normal ear; we observed no glume induration. We noted also that sessile spikelets rarely branched, while pedicellate ones often formed short branches bearing two to six spikelets. Our standard stock has an average condensation index of 1.3; spikelets may occur at a given node in pairs, in 4's, in 3's and 5's and occasionally in 6's. As in Phipps' stock, both florets of each spikelet always developed, and thus each node had at least four and occasionally as many as twelve florets in addition to possible extra ones formed on branches of proliferated pedicellate spikelets. Phipps mentioned that careful study of his material showed "a few multi-flowered spikelets."

Silks were produced only from pistils, and such florets were always imperfect. No glumes were modified into silks, as Phipps reported. It is doubtful if his observation is accurate, because he noted "the basal parts of such glumes were normal." The silk-like structures were most likely awns, and if so, they were probably produced not on glumes but upon lemmas. We observed no such structures in this mutant, but in a mutant combination not reported on here, awns are developed on the lemmas. In some tassels, spikelets were sterile, producing neither silks nor stamens. These sterile spikelets were most common on branches between the proximally located obviously staminate areas and the distally located obviously pistillate areas. Characteristic of our Tassel-seed 4 stock were both its generally light set of fruit in the tassel and production of staminate and pistillate florets in widely varying amounts. No cupules were developed adaxial to any spikelet pairs of the tassel.

Ears of Tassel-seed 4 were often shorter than normal because of failure of the tip to mature; they developed better if tassels were removed early. In our stocks, no excessive development of silks was noted, but Phipps reported that some glumes were modified into silks. Development of second florets, referred to by Phipps as common, was apparently much less common in our stock, and regular rowing was not obscured. Glumes were usually less indurated than in normal ears.

##### 5. *Tassel-seed 4<sup>a</sup> (ts<sub>4</sub><sup>a</sup>).—*

This allele of Tassel-seed 4 was found by E. G. Anderson in a background stock of CC5 × L317 which had been exposed to radiation at Eniwetok. Crosses made by the junior author between this mutant and Tassel-seed 4 showed the two types to be allelic.

The tassel of Tassel-seed 4<sup>a</sup> resembles that of Tassel-seed 4, but the quantity of seed set is much greater. Pollen is much more freely produced than in Tassel-seed 4. Pistillate florets which set fruit are always borne on pedicellate spikelets and are generally imperfect, but some perfect florets have been found which always appeared to set fruit. In general, pistillate florets are confined to the outer third of branches. The central spike is sometimes all staminate, with several extra florets produced on short branches which are proliferations of pedicellate spikelets. Cupules are sometimes weakly developed on the culm of the central spike, but their presence is not universal. Average lengths of glume are about half again as great as those of Tassel-seed 4.



In Tassel-seed 4<sup>a</sup> a few pedicellate spikelets have a tendency to proliferate slightly in the upper (distal) third of the ear. After kernels are removed, the right-angled insertion and excessive lengths of the glumes, paleas and lemmas of this allele give the cob a markedly different appearance from that of Tassel-seed 4.

6. *Tassel-seed 5* ( $Ts_5$ ) (pl. 25, fig. 1).—

Although this mutant is attributed to Emerson (1932), the only mention of Tassel-seed 5 in his paper was its inclusion on Chromosome 4 of a linkage map (see his fig. 1, p. 145). Emerson *et al* (1935), in a brief description, noted that it contained both silks and anthers but was not compacted as in Tassel-seed 4. In our material, tassels were very close to normal proportions, but they were never exerted as far as in normal sibs. Apparently this condition was due to lack of elongation of the internode directly below each tassel, as the plants appeared to be normal in height (Table I and fig. 1). Silks are much shorter and more scattered than in previously discovered tassel-seed forms. Their occurrence varies from very few being located in small branch areas (either basal or terminal), to being uniform over the entire tassel.

Spikelets may bear either staminate, pistillate, or perfect florets, but these types occur in specific places. Imperfect pistillate spikelets are usually located in proximal parts of lower branches, and when they occur on central spikes, it is only in their lower regions. Cupules are well developed adaxial to such spikelets, which most often occur as sessile members of spikelet pairs; the pedicellate ones are always both imperfect and staminate. The imperfect pistillate florets form most of the caryopses. Perfect spikelets are never associated with well-developed cupules, and seldom set fruit unless there are few or no imperfect pistillate spikelets present. Even here, however, fruits are formed predominantly on sessile spikelets. If a fruit is set in such a floret, the stamens are generally not exerted, but examination shows their anthers to be full of pollen and occasionally dehiscent inside the palea and lemma. Imperfect staminate spikelets occur wherever the other two forms are absent; they never have any trace of silks, and their stamens shed pollen copiously. Silks not pollinated quickly withered.

The ear of Tassel-seed 5 in our strain developed very few second florets, but Emerson *et al* noted that "secondary florets develop in ears." Otherwise, the ear closely resembles that of our Standard stock.

7. *Tassel-seed 6* ( $Ts_6$ ) (pl. 25, fig. 2).—

The first apparent reference to this dominant mutant was made by Emerson (page 14 of the Maize Genetics Cooperation Newsletter for January, 1933). In subsequent 'Newsletters', he established that this mutant is located on Chromosome 1, but no description of its morphology has been published.

Plants of Tassel-seed 6 average about one foot shorter than normal sibs. Tassels appear at the same time, but they are only half as long and are borne on peduncles whose average length is only three-fifths as great as those of Standards. In general



appearance, the tassels resemble those of Tassel-seed 4, but they usually set a considerably greater number of fruits. Branches are numerous, short, thin, and lax, with no cupules developed adaxial to any spikelet pairs. They end in many small florets which rarely form fruits and which may be borne on whorled instead of distichous spikelets. Spikelet pairs are closely set on both branches and central spike. Scarcely any distinction exists between pedicellate and sessile individuals, as each one forms several closely packed florets. Short branches with 4 to 12 spikelets are developed on the central culm, giving it a thickened appearance. Glumes are hyaline, without chlorophyll, and extremely short, averaging about 5 mm. in length.

Tassels of this mutant have two general forms. Approximately half of them are entirely pistillate; the others produce staminate spikelets on proximal branch areas and on the lower third of their central spikes. Tassels of this latter sort may have their remaining spikelets constructed in one of three different orders which occurred in our samples with equal frequency: (1) florets bearing silks might also bear stamens and thus be perfect; (2) they may bear no stamens and be imperfect, or (3) a zone of perfect florets of variable length may grade off into a tip which is entirely imperfect. Stamens in perfect florets often neither extruded their anthers nor shed pollen, but those in staminate florets invariably shed good quantities of pollen. Silks are produced only from pistils, but an occasional lemma near a branch tip may develop a short awn.

Ears of Tassel-seed 6 are not well developed unless the tassel is removed early. There is the same characteristic production of second florets found in other tassel-seeded forms, so that regular rowing is often obscured. In other respects, ears are comparable with those of Standard plants.

8. *Tassel-seed 7* (*ts<sub>7</sub>*) (pl. 26, fig. 1).—

This mutant was found by E. G. Anderson at Pasadena in material which had been exposed to radiation at Bikini. (See Anderson *et al*, 1949, for a further discussion of radiation effects.) It is not known to which chromosome it should be assigned. Tassels have proportions and dimensions of normal ones, and, like Tassel-seed 5, have few functional pistillate florets. Silks are generally short and evenly distributed; their occurrence varies from almost none to profuse. Each silk arises from a pistil in a perfect floret; florets which do not produce silks are imperfect and staminate, producing pollen freely. Only two florets are borne on each spikelet. No cupules are developed in the tassel. The number of fruits seldom exceeds twelve per tassel, and on about half the tassels they are not formed at all.

The ear of Tassel-seed 7 commonly bears up to six short branches at its base. These branches are produced from pistillate spikelets, and an adaxial cupule is present above each one. The sessile spikelet of such a pair is generally not fully developed. These basal branches do not form any viable kernels. Silks form only slightly if at all, even though the branches remain meristematic after cessation of growth elsewhere throughout the plant. Occasionally, two or three small



branches are found on the shank below an ear. These sub-ear structures have always been sterile, and none of them developed beyond the point at which pistillate spikelets could be easily recognized.

9. *Tassel-seed*  $\delta$  ( $ts_8$ ) (pl. 26, fig. 2).—

This mutant, found by E. G. Anderson at Pasadena, was segregating in a culture of chromosome translocations. It is known to be linked to white endosperm ( $y_1$ ). Both  $ts_8$  and  $ms_1$  tassels are male-sterile, in chromosome 6 and linked to  $y_1$ , but the two forms are not allelic. Further, since  $Ts_8$  sets no fruit but produces silks and since Emerson *et al* (1935) mentioned no male-sterile forms which so behaved, the material is here described as an eighth tassel-seed form. In over-all appearance, plants resemble normal sibs. Tassels are of standard proportions and size, but glumes are occasionally shorter than normal and the spikelets never swell as time for anthesis approaches. Silk production varies from none to a profusion as great as may occur in Tassel-seed 7. Four-fifths of our population of this mutant had tassels in which no stamens were formed; in the remaining one-fifth, they were formed but their anthers were empty. No stamens are ever exerted. Silks arise from abortive pistils. Three florets per spikelet may send out silks, but no fruits are ever set regardless of ample exposure to pollen. Branch tips are often undeveloped.

The ear of Tassel-seed 8 produces a great profusion of silks; 4 to 6 are formed by each spikelet. The first silk formed (from the lowest flower) is of greatest diameter, and its pistil forms a caryopsis. Each of the others sends out a silk which generally is exerted, but no fruits are formed. Kernels are arranged in rows, and, except for the fact that many extra silks protrude between the tightly packed kernels, a mature ear resembles that of a Standard plant.

10. *Male-sterile* ( $ms_1$ ) (pl. 27, fig. 1).—

This mutant was reported by Singleton and Jones (1930) and listed by Emerson *et al* (1935) as occurring on Chromosome 6. Singleton and Jones noted that tassels of male-sterile plants were more slender than normals, that anthers failed to extrude, and that no pollen was shed. They also reported that Beadle found meiosis essentially normal but that the haploid nucleus did not go through the first mitotic division, and by the time pollen should be shed it was difficult to find even the remnants of spores. Emerson *et al* noted further that shriveled anthers were exerted much later than in normal sibs.

In our material, no stamens were exerted. In other respects, tassels of  $ms_1$  resembled those of our Standards. There was a tendency for the tassel to emerge sooner than with normals, and this tendency was reflected in slightly longer pedicels (Table I and fig. 1) since elongation ceased at the same time as in normal sibs.



The ear is normal. Singleton and Jones reported that  $ms_1$  is closely linked to the white endosperm locus ( $\gamma_1$ ) with about 5 per cent recombination. Our material behaved in the same fashion; white kernels almost invariably produced male-sterile plants.

11. *Branched-silkless* (*bd*) (pl. 28, fig. 2).—

First described by Kempton (1934), this mutant is listed by Emerson *et al* (1935) as occurring on Chromosome 7. Kempton noted that the division of the tassels into a central spike and branches is as definite as in normals, but that the tassels have a thickened appearance suggesting those of Tunicate plants. He attributed this thickening to development of short branches in place of paired spikelets, a condition which also occurred in our material. He also mentioned the fact that this branching was most common on central spikes, and that on the branches there was more tendency toward retaining a pedicellate-sessile form.

Kempton made no mention of sterility, nor did his illustrations show any, but in our material sterile areas occurred at branch tips and sometimes at the tip of the central spike. Not uncommonly lowermost branches were sterile throughout. In sterile areas, spikelets were less developed as distance from the central culm increased. Kempton noted that many plants shed pollen in good quantity, but stamens often were not fully exerted.

Ears of *Branched-silkless* are of two forms, a fact which Kempton likewise noted; his figures show each type clearly. In one type, each spikelet primordium develops into a short branch bearing female spikelet rudiments which never develop beyond the earliest stages. In the other type, such branch development is confined to the basal quarter of the ear, the upper three-fourths being composed of sterile spikelets with elongated and sometimes thickened glumes. That these branches develop from spikelet primordia on an otherwise normal cob can be easily shown by removal of the branches; underlying each pair adaxially is a well-developed cupule. It is this latter type which may occasionally produce a scattering of silks too short to become exerted. Kempton stated that his material was wholly without silks, but Emerson *et al* mentioned that the ear occurs "often without silks."

12. *Club* (*club*) (pl. 27, fig. 2).—

This mutant was first noted by E. G. Anderson and segregated from non-irradiated genetic stocks at the Caltech farm in Arcadia. Its chromosome length is unknown.

The tassel is shorter than normal, with branches held at angles approximating 45°. Branch ends do not droop and their thickly set spikelet pairs are fertile throughout. The central spike is exceedingly thick, and it is on account of this character that the mutant was named. This thickening is brought about by a shortening of internodes, so that the spikelets stand nearly at right angles to the central culm. Further, these closely spaced spikelets occur singly or in pairs; there is no pedicellate branch development such as is found responsible for creation of thickened portions of the central spike of *Branched-silkless*.



The ear of Club generally matures a week later than the tassel. Its silks are profuse, and there are 4–6 silks per spikelet, each from a rudimentary pistil—a condition also found in ears of Tassel-seed 8. However, Club ears are fasciated, the branching strongly resembling a type listed by Kempton (1923) as Bearsfoot (see his fig. 1 for a clear illustration). It is apparently caused by one or more incomplete divisions of the growing point when the ear is partly formed, followed by simultaneous development of each new point into a more or less independent ear tip. The upper half of such an ear is generally hollow, and no spikelets are formed on the inside walls.

13. *Vestigial glume* (Vg) (pl. 28, fig. 1).—

First reported by Sprague (1939), Vestigial glume was found to be a dominant mutation on Chromosome 1. It is easily noted in the tassel, where the hyaline outer glumes range from awl-shaped vestiges to nearly one-third normal length. Sprague pointed out that “flowering glumes” (lemmas) and “palets” (paleas) were also reduced in size, with the result that the stamens were nearly completely exposed. In our material, as in his, anthers generally dried up before dehiscence, but occasionally a plant shed viable pollen. Many specimens in our stock had sterile areas (i.e., no stamens were formed) at tips of branches and central spikes, in some cases involving the outer sixth of all branches. Generally, over-all tassel size was smaller and tassel construction, as exemplified by thickness of central culm and branches, was lighter than in normal sibs.

The ear of Vg is easily recognized, as Sprague pointed out, after removal of kernels. There are no chaffy upper and lower glumes, paleas or lemmas present, only short pedestals, each with a low, hard ridge on both upper and lower sides. Above each spikelet pair, in an adaxial position, is a cupule with somewhat reduced rachis-flaps (Lenz, 1948).

14. *Tunicate* (Tu) (pl. 22, fig. 2).—

According to Collins (1917a), this mutant has been reported from several sources and its origin is not known. Recently, it has been cited in connection with theories of maize origin (Mangelsdorf, 1948; Mangelsdorf and Smith, 1949). Cutler (1944) suggested that its widespread occurrence among Indian tribes was because of mystical significance attached to it. Emerson *et al* (1935) listed the character as occurring on Chromosome 4.

Tassels of heterozygous Tunicate plants have normal measurements in all visible parts except the glumes. The glumes are one-fifth to one-fourth longer than those on Standard tassels and enclose paleas and lemmas similarly elongated. The stamen length being normal, the anthers, especially in the central spike, are not fully exerted and therefore are not pendant at anthesis. Pollen is shed abundantly.

Ears of heterozygous Tunicate plants are easily classified. Collins (1917a, b) stated that “the glumes of the female inflorescence, or ear, are developed so that each seed [fruit] is entirely enclosed.” Emerson *et al* (1935) likewise attributed



these covers to glumes. In our stock, paleas and lemmas were also elongated, and in many basal spikelets, paleas and lemmas of both upper and lower florets were noted. No fruit occurred in these lower florets, however, and regular rowing was externally apparent. The rachis of a Tunicate cob is rather flexible. Cupule development adaxial to each spikelet pair was not excessive in comparison with Standards; but in the Tunicate ear of Guarani maize sent to the senior author by Dr. P. C. Mangelsdorf, the cupules are much more apparent than is normally the case.

Homozygous Tunicate plants, according to Emerson *et al* (1935), are usually female-sterile. No homozygous plants were available in our collection.

An allele of Tunicate, *tu<sup>h</sup>*, was reported by Mangelsdorf (1948) as being present in *Maiz chapolote*. How this allele would behave with our Standards as background was not determined.

15. *Ramosa 1* (*ra<sub>1</sub>*) (pl. 29, fig. 1).—

This form was originally described by Gernert (1912) under the name of *Zea ramosa*, and was listed by Emerson *et al* (1935) as *Ramosa-ear 1*, located on Chromosome 7. Gernert's description of the tassel was brief. In his stocks, tassels were slightly smaller than normal, invariably much branched and cone-shaped. Collins (1917a, b) noted that branches were much more numerous than normal. Kempton (1921) reported 400 as an extreme number; the branches gradually decreased in size upward, the transition from branches to pairs of spikelets being imperceptible. A short central spike was characteristic in our specimens—a fact which Kempton had likewise noted in his plants but which Collins did not mention. It was not possible, according to Collins, to distinguish between plants heterozygous for *Ramosa 1* and normals. However, in our material, it was quite simple to separate them; in five  $F_1$  families of *Ramosa 1*  $\times$  Standard, four with 10 plants and one with 9 plants, separation was easily made into 24 normal and 25 heterozygous individuals. Resemblance of tassels of homozygous *Ramosa 1* plants to grass panicles is striking (Kempton's plate 13 is typical). Tassels of plants heterozygous for this character were intermediate between a pyramidal paniculate tassel and a normal one, identical to one figured by Kempton in his plate 14.

The ear of *Ramosa 1* was described by Gernert as being much branched, without male florets, covered with husks, and composed of a mass of kernels borne on numerous irregular branches. His description applies to our specimens as well, except for two other points: (1) branches on a *Ramosa 1* ear are about as numerous and have much the same irregular whorled arrangement as do those of the tassel; (2) there are no adaxial cupules at the junctions of ear branches and central culm. Cupules were present, however, adaxial to each spikelet pair of the branches. No other ear among the mutants in this collection is so organized. It was also a common occurrence for tips of those branches originating near the upper part of the ear to be sterile.



16. *Ramosa 2* ( $ra_2$ ) (pl. 29, fig. 2).—

The only published reference to this mutant is found in Emerson *et al* (1935), which simply listed *Ramosa 2* as being located on Chromosome 3 and credited its discovery to Brink.

*Ramosa 2* has a tassel characterized by stiff upright branches which remain closely appressed to the central culm. The central spike region does not bear short-pedicelled spikelet pairs; instead the spikes are borne on branches which decrease in length from base to apex. There is a pronounced transition from well-developed tassel branches bearing many pairs of spikelets to smaller branches bearing fewer spikelets, some of which appear to occur singly. As one proceeds acropetally, these multi-spikeleted branches are replaced by stalks each bearing only one pair of spikelets which are themselves borne on pedicels longer than normal. In the adaxial area of each of these branches and stalks, a small cupule-like depression in the central culm can be observed which is generally of a different color from the surrounding surface. Although these depressions and short stalks are not confined to *Ramosa 2*, they are here most common and best developed. The spikelet pairs in proximal areas of well-developed lower branches are likewise stalked and also have abnormally long pedicels, but there is no adaxial depression.

Pollen is shed freely, but much of it remains within the confines of the tassel because close proximity of branches does not allow unrestricted air passage. Each spikelet has two male florets, and each of these has three functional stamens. Tassel-seed 4<sup>a</sup> might possibly be confused with *Ramosa 2*, as its tassels sometimes show the same tendency to have numerous stiff, erect branches and stalked spikelet pairs in the central culm region, with an abundance of pollen produced. It can be separated from *Ramosa 2* by the lack of stalked spikelet pairs on lower branches and the fact that each of its branches end in a few sterile undeveloped spikelets.

The ear of *Ramosa 2* sometimes ends in a staminate structure looking like a normal central spike. Most commonly, it produces scattered branches on the upper (distal) half of the cob, which in turn bear female spikelets in pairs. These branches are nearly always found in younger ontogenetic stages than the rest of the plant and consequently set seed only rarely. A branch originates by growth of what would normally be the pedicellate spikelet of a pair of kernel-bearing spikelets. No instances were observed in which the sessile spikelet of such a pair formed anything but a normal caryopsis. The spikelet pairs themselves are borne on short stalks; the cupule is bent at nearly right angles, and is adherent half to the stalk and half to the cob. In addition, these stalks are spaced rather widely apart, so that a cob of *Ramosa 2* from which the chaff has been removed resembles a similarly treated cob of *Coroico* maize (Cutler, 1946).

## SUMMARY

Morphological studies have been made on tassels and ears of sixteen mutant forms of maize. Four of these forms are reported for the first time, and the others, for which descriptions were either inadequate or non-existent, are here



described. Each genetic form was introduced into a standard background derived from the inbreds CC5 and L317. The mutants studied included nine tassel-seeded forms:  $ts_1$ ,  $ts_2$ ,  $Ts_3$ ,  $ts_4$ ,  $ts_4^a$ ,  $Ts_5$ ,  $Ts_6$ ,  $ts_7$  and  $ts_8$ . Others studied were Male-sterile ( $ms_1$ ), Branched-silkless ( $bd$ ), Club ( $club$ ), Vestigial glume ( $Vg$ ), Tunicate ( $Tu$ ), Ramosa-1 ( $ra_1$ ) and Ramosa-2 ( $ra_2$ ).

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