The Inflorescences of Maize

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SINCE the discovery of maize, in 1492, by two explorers sent out by Columbus, the morphological peculiarities of the ear and tassel of maize have been of special interest to some and of general interest to all who are acquainted with the maize plant. Early descriptions and drawings of the maize plant gave attention to the inflorescences. Lyte's description [*New Herbal,* 1619], quoted by Arber (*1*), Mangelsdorf and Reeves (*2*), and Mangelsdorf (*3*), of the inflorescences of maize is vivid and picturesque.

> This corne is a marvelous strange plante. . . . Nothing resembling any other kind of grayne; for it bringeth forth his seede cleane contrarie from the place whereas the flowers grow, which is agaynst the nature and kindes of all other plants, which bring forth there fruit there, whereas they have borne their flower . . . at the highest of the stalks grow idel and barren eares, which bring forth nothing but flowers or blossome. . . . The fruitful ears do grow, upon the sides of the stems amongst the leaves, which ears be great and thick, and covered with many leaves so that one cannot see the ears. . . . The grayne or seed which groweth in the ears, is about the quantitie or bignesse of a Pease, of colour in the outside, sometimes browne, sometimes redde, and sometimes white, and in the inside it is in colour white, and in taste sweet, growing orderly about the eares, in nine or ten ranges or rows.

This is a good description of the major characteristics of the ear and tassel even by present standards.

The main purpose of this paper (*4*) is to consider, from several aspects, the inflorescences of normal dent maize, especially of the ear, which is annually the source of billions of bushels of food and feed. However, it was the morphological differences between the ear and the tassel and, also, the unique characteristics of the maize inflorescences in contrast with the inflorescences of other cereal grasses that impressed the first observers. The unique characteristics of the maize ear and tassel continue to be of great interest to all who work with the maize plant. From a practical standpoint, the capacity of the maize plant to produce seed is affected by certain morphological characteristics of the ear and by certain intraplant relationships among the ear, the tassel, and other parts of the plant. Therefore, to provide a botanical basis for understanding this great food plant, the morphological features that characterize it and distinguish it from other cereal grasses are described as clearly as possible within the limited space available here. In addition, the chemical composition of the maize kernel and its modification by selection are discussed briefly. Finally, an attempt is made to show why the maize plant is superior as a producer of cereal grain.

The Mature Maize Plant

At maturity the above ground parts of a maize plant consist of the stem, foliage leaves, tassel, and ear (Fig. 1). The stem is divided into nodes and internodes, which are of varying lengths. The foliage leaves are in two ranks, one at each node, and they alternate

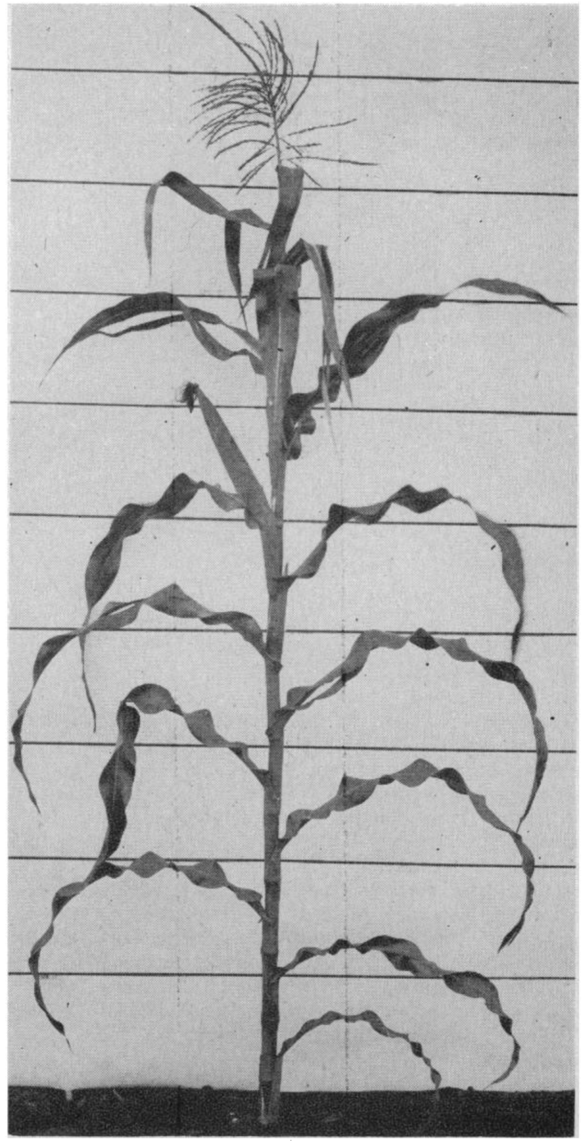

Fig. 1. A maize plant showing the alternate, two-ranked arrangement on the main stem, the tassel, terminal on the main stem, and the lateral axillary branch on which the ear develops.

on the stem. The tassel, which produces only pollen, terminates the stem. A lateral axillary branch (or branches), in the upper portion of the plant, is terminated by the ear, which produces only seed. The lateral ear-bearing branches have short internodes, and they have modified leaves (husks) whose arrangement on the branch is the same as on the main stem.

Since maize is a grass, the unit of the inflorescence is a spikelet (Fig. 2). In maize the spikelets are in

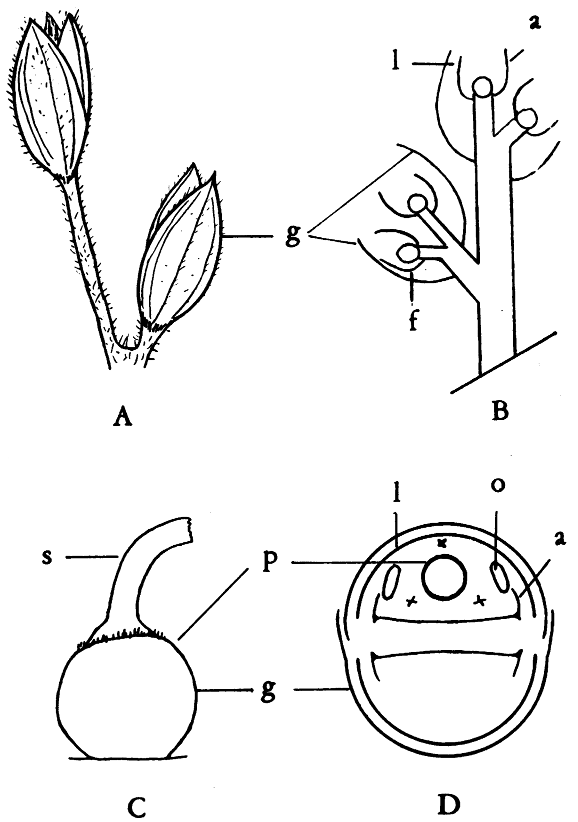

Fig. 2. (*A*) A pair of spikelets from a tassel showing the pedicellate spikelet on the long stalk and the sessile spikelet on the short stalk. (*B*) Diagram of a pair of spikelets from a tassel. A spikelet is a short branch that originates from another branch, the spikelet-forming branch. The spikelet is the portion of the diagram that is enclosed by the sterile glumes and the flower is the portion of the diagram that is enclosed by the lemma and palea, the flowering glumes. (*C*) A pistil from an ear, enclosed by two sterile glumes, which in the ear are short and thick. (*D*) Diagram of a cross section through a pair of spikelets from an ear. Only one of the pair of flowers in the spikelet of an ear has a functional pistil. [*a*, palea; *f*, flower; *g*, sterile glumes; *l*, lemma; *o*, lodicule; *p*, pistil; *s*, style (silk)].

pairs. A spikelet is a condensed branch consisting of a short stem, the rachilla, upon which are placed two leaflike structures, the sterile glumes, so named because they do not bear flowers in their axils (Fig. 2*A*–*D, g*). In the tassel the sterile glumes completely enclose the flowers, but in the ear they only partly enclose the flowers (Fig. 2*C, g*). Two flowers are produced in each spikelet.

In the tassel both flowers of a spikelet produce stamen, but in the ear only one flower of a spikelet produces a pistil. Each flower has a pair of glumes, the lemma and the palea, called the flowering glumes (Fig. 2*B* and *D, l* and *a*). In the tassel the flower is enclosed by its glumes, but in the ear the flower is only partly enclosed by its glumes.

The major characteristics of the maize tassel and ear are shown in Figs. 3 and 4. Several of the many ways in which the ear and tassel differ from each other are listed in Table 1. This table also shows that the ear and tassel are alike in two respects. First, both have paired spikelets; and second, the ear and central axis of the tassel are symmetrical structures with the spikelets arranged upon them in many rows. In addition to these characteristics, the ear and tassel show a number of correlations in development (*5, 6*), a list of which is given in Table 2.

Inflorescences of Maize and Other Grasses Compared

The ear and tassel of maize are morphologically unique. The combination of a symmetrical, many-rowed central axis with asymmetrical, two-ranked basal branches found in the tassel does not exist among other grasses. Asymmetrical, two-ranked branches are found in the terminal inflorescences of *Euchlaena* (teosinte) and *Tripsacum*, two close relatives of maize, and in *Chloris* (finger grass), *Eleusine* (goose grass), and *Paspalum*. The symmetrical, many-rowed characteristics of the ear and the central axis of the tassel are also found in the inflorescences of

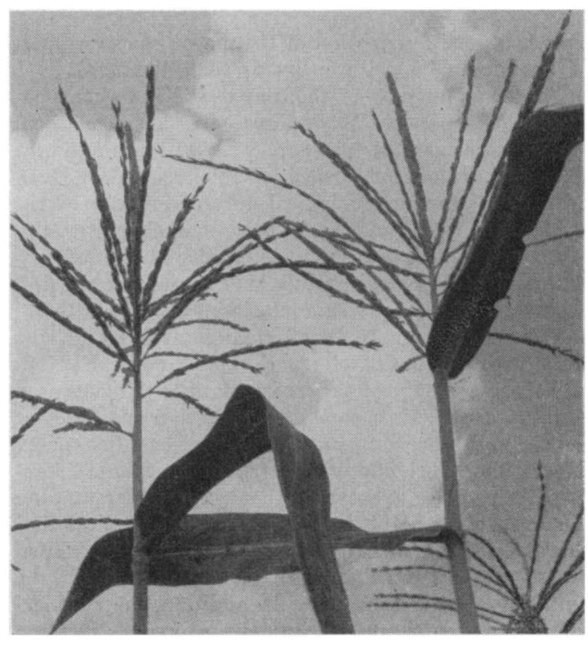

Fig. 3. Maize tassels which are terminal, staminate inflorescences having a symmetrical, polystichous central axis and asymmetrical, distichous lateral branches.

Pennisetum glaucum (pearl millet) and *Setaria lutescens* (yellow bristle grass). The paired spikelets of maize are found in *Tripsacum, Euchlaena,* and in the many members of the tribe *Andropogoneae,* to which sorghum and sugar cane belong. The characteristic of maize that distinguishes it from other grasses is the presence of two spikelets in the ear, each with a terminal, fertile flower and a lateral, aborted flower. A terminal, staminate inflorescence and a lateral, pistillate inflorescence, as found in maize, are found in only one other grass, *Euchlaena,* a close relative of maize (*7*). Other cereal grasses, including wheat, oats, barley, rye, rice, millet, and sorghum have inflorescences containing perfect flowers.

Development of the Maize Plant

There are four major stages in the development of the maize plant, terminating with the mature seed. They are the vegetative, the transitional, the reproductive, and the seed stages. In each of these stages, the developmental activities are different (*6, 8, 9*).

In the vegetative stage, the tip of the main stem remains short (Fig. 5*A*); there is no internode elongation; and leaf primordia arise one above the other in alternate succession at a certain distance from the tip of the stem. Axillary branches are produced, and leaves arise from their tips in the same order as those of the main stem (Fig. 5*C*).

The transitional stage is of short duration and consists of an elongation of the tip of the stem (Fig. 5*B*), with no apparent differentiation of lateral organs. The transitional stage occurs in the main stem which

Table 1. Differences between the ear and tassel.

Characteristics	Ear	Tassel
General		
Position on the plant	Lateral	Terminal
Long, basal asymmetrical branches	Absent	Present
Sex	Pistillate	Staminate
Fertile flowers per spikelet	One	Two
Sterile glumes	Short-thick	Long-thin
Flowering glumes	Short-thin	Long-thin
Central axis only		
Sclerenchyma zone	Present	Absent
Rachis flaps	Present	Absent
Longitudinal grooves between spikelet rows	Present	Absent
Alveole	Present	Absent

gives rise to the tassel and in the lateral branch which gives rise to the ear.

The reproductive stage begins with the initiation of branch primordia at the base of the elongated, transitional stem tip (Fig. 5*D, E*). At the same time that branch primordia are forming in the tip of the stem, the basal internodes of the main stem begin to elongate (Fig. 5*C*). Elongation of the internodes of the stem proceeds from the base toward the tip of the

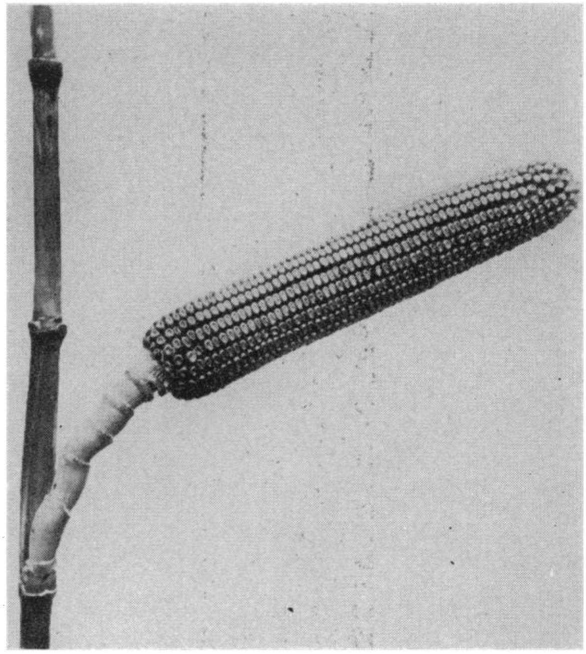

Fig. 4. Part of the main stem and ear with the leaves and husks removed. This photograph shows clearly that the maize ear is a symmetrical, polystichous structure borne on a condensed, lateral, axillary shoot.

stem. Elongation of the main stem increases the height of the plant, resulting in the emergence of the tassel from the leaves that envelop it, and terminates with the maturity of the tassel.

Branch primordia and their subtending ridges are the first lateral parts of the inflorescence to appear on the elongated tip of the stem of either the main stem or the lateral branch (Fig. 5*D, E*). In the tassel the branch primordia are of two kinds: those at the base of the tassel that elongate to become the long branches, and the spikelet-forming branches on the central axis and on the long branches of the tassel (Fig. 5*E, F*). All branch primordia of the ear are spikelet-forming branches (Fig. 5*D, E*).

In both the tassel and the ear, the spikelet-forming branches divide into two spikelet initials (Fig. 6*A, B, E*). One spikelet initial terminates the spikelet-

Table 2. Correlations in the development of the ear and tassel.

Tassel	Ear
Internode condensation	Increased row number
Extreme condensation of central axis	Short blunt ears
Biparted and triparted central axis	Branchlike divisions of the ear tip
Two or many rows of branches and spikelets, central axis	Two or many rows of spikelets in ear
Tassel branch length	Ear length
Branch length pattern	Ear shape
Tertiary branches	Irregular rowing

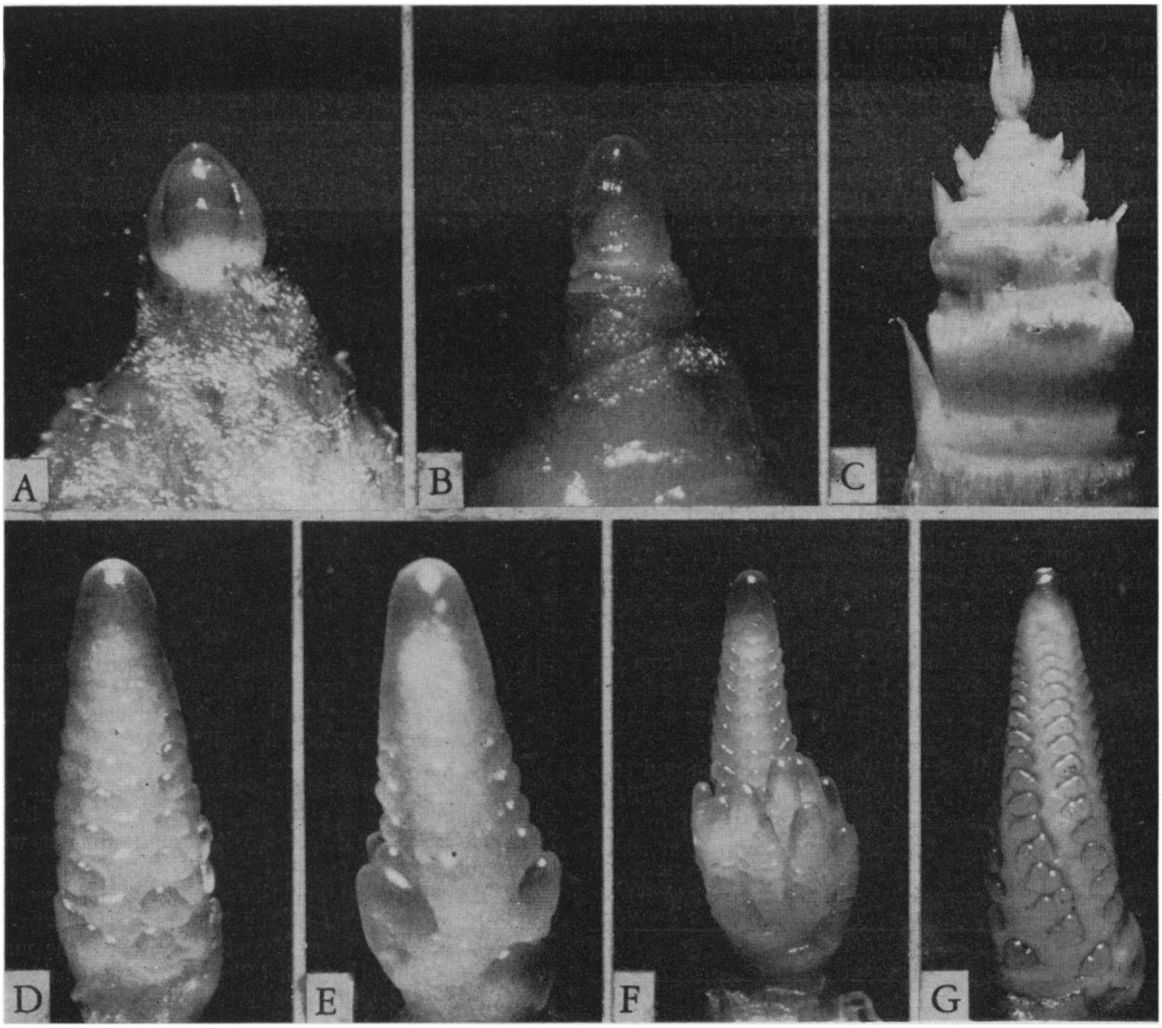

Fig. 5. External appearance of shoots of maize in the vegetative, transitional, and floral stages. (*A*) Main shoot in the vegetative stage having four leaves visible. Leaf primordia partly enclose the shoot apex (×44). (*B*) Main shoot in the transition stage, elongating, preceding the initiation of primordia of spikelet-forming branches (×35). [Photo by E. R. Leng, University of Illinois.] (*C*) Main stem with foliage leaves removed to show the tassel and the lateral axillary shoots (×7). (*D*) Ear shoot, showing spikelet-forming branches as protuberances, subtended by ridges (×49). (*E*) Early stage in the development of the tassel, showing long branch primordia at the base and spikelet-forming branches toward the apex (×44). (*F*) Spikelet-forming branches can be seen on the central axis and on the lateral margins of the long branches of the tassel primordium (×22). (*G*) Part of the spikelet-forming branches at the base of the ear primordium have divided into two spikelet initials (×22).

forming branch, and a stalk develops beneath it, producing the pedicellate spikelet (Fig. 2*A, B*). The other spikelet initial is a lateral branch, and since no stalk, or only a short stalk, develops beneath it, this spikelet is called the sessile spikelet (Fig. 2*A, B*). It is easier to distinguish the pedicellate from the sessile spikelet in the tassel than it is in the ear where both spikelets appear to be sessile. The pedicellate (terminal) spikelet is always ahead of the sessile (lateral) spikelet in development.

Two flowers are produced in each spikelet, a terminal and a lateral flower (Figs. 6*C, D* and 2*B*). In the tassel both flowers are functional, each containing three anthers and an aborted pistil (Fig. 6*G, J*). In dent maize, almost without exception, only the terminal flower of the spikelet of the ear develops (Figs. 6*F* and 2*D*). Pistils form in the functional flowers of the ear, but the stamens abort (Fig. 6*H*). Thus, the tassel functions as a staminate, and the ear functions as a pistillate inflorescence.

Development of the maize kernel begins with the fertilization of the egg and endosperm nuclei, within 26 to 28 hr after pollination (Fig. 6*I*). The endosperm nucleus begins to divide immediately after fertilization, but the first division in the fertilized egg does not occur until 10 to 12 hr later. Twenty days

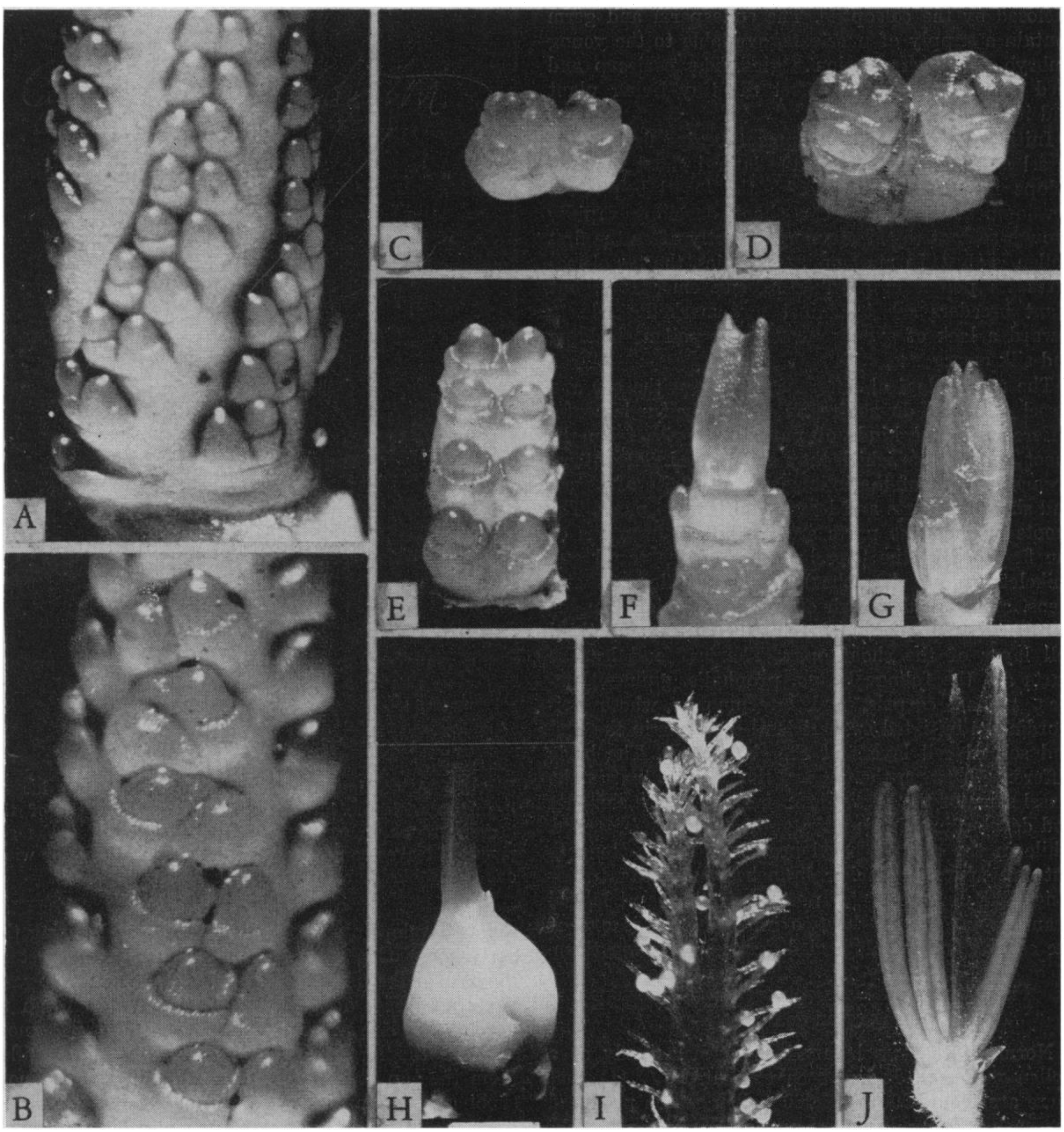

Fig. 6. Various stages in the development of spikelets and flowers of the tassel and ear. (*A*) A section of the base of an ear primordium showing the pedicellate (terminal) spikelet primordia with transverse ridges, glume initials, and the sessile (lateral) spikelet primordia without glume initials (×43). (*B*) Section of the central axis of the tassel, showing stages in the development of spikelet primordia comparable to *A* (×69). (*C*) Pair of pistillate spikelets, terminal and lateral flowers are differentiating (×47). (*D*) Pair of staminate spikelets, flowers as in *C* (×47). (*E*) Paired pistillate spikelets on a dissected portion of an ear (×43). (*F*) A pistillate spikelet, showing a terminal, fertile and a lateral, aborted flower. The silk on the fertile flower has a biparted tip (×34). (*G*) Staminate spikelet, outer glumes removed, showing the stamens of the two flowers enclosed by the thin flowering glumes (×9). (*H*) A pistil and portion of the silk (×17). (*I*) Biparted tip of a silk (style) showing pollen grains germinating on the stigmatic branches (×24). (*J*) A staminate spikelet, outer glumes and lemmas removed, to show the two functional flowers with stamens but no pistils (×9).

after pollination 89 percent of the seeds will germinate, but the percentage of strong seedlings is low (*10*). About 45 days after pollination the maize kernel reaches full maturity.

The maturity of the maize kernel marks the end of the last stage of development, and the maize plant begins to die. The maize kernel contains a young plant with a root and a shoot with four to five leaf initials, enclosed by the coleoptile. The endosperm and germ contain a supply of nutrients, available to the young embryo when germination begins. The pericarp and seed coat enclose and protect the tiny living plant and its food supply.

Initiation of floral development begins first in the tassel and slightly later in the lateral shoot that develops into the ear. Although the tassel begins its development first, the ear shoot develops rapidly enough so that the silks emerge shortly after the first pollen is shed. In most maize varieties, the tassel matures its pollen in advance of silk emergence, but plant breeders select against any marked tendency toward a lack of synchronization in pollen shedding and silk emergence.

The morphological differences between the ear and tassel of maize do not result from any fundamental difference in the kinds of parts that arise from the shoot apices from which they are derived. The lateral organs of each of the inflorescences consist of shoots and shootlike parts and leaves and leaflike parts. The shoots or shootlike parts are the lateral branches of the first order (the long branches of the tassel and spikelet-forming branches), spikelets, flowers, stamens, and lodicules, each of which is initiated in the parent axis by periclinal cell divisions in the third cell layer of the shoot apex. The leaf and leaflike parts are the foliage leaves, prophylls, glumes, lemmas, paleas, carpels, and integuments, whose primordia are initiated by periclinal divisions in the first and second cell layers of the shoot apex. The basic difference between the ear and the tassel is that in the tassel some of the lateral branches at its base elongate and develop into long, unilateral, distichous branches, while in the ear the basal branches do not elongate but are spikelet-forming branches from the beginning. The developmental pattern of the basal lateral branches in each of the two inflorescences is one of the essential morphological differences between them.

Functional and Developmental Relationships in the Ear and Tassel

Normally the tassel functions in maize only as a pollen producer. It has been estimated (*1, 11*) that there are from 9000 to 25,000 pollen grains produced for each silk produced by an ear. Kiesselbach (*11*) states that it has been calculated that an average tassel of the variety Nebraska White Prize would produce 25 million pollen grains. The period of pollen shedding varies in length, but it is, on the average, about 10 days. The length of the pollen-shedding period and the amount of pollen shed usually insure the fertilization of each functional pistil on an ear. Although many pollen grains may fall upon a silk, germinate, and send pollen tubes down the silk toward the embryo sac, only one pollen tube enters the embryo sac to provide the two sperms necessary for fertilization.

Ears develop from one or more of the upper axillary shoots of the stem (Figs. 5*C* and 7). The shoots formed at the base of the stem may remain nonfunctional or develop into tillers (suckers). Axilliary shoots develop in acropetal succession, and during the early stage of plant development they are largest at the base of the plant and progressively smaller toward the apex (Fig. 5*C*). Later, when the ears begin to develop, the size sequence changes, so that the topmost shoot is the largest, and the shoots become smaller from the top to the base of the plant. The topmost shoot or the topmost two or three shoots, depending upon whether they are single- or multiple-eared types, in turn take precedence in their development. The axillary shoots above and those below the one that becomes the ear (or ears) are inhibited by their development. The axillary shoots above the ear shoot (or shoots) are so inhibited that they cannot be seen except at very early stages in the development of the plant. What determines which axillary shoot or shoots will develop into ears is not definitely known, but it is correlated with tassel initiation. When tassel initiation begins, the last-formed axillary shoot (or shoots) too far advanced in development to be inhibited at tassel initiation becomes the ear shoot (or shoots).

Fig. 7. A portion of the main stem and two lateral branches with the husks pulled back at the tip of the larger branch to expose the tip of the ear. Husks are modified leaves consisting of the leaf sheath either without a leaf blade or with a reduced leaf blade.

Developmental patterns of the topmost ear shoots in single- and multiple-eared types show interesting contrasts. Freeman (*12*) showed that, at an early stage of development, the five topmost shoot primordia of a single-eared type had a large top shoot and, successively toward the base of the plant, four much smaller shoots, indicating a dominance of the topmost ear shoot. In multiple-eared types, the size of the ear shoots graded downward in size from the topmost shoot, indicating no dominance among the shoots.

Some interesting relationships in the development of ear shoots on single- and multiple-eared types have been shown by Lyons (*13*). He studied one-, two-, and three-eared maize types. If the topmost ear shoot was covered to prevent pollination, the number of normal ears produced in the one-eared type was none; in the two-eared type, one; and in the three-eared type, two. If two top shoots were covered, the two-eared type produced no normal ears, and the three-eared type, one ear. When the topmost shoots that normally produce the ears on two- and three-eared types were covered, lower shoots on a few plants produced ears varying from a few seeds to medium-sized ears. However, most plants failed to produce seed on the lower shoots, even though silks were exposed. Removal of the topmost one or two shoots of the one-eared type shifted the ear production to the next lower remaining shoot or shoots. In the two-eared type, removal of the topmost one, two, or three shoots shifted ear production to the next lower pair of shoots. In the three-eared type, removal of the two top shoots shifted ear production lower on the plant to the third, fourth, and fifth shoots. It would appear from these studies that a certain ear type will produce only a definite number of ears. Ear shoots, even though unfertilized, inhibit normal ear development in the next lower ear shoots, but when ear shoots are removed in certain combinations, development of ears on other shoots lower on the plant can take place.

The number of ears per plant is an inherited characteristic that can be affected by selection. Selection for two ears per plant was begun in on open-pollinated field of a normally one-eared, yellow dent corn at the Illinois Agricultural Experiment Station in 1905 and continued through 1927. Each year ears from plants having two ears per plant were selected, and the seed was mixed together to provide seed for the next crop. The percentage of two-eared plants increased from 6.7 percent to 80.1 percent in 1927. The percentage of two-eared plants varied from year to year, but after 1920 it was never below 48 percent.

Selection for height of ear was begun at the Illinois Agricultural Experiment Station in 1903 and was discontinued in 1928. High- and low-ear strains were established by selecting, from a field of open-pollinated yellow dent maize (Leaming), ears from plants that had their ears highest or lowest on the plant (*14*). At the beginning of the experiment, the ear height of the high-ear strain averaged 56.4 in. from the ground, and that of the low-ear strain averaged 42.8 in. from the ground. The greatest difference in ear height was obtained in 1927, 1 yr before the experiment was discontinued, when the average ear height of the high-ear strain was 120.5 in. from the ground, and that of the low-ear strain was 8.1 in. from the ground, a difference of 112.4 in. The greater ear height of the high-ear strain resulted from more and longer internodes below the ear, whereas the low-ear strain had fewer and shorter internodes below the ear, but the height of the plants from ear to tassel was the same in both strains.

The high-ear strain was 10 to 14 days later than the low-ear strain. The yield of both strains was less than normal corn. While the high-ear strain, owing to its extreme height, leaned badly or fell to the ground, the low-ear strain had a stiff erect plant. Owing to its short, stiff, erect stalk, the low-ear strain was used to produce stiff-stalked inbred lines, one or two of which have been used in the production of commercial hybrids. The high-ear strain has been of no value as a source of breeding material in the production of commercial hybrids.

Ear Size and Factors Affecting It

The maize ear is a large inflorescence (Fig. 4). A good commercial hybrid grown at a planting rate of four plants per hill (16,000 plants per acre) will have from 750 to 800 kernels per ear, or a seed yield of 225 to 250 g per ear. Eight hundred kernels per ear is equivalent to 14 average oat panicles containing 60 kernels per panicle or 20 average wheat heads containing 40 kernels per head. One ear of maize producing 250 g of grain is equivalent to the weight of grain produced in 300 average-sized oat panicles or 200 average-sized wheat heads. The marked superiority of the maize ear as a seed producer lies not so much in the number of kernels per ear as in the weight of the kernel, which results in a high total weight of seed per ear.

The number of kernels per ear is determined by the number of rows of kernels (Fig. 8) and the number of kernels per row (Fig. 9). An ear having 800 kernels would require an 18-rowed ear with 45 kernels per row. Kernel-row-number has been found to vary from four rows in a distichous type to 30 or more

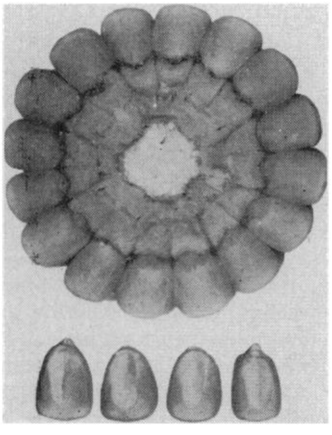

Fig. 8. Four maize kernels and a cross section of a maize ear demonstrating the many-kernel-row characteristics of the ear.

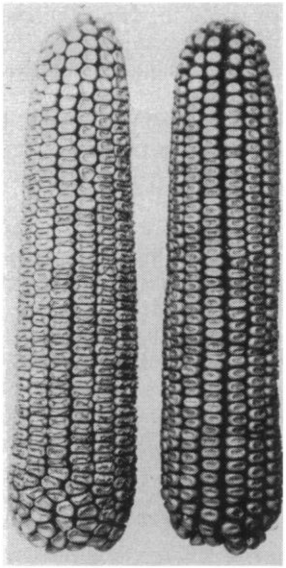

Fig. 9. From the photograph it would appear that the maize ear on the left has 12 rows of kernels and the ear on the right has 14 and that each ear has approximately 50 kernels per row. Based on these figures, the total kernels per ear would be 600 (left) and 700 (right).

in a fasciated type. Most commercial hybrids have about 16 to 18 rows of kernels. According to Anderson and Brown (*15*), row-number is affected by the degree of condensation or telescoping of the successive internodes. As the condensation index increases, there is an increase in the kernel-row-number. It is thought that maize types with a kernel-row-number of 16 or less do not carry condensation factors. Kernel-row-number will vary among plants of a given strain or variety, the range of variation depending upon the genetic purity of the type for row number. However, there is usually a predominance of a certain kernel-row-number that characterizes the type (*16*). Kernel-row-number is the first ear characteristic determined; it is determined when the spikelet-forming branch primordia are initiated in the circumference of the base of the ear shoot primordium (*6*). If several ear shoots on the same plant are examined, beginning with the topmost and proceeding downward, it will usually be found that the topmost shoot has the greater kernel-row-number (*12, 17*). The number of kernels per row is determined by the growth in the length of the ear shoot. As the ear shoot grows in length, spiklet-forming branch primordia are formed in acropetal succession beneath the apex of the shoot. The duration of the period of growth of the ear shoot in which functional spikelet primordia are produced has not been determined. In fact, little is known about the cause of variability in kernel-row-number and in the number of kernels per row even though their direct relationship to variation in seed yield can be clearly demonstrated.

Lateral shoots are produced in the axil of each leaf. Each axillary shoot is a potential branch that may develop into a negative shoot (tiller, sucker) or into an ear shoot (Figs. 7 and 10). If the tiller develops during the early stage of plant growth, it may become almost as large as the main axis and produce an ear in the same manner as the main axis, or it may produce seed mainly in the central axis of its tassel.

The value of the tillers on corn plants has been questioned for many years; they have been called suckers, owing to the early belief that they were parasitic and, hence, reduced the grain yield. However, investigations cited by Dungan (*18*) showed that plants with tillers yielded more than plants without tillers, although the difference was not significant. When all the leaves were removed from the main stem at the early milk stage of seed development, the plants with tillers were significantly superior to plants without tillers in yield of grain, test weight per bushel of the seed, weight of 100 kernels, diameter of ear, length of ear, and weight of the ear-bearing stalk. Using ears from single-plant hills, Carter and Dungan (*19*) compared ears from plants with tillers and ears from plants without tillers and found that the plants with tillers yielded 14.5 percent more grain. Based on 5 yr work, Kiesselbach (*11*) showed that the main stalk of tillered plants yields only 2 percent more grain than plants without tillers, but, if the grain yield of the tiller is included, the total yield of grain per plant is 42 percent greater. Hybrid corn breeders have tended to select for the nontillering habit for several reasons, one of which is that maize that does not tiller is easier to harvest. However, the question of whether

Fig. 10. A maize plant with leaves and a maize plant with leaves removed to show the development of the basal axillary shoots, which at this stage of development are called tillers or suckers. [Photo by H. R. Lathrop, Ext. Agron., Purdue University.]

or not the capacity to tiller is a desirable characteristic has not been clearly answered.

A maize variety may produce one, two, or more ears per plant. Under favorable growing conditions, the ear of the single-eared type is usually larger than each of the individual ears of the multiple-eared type, but the total yield of a plant of a multiple-eared type may be greater than that of the single-eared type. The Illinois two-eared strain of maize was grown in two yield tests at the Illinois Agricultural Experiment Station. One test was conducted during a period of 18 yr by the plant-breeding division, and the other test was conducted during a period of 13 yr by the crop-production division. The 18-yr average was 58.1 bu/acre for the two-eared strain and 55.5 bu/acre for Reid Yellow Dent (essentially a one-eared strain), a difference of 2.60 bu/acre in favor of the two-eared strain. In the 13-yr test, the two-eared strain yielded 75.8 bu/acre and Reid Yellow Dent yielded 71.2 bu/acre, a difference of 4.6 bu/acre in favor of the two-eared strain. In the latter test, the maximum yield of the two-eared strain was 102.3 bu/acre and that of Reid Yellow Dent was 85.0 bu/acre, both occurring the same year, 1923. The significance of these differences has not been determined. It can also be shown that certain multiple-eared types of maize will outyield certain single-eared types when environmental conditions are limiting. However, in spite of some evidence that multiple-eared types yield more than single-eared types, published evidence was not found which would show that if two types of maize were genetically alike, except for the number of ears per plant, the multiple-eared type would always yield more than the single-eared type.

The Maize Kernel

A maize kernel is a fruit composed of the fruit coat and the seed. The fruit coat, called the pericarp, consists of several cell layers. The seed consists of three major parts—seed coat, endosperm, and embryo—each of which can be further subdivided (*20*). Approximately 82 percent by weight of a kernel of dent corn is endosperm, 11 percent is germ, and 7 percent is pericarp, seed coats, and tipcap.

The major chemical components of the maize kernel are carbohydrates, protein, oil, and ash. A medium-protein corn contains about 83 percent carbohydrate, 10 to 11 percent protein, and 4.3 percent oil. Although all parts of the seed contain carbohydrates, protein, and fat, the endosperm may be characterized as high in carbohydrate (starch), medium in protein, and low in oil. On the other hand, the germ is high in oil, high in carbohydrate, and low in protein (*21*).

The percentage of protein or oil can be increased or decreased by selection. This has been demonstrated by 50 generations of selection in the Illinois chemical strains of maize. Selection was begun in 1896 in an open-pollinated variety, Burr White. The original variety had an average oil content of 4.70 percent and an average protein content of 10.92 percent. After 50 generations of selection, the average oil content of the Illinois high-oil strain was 15.36 percent and that of the Illinois low-oil strain was 1.01 percent; and the average protein content of the Illinois high-protein strain was 19.45 percent and that of the Illinois low-protein strain was 4.91 percent. Progress is still being made in selection in the high-oil and high-protein strains; however, little progress appears to have been made for the last 15 to 20 generations of selection in the low-oil and low-protein strains. Recovered lines from backcrosses of the high-chemical strains to standard inbred lines have been used in hybrid combinations. Hybrids have been produced that yield well and produce more oil or protein per acre than the standard commercial hybrids with which they were compared (*22*).

Maize, a Superior Seed Producer

In its range of adaptation, maize as a seed producer is superior to other cereals grown under the same conditions. There are three major factors that contribute to its superiority in seed production: (i) the maize plant is large, (ii) branching is suppressed, and (iii) seed production is confined to a lateral pistillate branch. Weatherwax (*7*) was of the opinion that the superiority of maize as a seed producer lay in the suppression of all but a few branches and in an exceptionally large seed.

The maize plant is much larger than the plant of any other cereal grain, except certain varieties of non-dwarf grain sorghums. At tasseling, a plant of a good hybrid will have from 16 to 18 functional leaves (Fig. 1). Based on an average of 18 F_1 hybrids, Sprague and Curtis (*23*) found that a maize plant could have a leaf surface of 5.7 ft^2. On this basis, an acre of maize at a population of 14,000 plants per acre would have 1.85 acres of leaf surface. Kiesselbach (*11*) estimated that the leaf surface per acre of corn amounted to 1.64 acres. Based on the average of five grain sorghum varieties grown for 5 yr, Swanson (*24*) found that the leaf surface per acre of grain sorghums ranged from 0.55 to 2.6 acres. No data were found on the extent of the leaf surface in an acre of wheat or oats grown in the United States. From data given by Watson (*25*) on the leaf surface of wheat varieties grown in England, it was calculated that an acre of wheat could have from 1 to 1.2 acres of leaf surface. All estimates of leaf surface are based on one side of the leaf. From the few data available, it does not appear that the leaf surface per acre is the important factor in the superiority of maize as a seed producer.

In maize an extensive, well-organized vascular system is found, both in the large solid stem and in the lateral shoot and ear. The maize plant also has a large and extensive root system. It has been reported by Martin and Hershey (*26*) that the diameter of the main stem is highly and positively correlated with the number of vascular bundles in the stem and with the number and size of the uppermost whorl of soil roots. Concomitant with the over-all size of the maize plant is the corresponding size of the separate parts, all of which contribute to the development of a large amount of seed per plant and a high seed yield per acre.

It has already been pointed out that branch development in maize is suppressed to the point where only one or more lateral branches develop (Figs. 1 and 7). Plant breeders have contributed by selecting nonbranching types. The vegetative development of the lateral ear-bearing branch is also suppressed to the point where there is little or no internode elongation, and leaf development is restricted to the development of the leaf sheath (husks) without a blade, or only a very small one. The ear-producing branches are pistillate, only seed being produced. This combination of characteristics aids in the concentration of the growth potentials of the plant into seed production.

The position of the ear shoot or shoots on the plant may also be an important factor in the high seed yield of the maize plant. The topmost ear shoot is placed so that there are six to seven morphologically younger leaves above it. Below the topmost ear shoot there may be ten or more morphologically older leaves. Thus there is a large photosynthetic area both above and below the ear, so that materials essential for growth can move downward and upward. Other cereal grains develop their seed in terminal inflorescences with all the leaves below them. The importance of the leaves above the ear shoot is shown by some data obtained by Dungan and Woodworth (*27*). They found that the removal of the topmost one to four leaves with the tassel, when hand tasseling was done, reduced the seed yield. The reduction in yield below that of plants with tassels was 8.3, 15.3, 18.0, and 29.0 bu/acre for the removal of the first, second, third, and fourth leaves, respectively.

All the factors that contribute to the superiority of maize as a seed producer have not been mentioned. It seems that the plant characteristics that are discussed here make an important contribution to the superiority of maize as a seed producer. However, few or no data are available that bear directly on the question. Although much has been learned regarding the maize plant, much is yet to be learned regarding the correlation between morphological and physiological characteristics of maize in the production of seed.

Summary

1) The development of the maize plant, from germination to the maturation of the seed, is divided into the vegetative, transitional, reproductive, and seed stages. The ear and tassel differentiate and develop in the reproductive stage.

2) The mature tassel is a terminal, staminate inflorescence consisting of a symmetrical, many-rowed central axis and asymmetrical, two-ranked lateral branches. Paired spikelets, one terminal (pedicellate) and the other lateral (sessile), each containing two functional staminate flowers, are borne on the central axis and the lateral branches.

3) In contrast with the tassel, the ear is a pistillate inflorescence produced on a lateral branch. The ear consists of a symmetrical, many-rowed axis on which are paired spikelets, each containing two flowers. In the mature ear, it is difficult to distinguish the pedicellate from the sessile spikelet. There are two pistillate flowers in each spikelet of the ear, but only the terminal flower is functional, while the lateral flower aborts.

4) The mature ear and tassel appear to be different kinds of inflorescences, but if they are examined at the earliest stages in their development they will be found to be basically alike. The differences in the appearance of the two inflorescences at maturity are the result of differences in the differentiating and development of their parts.

5) Each of the morphological characteristics found in the maize inflorescences, except one, is present in other grasses, but the collection of morphological characteristics found in the ear and tassel is unique. One morphological characteristic not found in other grasses but found in the maize ear is the presence of a terminal, fertile, and aborted, lateral flower in each of the paired spikelets.

6) Axillary shoots are produced in acropetal succession in the axil of each leaf. Some of the axillary shoots that are produced at the beginning of the development of the plant may develop as tillers (suckers). The last-produced axillary shoot (or shoots) that is far enough advanced in its development at the initiation of the tassel develops into the ear (or ears).

7) The amount of seed produced per ear is determined by the number of rows of kernels and the number of kernels per row. The number of rows of kernels is determined at the beginning of the initiation of the ear, but the number of kernels per row may vary with the strain and with changes in the environment. Under comparable condition, seed produced per ear is less in plants without tillers than in plants with tillers. The average seed yield per ear is less in multiple-eared types than single-eared types growing under similar conditions.

8) The three major parts of the maize kernel are endosperm, 82 percent; germ, 11 percent; pericarp, seed coats, and tip cap, 7 percent. The composition of the maize kernel is 83 percent carbohydrate, 10 to 11 precent protein, and 4.3 percent oil. Fifty generations of selection for high- and low-protein strains and high- and low-oil strains produced marked changes in the chemical composition of the maize kernel. Beginning with 4.7 percent oil, after 50 generations of selection, the high-oil strain has 15.36 percent and the low-oil strain has 1.01 percent of oil. The protein content was 10.92 percent at the beginning of the selection and reached 19.45 percent in the high-protein strain and 4.91 percent in the low-protein strain after 50 generations of selection. Recovered inbred lines from backcrosses to the high strains have resulted in good-yielding hybrids that produce more protein or oil per acre than standard hybrids.

9) Several factors contribute to the superiority of maize over other cereals as a seed producer. The maize plant is large and, concomitant with its size, it has

a large leaf surface, large stem, large root system, and an extensive vascular system. Branching is restricted to a few lateral, pistillate branches in which vegetative development is suppressed. The lateral ear-producing branch (or branches) is so placed on the plant that there are many leaves above and below it. The ear is large in diameter and has seeds that are many times larger than those of other cereals. All the afore-mentioned characteristics, many of which are not present in other grasses, contribute to making the maize plant a superior seed producer.

References and Notes

1. A. Arber, *The Gramineae: A Study of Cereal, Bamboo, and Grass* (Cambridge Univ. Press, New York, 1934).
2. P. C. Mangelsdorf and R. G. Reeves, *The Origin of Indian Corn and Its Relatives.* Texas Agr. Expt. Sta. Bull. 574 (1939).
3. P. C. Mangelsdorf, *The Origin and Nature of the Maize Ear.* Botan. Museum Leafl., Harvard Univ., 12 (1945).
4. Presented in the symposium "Species that feed mankind," AAAS meeting, Boston, 27 Dec. 1953.
5. E. Anderson, *Ann. Missouri Botan. Garden* **31**, 325 (1944).
6. O. T. Bonnett, *Developmental Morphology of the Vegetative and Floral Shoots of Maize.* Illinois Agr. Expt. Sta. Bull. 568 (1953).
7. P. Weatherwax, *Am. Midland Naturalist* **16** (1935).
8. O. T. Bonnett, *J. Agr. Research* **60**, 25 (1940).
9. ———, *Ann. Missouri Botan. Garden* **35**, 269 (1948).
10. B. Koehler, G. H. Dungan, and W. L. Burlison, *J. Am. Soc. Agron.* **26**, 262 (1934).
11. T. A. Kiesselbach, *Progressive Development and Seasonal Variations of the Corn Crop.* Nebraska Agr. Expt. Sta. Research Bull. 166 (1950).
12. W. H. Freeman, *The Relation of Size, Shape and Position of the Maize Ear at Early Stages of Development to Kernel-Row-Nnumber.* Master's thesis, Univ. of Illinois (1940).
13. J. C. Lyons, *The Influence of Uppermost Axillary Shoots and Plant Growth Substances on the Development of the Lower Axillary Shoots of Dent Corn.* Ph.D. thesis, Univ. of Illinois (1952).
14. Louie H. Smith, *The Effect of Selection Upon Certain Physical Characteristics in the Corn Plant.* Illinois Agr. Expt. Sta. Bull. 132 (1909).
15. E. Anderson and W. L. Brown, *Ann. Missouri Botan. Garden* **35**, 323 (1948).
16. R. A. Emerson and H. H. Smith, *Inheritance of Number of Kernel Rows in Maize.* Cornell Univ. Agr. Expt. Sta. Mem. 296 (1950).
17. D. E. Alexander, *Agron. J.* **44**, 430 (1952).
18. G. H. Dungan, *J. Am. Soc. Agron,* **23**, 662 (1931).
19. D. O. Carter and G. H. Dungan, *Trans. Illinois State Acad. Sci.* **25**, 114 (1933).
20. M. J. Wolf *et al., Cereal Chem.* **29**, 321 (1952).
21. C. G. Hopkins, L. H. Smith, and E. M. East, *The Structure of the Corn Kernel and the Composition of Its Different Parts.* Illinois Agr. Expt. Sta. Bull. 87 (1903).
22. C. M. Woodworth, E. R. Leng, and R. W. Jugenheimer, *Agron. J.* **44**, 60 (1952).
23. H. B. Sprague and N. Curtis, *J. Am. Soc. Agron.* **25**, 709 (1933).
24. A. F. Swanson, *J. Am. Soc. Agron.* **33**, 908 (1941).
25. D. J. Watson, *Ann. Botany (London)* **11**, 41 (1947).
26. J. N. Martin and A. L. Hershey, *Iowa State Coll. J. Sci.* **9**, 275 (1935).
27. G. H. Dungan and C. M. Woodworth, *J. Am. Soc. Agron.* **31**, 872 (1939).

A New University

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THE current issue of the *Annual Review of Physiology* has just come into my hands. In the prefatory chapter, Otto Loewi deplores the trend that science and its literature have taken. As I read, and so wholeheartedly approved, I wondered whether this trend, which seems inescapable in our modern life, need necessarily affect all living and thinking. Loewi's plea for a greater emotional appeal in science is, in reality, a groping for something of basic moral value. He says:

> A scientific worker nowadays rarely finds it possible to publish papers which have a personal touch; [he is not permitted] to discuss the origin and development of his problem, to draw conclusions of hypothetical character . . . such revelations are not found in the ordinary papers which fill the scientific journals.

Loewi then quotes a remark made by one of his students:

> For me the most exciting papers are those which describe exactly what the individual scientist experienced from the beginning to the end of his experiments, the mistakes he made and how he learned through them what the answers were.

One of my own former students, now a research worker in his own right, came to me the other day and, as he handed me a manuscript, said: "What shall I do? This is a good article, the best I've written. The editor accepted it provided that I omit all discussion and my conclusion. That leaves only the data!" "That is all the editor and his critics want," I said. "Send it to Europe." He did and it was accepted in full. These two students have struck at the very roots of our university and of our social life as well.

I had a chapter on adsorption. The critic objected to irrelevant facts: "Cut the history and the ancient guessing, and tell the student what adsorption *is,* then stop." Do we know what adsorption is? That master of adsorption chemistry, Herbert Freundlich, thought otherwise. He taught that the adsorption bond can be anything from primary valence to the loose attraction between gases and metals. The critic also objected to my insistence that adsorption is often nonstoichiometric. "A discarded view," he said. For me, the nonstoichiometric proportion between adsorbent and adsorbate is the very essence of adsorption and of colloid science in general. I turned to the writings of America's foremost authority on adsorption and found such statements as