A morphological study of the structure and development of the stem and ears of Zea mays L.

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UMI®
A MORPHOLOGICAL STUDY OF THE STRUCTURE AND DEVELOPMENT
OF THE STEM AND EARS OF *ZEA MAYS* L.

By

Arthur Leroy Hershey

A Thesis Submitted to the Graduate Faculty
for the Degree of
DOCTOR OF PHILOSOPHY
Major Subject - Plant Morphology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of the Graduate College

Iowa State College
1934
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INTRODUCTION

These investigations deal with the ontogeny of the corn plant with special emphasis upon the structural development of the stem and axillary buds. The investigations had two main objectives under consideration: first, to determine the origin, sequence in development, and histological features of the various stem structures; second, to ascertain the sequence in the origin and the ultimate development of the axillary buds at the different nodes.

Information in regard to the above structural features of Zea mays should be of value in the investigations of pathological and physiological problems of the plant. The work of Platz (15), Kyle (11) and others suggests that a knowledge of the ontogeny and morphological development of the host is essential to an understanding of the relationships existing between the plant and the ability of the smut organism to enter the tissues of the host. Investigations of Harrison and King (9) on the effect of toxic salts on corn seedlings show that physiologically there are also definite, critical stages in the development of the maize plant.

Information concerning the ontogeny and structural development of the vegetative and reproductive organs of Zea mays should be of value to investigators endeavoring to increase the
-4-

efficiency of the plant. A knowledge of the various kinds of
tissues as to time of formation, sequence of development, and
functional relationships is pertinent to an understanding of
the internal factors which are important in determining the
growth and productivity of the plant.
REVIEW OF PERTINENT LITERATURE

Development of the Stem

The germination of maize and organization of the vascular system of seedlings have been followed by Avery (3). He considered the scutellum to be the cotyledon while the coleoptile is homologous with a foliage leaf, and is the second leaf of the plant. He did not accept the term "mesocotyl" as used by Sargent and Arber (17), but considered the elongated structure between the cotyledon and coleoptile to be the first internode of the axis. The root-to-stem transition, according to Avery, occurs mostly in the first internode and may even continue into the third and fourth internodes. The scutellum is also interpreted as a cotyledon by Weatherwax (25,26). He considered the coleoptile a foliage leaf which occupies morphologically a terminal position during the development of the embryonic axis, while the cotyledon originates as a lateral organ.

In a study of the formation of the staminate inflorescence, Longnecker (12) found that very little elongation of the stem occurs previous to the fortieth day after planting. He described this early period of growth as being characterized by the differentiation of leaves, tassel, and axillary buds. Eldredge (7) found that the growing point of the stem of corn does not extend
above the ground level before the plants are approximately two feet high and have eight or nine leaves exposed (mean date June 22), but the increase in length of the stem was very rapid during the following twenty days.

Strasburger (18,19), who was the first to study the vascular system of corn in detail, gave a very detailed account of the origin and formation of the closed vascular bundles of maize. He showed that the cells in the central region of the young bundles have the characteristics of a typical cambium tissue which later differentiates to form the parenchyma layer of radially arranged cells separating the xylem and phloem. He found the cambium more prominent in bundles just above the node than farther up in the internode. Anderson (1) also called attention to the radial arrangement of the cells between the xylem and phloem in mature vascular bundles of Zea mays. Chrysler (4) found that the most of the bundles in an aerial node of Zea are collateral, but the amphivasal type is present at the point of origin of axillary buds and are very numerous and large in the nodes of the axillary branches bearing pistillate inflorescences. He considered the amphivasal type of bundle as being formed by the fusion of collateral bundles and indicating that Zea mays is a highly organized member of the Gramineae.

By placing the cut ends of corn stems in methylene blue, Evans (8) was able to follow the course and branching of the vascular bundles in the nodes and internodes. He decided that
the complex vascular arrangement in the node is a result of divisions, subdivisions, and anatomosing of small bundles which originate from the large vascular bundles passing through the node. He found that most of the large vascular bundles give off small branches as they enter the node. According to Evans, a bundle seldom passes through more than two or three nodes without branching.

Development of Axillary Buds

Aside from the buds which form the mature ears of the plant, no attention has been given to the origin and ultimate development of the lateral buds of maize. Longnecker (12) mentioned incidentally that the axillary buds appear about the twentieth day after planting and are generally noticeable in the axils of the leaf primordia by the twenty-third day. Weatherwax (24) called these buds "potential" branches which may develop into ear-bearing shoots if the plant is subjected to proper physiological conditions. However, he reported no experiments to prove that such results are actually attainable. Osborn (14) described the small axillary buds as microscopic growing points which gradually differentiate the husks and pistillate primordia acropetally.

Weatherwax (23, 26) and Miller (13) have studied the differentiation and development of the pistillate spikelet and found that the order of differentiation of the parts of the spikelet
are as follows: lower empty glume, upper empty glume, lemmas, rudiments of sterile flower, stamens, palet, and ovary wall of fertile flower, and rudimentary stamens and palet of sterile flower. Weatherwax (23) made a comparative study of the staminate and pistillate inflorescences and found that the two inflorescences are morphologically homologous structures, but that differences which appear at maturity are due to suppression of different essential organs in the flowers. His investigations show that the pistils of staminate flowers and stamens of pistillate flowers are aborted, but that the stamens of the pistillate flowers often develop microspore mother-cells before degeneration of the stamens occurred.
MATERIALS AND METHODS

Planting and Cultivation

This problem was conducted during the years of 1929 to 1932 for the purpose of determining the development of the stem and ears of Zea mays under field conditions. Average maturing, open pollinated strains of Reid’s Yellow Dent corn including Osterland, McCullock, and Steen varieties, were selected for study. The corn was planted between May 13 and May 21 of the various years. The seeds were planted in plots eighty hills long and twelve hills wide at the Botany experimental farm near Ames.

The kernels were planted by hand, four or five in a hill, and when the seedlings were two weeks old they were thinned to three in a hill. The rows and hills were forty inches apart. The corn was given three to four cultivations during the season and kept comparatively free from weeds.

Collecting and Recording Data

In order to secure plants grown under comparable environmental conditions of shade and moisture, the plants for study were selected from inside rows of the plots and always from hills containing three plants. Growth measurements of 20 plants were
made every five or seven days. These measurements and observations included length of stem, height to the tip of the highest cut-stretched leaf, number of leaves unrolled or appearing, length of internodes, diameter of lower internodes, number and size of axillary buds, whorls of roots, and number of vascular bundles formed. Age of plants was reckoned from the date of planting.

During the first fifty days it was necessary to cut the plants longitudinally in order to measure the length of the stem. This permitted the recording of stem length from the time of germination to maturity. The diameters of the lower internodes were measured by means of calipers and recorded in millimeters. These measurements were made of plants which had the leaf sheaths removed. Length of internodes was recorded in inches.

The number of vascular bundles in the first two internodes above the ground level was determined by counting the number of bundles in cross-sections taken from the middle of the internodes. A projection microscope was used in making the counts after the first thirty days. Permanent slides were made and used for the earlier stages. All of the coefficients and correlations were calculated according to methods suggested by Wallace and Snedecor (21).

**Histological Methods**

During the first forty days of growth it was necessary to
-11-
preserve the entire stem in order to study the various stages of its development. The plants were collected every five or seven days and the leafy tops removed above the growing point of the stem. The two sides of the short stem were cut away parallel with the axillary buds, in order to permit more rapid penetration of killing fluids and reagents. The sections were placed immediately in an acetic-formalin-alcohol killing fluid, the air exhausted under pressure, and allowed to remain in the fluid for twenty-four hours. The standard procedure for paraffin method was then followed.

After the forty-eighth day the axillary buds were removed from the stem, placed in an acetic-formalin-alcohol killing fluid, cleared and embedded in paraffin. The axillary buds from each of the various nodes were embedded separately. This provided material for a chronological study of the average development of the buds at each node.

Longitudinal and transverse sections were made with the microtome. The young stems were sectioned 15 to 18 microns in thickness, and the axillary buds were cut 12 to 15 microns in thickness. The majority of the sections were stained in Meyer's haemalum and safranin; others were stained with safranin and counter-stained with fast green dissolved in 95 per cent alcohol.

Detailed drawings of vascular bundles were made with the aid of a camera lucida. Outline drawings of indicated magnification were made by use of a small Leitz micro-optican.
The mature kernel of corn is composed of the embryo, endosperm, and pericarp. The embryo consists of the scutellum, plumule, epicotyl, and radicle. The plumule consists of a small growing point surrounded by six or seven embryonic leaves and the coleoptile. (Fig. 7).

During germination the radicle is the first to force its way through the pericarp. The emergence of the radicle is soon followed by the emergence of the coleoptile which encloses the apical meristem and young leaves. The coleoptile is pushed upward by the elongation of the first internode (3) or mesocotyl (7), until the coleoptile node is within one or two inches of the surface of the soil. The young leaves elongate and usually make their appearance through the tip of the coleoptile five or ten days after planting. In the meantime a whorl of roots appears at the coleoptile node. About twenty days after planting a second whorl of roots is usually recognizable at the next node above the coleoptile node. (Fig. 9).
tures below the coleoptile generally begin to degenerate and soon become non-functional. Consequently the subsequent development of the plant is confined to the coleoptile node and plun- ular structures.

The first two leaves above the coleoptile node remain relatively small as compared with the later leaves, and usually die and disappear before the plants are sixty days of age. In the varieties under observation the primordia of fourteen to sixteen leaves were commonly differentiated from the apical meristem before the plants were thirty days of age. (Fig. 11).

The first primordia of axillary buds appeared in the axils of the basal leaves about twenty days after date of planting (Fig. 10) and all the axillary buds were usually differentiated by the time the plants were thirty days of age. About thirty days after planting the apical meristem was transformed into the primordium of the tassel. This change was apparently accompanied by a checking of the further formation of axillary buds. The inhibiting of the further differentiation of axillary buds occurred sufficiently early that no axillary primordia were formed in the axils of the upper leaves. In the variety studied, ten buds were usually formed before the transformation of the apical meristem into a tassel occurred, and the tenth or top bud, with one exception out of more than a hundred observations, was the bud which developed the main ear.

The tassel primordium elongated and formed a terminal fleshy
axis. Between thirty and thirty-five days after planting small lateral protuberances appeared in acropetal succession on the surface of the cylindrical axis of the tassel primordium. Usually within five days after their first appearance the lower protuberances elongated and thus formed the basal branches of the staminate inflorescence. Immediately following the formation of these lower branches, spikelets were differentiated on the central spike and basal portions of the branches of the tassel. (Fig. 14).

Prior to the fortieth day of growth the stem did not elongate very rapidly, seldom exceeding more than three to five inches in length and just emerging above ground level. The height to the tip of the upstretched leaves at forty days of age was usually over three feet.

The first forty days of growth may be regarded as the period of differentiation. During this period all the primordia of leaves, nodes, axillary buds, tassel, and the majority of the vascular bundles of the mature corn plant were differentiated (Fig. 14). Usually ten leaves were partially unfolded and five or six whorls of roots were apparent.

The period of differentiation was followed by a period in which occurred a rapid elongation of the stem and the development of the tassel and axillary buds (Figs. 13, 16). Figure 1 shows the average growth curve for the different varieties of yellow dent corn, three grown in 1929 and one grown in 1930. The graphs in figure 1 show that the stem elongated very little
Figure 1. Increase in length of stem and height of plants during 1929 and 1930.
during the first forty days after planting, but elongated very rapidly between the fortieth and seventieth day. During July (1930) the stem on the average increased in length from three inches to ninety-six inches. The differences in rapidity of growth as shown by a comparison of the graphs of 1929 and 1930 were probably due to differences in climatic conditions, 1930 being a very dry year. However, the general trend in development is similar for each year and for each variety.

About thirty days of age elongation of the stem by addition of cells from an apical meristem was discontinued and the apical meristem was transformed into the primordium of the tassel. Increase in height thereafter was due to the enlargement of cells already present and intercalary multiplication of cells of the internodes and tassel.

The tassels of thirty plants were measured at various ages in order to determine the rate of elongation of the tassel during the growing season (1929). The tassel usually attained its maximum length at about 70 days of age (time of shedding pollen) as shown in Table 1 and Fig. 2 (T).

Table 1. Increase in length of tassel.

<table>
<thead>
<tr>
<th>Days after planting</th>
<th>Length of tassel (inches)</th>
</tr>
</thead>
<tbody>
<tr>
<td>45</td>
<td>-1</td>
</tr>
<tr>
<td>52</td>
<td>3</td>
</tr>
<tr>
<td>62</td>
<td>16</td>
</tr>
<tr>
<td>72</td>
<td>22</td>
</tr>
<tr>
<td>82</td>
<td>22</td>
</tr>
</tbody>
</table>
Figure 2. Average length of tassel (T) and internodes (I-I) at various ages (1929).
A record of the increase in the length of each internode was also made of the three varieties of dent corn grown in 1929. Thirty plants were selected at various ages and the length of each internode was recorded in inches. (Table 2, Fig. 2).

Figure 2 shows that the tassel constitutes about one-fifth of the total length of the mature corn stem. The other four-fifths of the stem length are the results of the elongation of the internodes formed during the first six weeks of growth. Increase in the length of stem previous to the first fifty days of age was due to the slight elongation of the young tassel and first four internodes. According to Figure 2, during the following seven days the stem more than doubled its length by the elongation of the tassel and first eight internodes. Figure 2 further shows that the elongation of the internodes from the fifth to the twelfth, inclusive, was chiefly responsible for the increase in the length of the stem between the fifty-fifth and sixth-fifth day of the plant's growth. The remaining increase in height following the sixty-fifth day of age was chiefly due to the elongation of the five upper internodes.

The first three internodes attained their maximum length in about fifty-five days. The internodes from the fourth to the ninth, inclusive, reached their maximum length at the time the plants were about sixty-five days of age. The remaining internodes attained their maximum length usually by the time the plants were 80 days of age. Figure 2 shows that the rapid elongation of the stem was due primarily to the intercalary
Table 2. Length of internodes at various ages.

<table>
<thead>
<tr>
<th>Days after planting</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>0.7</td>
<td>1.2</td>
<td>0.6</td>
<td>0.4</td>
<td>0.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>48</td>
<td>1.0</td>
<td>2.2</td>
<td>3.0</td>
<td>2.6</td>
<td>1.2</td>
<td>0.5</td>
<td>0.4</td>
<td>0.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>55</td>
<td>1.3</td>
<td>2.6</td>
<td>3.3</td>
<td>4.4</td>
<td>5.6</td>
<td>5.5</td>
<td>3.8</td>
<td>1.9</td>
<td>0.9</td>
<td>0.6</td>
<td>0.4</td>
<td>0.3</td>
<td>0.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>65</td>
<td>1.4</td>
<td>2.7</td>
<td>4.0</td>
<td>5.2</td>
<td>6.0</td>
<td>6.6</td>
<td>7.0</td>
<td>5.7</td>
<td>5.0</td>
<td>4.6</td>
<td>3.5</td>
<td>2.7</td>
<td>2.2</td>
<td>1.0</td>
<td>-</td>
</tr>
<tr>
<td>70</td>
<td>1.4</td>
<td>2.7</td>
<td>4.1</td>
<td>5.2</td>
<td>6.0</td>
<td>6.7</td>
<td>7.0</td>
<td>6.9</td>
<td>6.5</td>
<td>5.2</td>
<td>5.7</td>
<td>5.5</td>
<td>5.0</td>
<td>3.6</td>
<td>4.3</td>
</tr>
<tr>
<td>80</td>
<td>1.4</td>
<td>2.7</td>
<td>4.1</td>
<td>5.2</td>
<td>6.0</td>
<td>6.7</td>
<td>7.1</td>
<td>7.2</td>
<td>6.8</td>
<td>6.5</td>
<td>6.5</td>
<td>6.5</td>
<td>5.9</td>
<td>6.1</td>
<td>5.6</td>
</tr>
<tr>
<td>120</td>
<td>1.4</td>
<td>2.6</td>
<td>4.1</td>
<td>5.2</td>
<td>6.0</td>
<td>6.7</td>
<td>7.1</td>
<td>7.2</td>
<td>6.8</td>
<td>6.5</td>
<td>6.5</td>
<td>6.5</td>
<td>6.2</td>
<td>6.2</td>
<td>6.0</td>
</tr>
</tbody>
</table>

(maturity)
multiplication and enlargement of cells in the internodes.

An intercalary meristem of five to seven layers of more or less isodiometric cells lies directly above each node. The parenchyma cells in the internodes are regularly arranged in rows which are parallel to the longitudinal axis of the internode and which may be traced back to the individual cells in the meristem from which they originated. The small, thin-walled parenchyma cells in unelongated internodes were much broader than long. During the period previous to the elongation of the stem, which was generally confined to the first forty days of the plant's growth, a multinucleate condition of the parenchyma cells, ranging from two to four nuclei per cell, was observed to be quite general in young stems. Mitotic figures were also observed in numerous parenchyma cells. Cell division, polynuclear parenchymatous cells, and cell enlargement are features connected with the increase in diameter of the internodes.

In order to determine the relationship between the elongation of the internodes and size of their diameters, a study was made of the rate in increase of the two internodes above the soil roots. These lower internodes were chosen because the supply of water and minerals of the plant depends upon the conductive capacity of the lower internodes through which all absorbed materials must pass.

The diameters of an internode were taken through two different planes; one passing through the grooved side of the inter-
node and one at right angles to the first. Correlation coefficient between these two diameters equalled 0.98 and indicates that the two diameters tend to be equal to each other.

Table 3. Increase in larger diameter of the two lower internodes.

<table>
<thead>
<tr>
<th>Internode</th>
<th>Days after planting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>48</td>
</tr>
<tr>
<td>First internode</td>
<td></td>
</tr>
<tr>
<td>Second internode</td>
<td>20 mm.</td>
</tr>
<tr>
<td></td>
<td>21 &quot;</td>
</tr>
</tbody>
</table>

Table 3 shows that the first and second internodes tend to reach their ultimate diameters about fifty-five and sixty-five days, respectively, after planting, thus attaining their maximum diameter nearly simultaneously with their maximum length as is shown by a comparison of tables 2 and 3. These observations are not in accord with Weatherwax (26) who states that "the elongation of the internode continues long after the ultimate diameter has been reached."

The internodes are able to increase their diameters over a period of time due to the activity of a peripheral meristematic layer in each internode (Fig. 3). This layer produces new cells which form vascular primordia or parenchymatous tissue. The presence of the peripheral meristem also accounts for the fact that there is a gradual gradation in the development of the vascular bundles from the central region of the internode where the bundles are most mature, to the peripheral region where the vascular primordia may be in the very early stages of differen-
Other rows of leaf traces are differentiated from a peripheral middle row of leaf traces of a leaf from the stem tissue.

- Overlapping leaf traces and forming the midrib of the leaf. In
- Retain penetration more deeply into the stem tissue or simply the
- Number, which is increased with smaller traces. The time of separa-
- Similarly, the leaf developed leaf traces, traces of more in
- Separation occurs. The time of development starts in beneath
- Age forms two epidermal-like layers between which the time of
- The leaf from the stem, the cells along the time of the
- Age as shown in Figure 2.* Each produces to the separation of
- Are separated from the main axis of the stem by tertarcal cleavage.

The leaves are first recognizable as bands of cells which

* is transdifferentiation into a leaflet parenchim. A

data as previously mentioned, the meristem area of the stem

Figure 2 in the very distal to the upper

A new formation, the remaining leaf primordia, may be recognized.

During the first thirty days after germination

stem are in a fully developed embryo, six to nine leaf primordia

meristem area trace which soon cover the entire epicotyl.

(Fig. 3B) The primordia appear as small lateral elevations of

between ten and fifteen days after the appearance of the silk,

The first leaf primordia are differentiated in the embryo

Differentiation of leaves.
Figure 3.

A. Cross section of young corn stem near a node showing the early cleavage in the formation of the edges of a young leaf. The branching of the vascular primordia in the node are also shown.

B. Cross section of young corn stem showing further cleavage of the young leaf from the stem tissue and the peripheral circle of leaf traces which will supply the leaf. Note the peripheral meristem (dark band) internal to the line of cleavage.
meristematic region preparatory to the formation of the next new leaf.

The leaf traces lie close to the upper surface of the leaf at the point of union of the leaf base with the stem. The larger traces penetrate deeply into the interior of the stem. Commonly they run horizontally with the node some distance before turning downward into the internode (Fig. 4). The explanation of the course of the large leaf traces as proposed by Arber (2) in other Monocotyledons is applicable to maize. According to Arber's theory, and verified by these investigations, the tapering form of the young stem of maize has a conical peripheral meristem which differentiates the large leaf traces and smaller provascular strands. The traces are early differentiated near the tip of the tapering stem and conform to its curvature. As the apex grows forward and the stem increases in diameter the traces are carried from the central part of the axis and turned abruptly outward into the leaves (Fig. 4).

Differentiation of Roots,

If Avery's (3) interpretation that the structure between the scutellum and coleoptile is the first internode of the maize seedling is correct, then the permanent root system of corn is entirely of stem origin. The root primordia originate from a region ten to fifteen cells beneath the epidermis and just above the node. The primordia first appear as small groups of meri-
Figure 4.

Portion of a longitudinal section of a corn stem showing the curved course of a leaf trace.
Figure 5.

Cross section through the peripheral part of a node showing a young root primodium. The meristematic tip is covered by a pronounced calyptrogen and a small root cap.
stematic cells which immediately undergo rapid division forming
typical meristematic root tips having a large calyptrogen and
small root cap (Fig. 5). The root primordium forces its way
through the thin layer of stem tissue until it becomes exposed
to the soil or air. The roots above the surface of the ground,
known as brace roots, also originate in this manner, but usually
become larger in diameter and more woody when mature than the
subterranean roots.

The number of whorls of roots arising from a stem varies
with the variety and environmental conditions. Eisele (6) noted
that the number of plants per hill influences the number of nodes
which produce roots as well as the number of roots which develop
at the various nodes. In plots with one plant per hill he found
that there was an average of sixteen prop roots from the first
node above ground, eight from the second node, and three from
the third node. In plots with five plants per hill he found that
the first node produced only five or six roots while the nodes
above produced no roots.

In the variety used for the present investigations (1930)
seven to nine whorls of roots were usually formed. The sequence
in the formation of the roots at the different nodes, reckoned
from date of planting, was as follows:

<table>
<thead>
<tr>
<th>Whorl</th>
<th>Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>First whorl (coleoptile)</td>
<td>15</td>
</tr>
<tr>
<td>Second whorl</td>
<td>20</td>
</tr>
<tr>
<td>Third whorl</td>
<td>30</td>
</tr>
<tr>
<td>Fourth whorl</td>
<td>35</td>
</tr>
</tbody>
</table>
Fifth whorl 40 days
Sixth whorl 50 "
Seventh whorl 55 "
Eighth and ninth whorls 60 to 70 days

Origin and development of the vascular system.

The origin of vascular bundles is easily observed in the young stem previous to the differentiation of the staminate inflorescence. The apical meristem consists of thin-walled cells with dense protoplasm (Fig. 6,A). At the base of the meristem these cells differentiate into numerous provascular strands. These strands are scattered throughout the stem with no definite arrangement, but are more numerous and less differentiated near the periphery. The cells of the provascular strands are small in diameter, elongated, and have relatively long nuclei which are located near the center of the cells. (Fig. 6,B). In longitudinal sections the strands appear as striated bands (Fig. 3,4). The cells of the vascular primordia maintain their ability to divide for a limited time allowing the young bundle to increase in size (Fig. 6, D and E).

The first noticeable, differentiation of the protoxylem was on the side of the strand nearest the center of the stem and consisted of an elongation and slight increase in diameter of one or two rows of cells, and the lignification of their walls in the form of rings. These rows of cells form the first annular vessels
Figure 6. Stages in the development of a vascular bundle in the young. X 375.

A. Meristematic cells of the apical meristem.

B. Cross section of young provascular strand.

C. Cross section of provascular strand showing differentiation of the protexylum (px) and protophloem (ph).

D. Cross section of young vascular bundle showing further development of the protoxylem (px) and increase in size of vascular strand.

E. Cross section of young vascular bundle showing increase in size of provascular strand and the first formation of the pitted vessels of the protophloem (ph).

F. Cross section of a vascular bundle previous to the lignification of the bundle sheath. Note the cambium-like tissue (cam.), enlarged pitted vessels (pv), and phloem (ph).

G. Longitudinal view of cells which will contribute to formation of the bundle sheath adjacent to the phloem.

H. Longitudinal view of young sieve cells and companion cells (F, ph).

I. Longitudinal view of the cambium-like cells (F, cam.).

J. Longitudinal view of a young pitted vessel (F, pv).

K. Longitudinal view of a young annular vessel (F, px).
of the young vascular bundle (Fig. 6, C, D). Subsequent differentiation is centrifugal with reference to the center of the stem, thus resulting in an endarch protoxylem (Fig. 6, E, F).

Simultaneously with the first appearance of the protoxylem the first differentiation of the protophloem becomes noticeable on the opposite side of the vascular primordia (Fig. 6 C). The cells on the outer side of the provascular strand thicken their walls, and are recognizable through all stages of vascular development by the refractiveness of their walls and resistance to stains (Fig. 6 D, E). The tissue between the protophloem and protoxylem remains meristematic and from the cells of this central area are differentiated the metaxylem, metaphloem, and a radial, cambium-like tissue.

Following the formation to the protoxylem and protophloem the young vascular bundle increases in size for a limited period without further differentiation while the surrounding cells form large parenchyma cells. A band of cells about the young vascular bundle remains intermediate in size, elongates and later forms the lignified bundle sheath. The lignification of the sheath cells occurs about the large leaf traces in the leaf earlier than around the bundles within the stem.

Immediately following the formation of the protoxylem and protophloem and enlargement of the vascular strand, the metaxylem is formed. The first metaxylem to differentiate consists of the pitted vessels, one on each side of the vascular bundle, and a spiral or annular vessel just above the annular vessels of the
protoxylem.

Differentiation of these three rows of cells is indicated by an increase in diameter of the cells, and formation of large vacuoles in their protoplasm. This is followed in the two lateral cells by the thickening of the walls characteristic of pitted or reticulated vessels, and in the centrally located cells by thickenings in the form of spirals. Further development of the vessels consists of reabsorption of end walls and disappearance of protoplasmic contents.

Meanwhile the homogenous cells between the xylem and protoxylem show signs of differentiation. The cells between the pitted vessels and above the spiral vessels assume a definite, radial arrangement resembling a cambium (Fig. 6, F-I). Cell division may occur in this region for a limited time. These cells remain parenchymatous and constitute a permanent tissue between the phloem and xylem in the collateral bundles. The presence of this cambium-like tissue is more noticeable just above the nodes than higher up in the internodes, being most highly developed in the larger bundles and leaf traces.

Simultaneously with the appearance of the cambium-like tissue in the central part of the young vascular bundle, the companion cells and sieve tubes become differentiated throughout the phloem region and assume the pattern characteristic of the phloem in Zea mays (Fig. 6, F, H).

The cells about the xylem vessels thicken their walls and form tracheids or small reticulated vessels. The lignification
of the tracheids and the bundle sheath marks the maturity of the vascular bundle.

The above descriptions are most applicable to the large bundles which are characteristic of the central region of the stem. All bundles in a cross section of an internode do not show the same degree of differentiation. The peripheral bundles are much smaller than those more centrally located in the stem, and are more variable in their ultimate stages of development attained. In these bundles the phloem is often much reduced and limited to the area between the pitted vessels; the protoxylem elements are fewer in number, the lateral, reticulated vessels being the most prominent; and the radial arrangement of the central cells is usually absent. These peripheral bundles develop relatively thick bundle sheaths which tend to fuse with each other into a continuous peripheral band of sclerenchymatous tissue which affords support for the plant.

As a vascular bundle passes through a node it generally expands in width and has an increased number of annular vessels and tracheids. The annular vessels remain in contact through the nodal region and the lacunae is absent. The bundle may branch just before entering the node as reported by Evans (3). This is very characteristic in nodes bearing roots, but is not so noticeable at the upper nodes. These observations show that the vascular structure of the node cannot be attributed entirely to the branching of the internode bundles as they pass through the node. Cross sections taken through the nodes of young plants showed that
most of the horizontal vascular structure of the node was developed from anastomosing provascular strands formed during the first four weeks of the plant's growth.

The bundles in the subterranean portion of the stem show great variation in size, shape, and arrangement of the cells in the vascular bundles. The bundles commonly approach the amphi-vasal type but the phloem is seldom completely inclosed by the xylem. The protoxylem elements are reduced in number and the reticulated vessels on the sides of the bundle increase in number, varying from two to eight.

During 1929 a study was made of the time and rate of development of the vascular bundles in Steen, McCullock, and Osterland's yellow dent corn. The two lower internodes above ground, which attain the maximum diameter of the plant, were used in this investigation. At fifteen days of age thirty per cent of the provascular strands had differentiated protoxylem and protophloem. Bundles of this degree of development were located near the central portion of the internodes, while the peripheral strands were less developed and more numerous toward the periphery. At thirty days of age, sixty-two per cent of the bundles had differentiated phloem and xylem tissues while numerous strands in the meristematic peripheral area remained undeveloped. About ninety per cent of the total number of bundles present at maturity were formed by the fortieth day. At maturity the first internode averaged 680 vascular bundles and the second internode averaged 750 bundles per cross sectioned area.
Correlation studies were made in 1929 on 580 plants grown under field conditions. Factors taken into consideration in these studies were age, height, diameters of lower internodes, and number of vascular bundles in the first and second internodes above the surface of the soil.

Table 4. Coefficients of correlation among various characters of the maize stem and their relation to age.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Number: vascular</th>
<th>Number: vascular</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Age in days</td>
<td>.96</td>
<td>.75</td>
</tr>
<tr>
<td>B Height of stem</td>
<td></td>
<td>.77</td>
</tr>
<tr>
<td>C Large diameter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D Small diameter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E Number of vascular bundles in first internode</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The correlation coefficients show highly significant correlations between all factors studied. Age and height of plants are important in determining the size of the diameters of the stem. However, size of diameters is of greatest importance in determining the number of vascular bundles in the two lower internodes. The number of vascular bundles formed in the first internode above ground level has a decided limiting influence on the number
of vascular bundles present in the second internode. These coefficients show that the vascular system of the first internode is very important for the maximum development of the plant. Any environmental or physiological factors influencing the normal differentiation of the vascular system of the lower internodes would produce a corresponding influence on the conductive system of the entire plant. Due to the fact that the first internode reaches its ultimate size during the first fifty days of growth makes this period one of great importance for the further development of the corn plant. Decrease in size of the diameter of the first internode places a limiting factor on the development of the stem which the plant is unable to overcome after the first thirty or forty days of growth.

Plants were also grown under different environmental conditions in order to study the effects produced on the development of the vascular system. The following table shows that a very marked reduction in the development of the vascular system may be caused by various environmental factors.

Table 5. Influence of environmental factors on development of vascular system in Osterland's yellow dent corn (1929).

<table>
<thead>
<tr>
<th>Plants</th>
<th>First internode</th>
<th>Second internode</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average number</td>
<td>Average number</td>
</tr>
<tr>
<td></td>
<td>of vascular</td>
<td>per cent of</td>
</tr>
<tr>
<td></td>
<td>bundles</td>
<td>reduction</td>
</tr>
<tr>
<td>1-3</td>
<td>490</td>
<td>0</td>
</tr>
<tr>
<td>3-5</td>
<td>666</td>
<td>22</td>
</tr>
<tr>
<td>5-10</td>
<td>496</td>
<td>27</td>
</tr>
<tr>
<td>10-15</td>
<td>380</td>
<td>44</td>
</tr>
<tr>
<td>15+</td>
<td>345</td>
<td>49</td>
</tr>
<tr>
<td>1-3 (shaded)</td>
<td>348</td>
<td>49</td>
</tr>
</tbody>
</table>
Study of the Axillary Branches as to Their Sequence in
Origin and Degree of Development Attained

In the plants included in this investigation a primordium of a lateral shoot was observed in the axil of each of the ten or eleven lower leaves of the plant. The upper one of these primordia produces the main ear. Only one plant out of more than a hundred observed showed a bud above the main ear. All the primordia of the axillary shoots are recognizable forty days after planting. Their succession in formation was acropetal and occupied the period from about the twentieth to the thirtieth day after planting. The cessation of the formation of lateral branches after the plants are about 30 days of age is probably associated with the transformation of the apical meristem into the tassel primordium and rapid development of the tassel.

At about twenty-five days of age the buds at the first three or four nodes are much more advanced in development than the upper buds (Fig.10). As the plant approaches fifty days of age the eighth and ninth buds are usually more advanced in development (Fig.20). There now follows a rapid increase in the development of the tenth or top bud, which leads in development after the plant is fifty-five days of age (Fig.22).

Development of top ear.

The early development of the axillary primordium that forms
the top ear is very similar to the development of the young stem, in that it differentiates leaf primordia, nodes and internodes, axillary buds and the primordium of a terminal inflorescence (Fig. 31). The terminal primordium of the lateral shoot develops the ear, the portion below forms the shank, and the leaf primordia develop the husks. The axillary buds in the husks were observed to develop small ears in certain hybrids grown in 1929.

The first indication of the transformation of the terminal ear primordium into a pistillate inflorescence is the appearance of rows of small elevations on its lateral surface. These protuberances appeared when the plants were about fifty days of age and developed acropetally forming the primordia of the spikelets. The tip of the ear remains meristemae for an indefinite time after the silks appear beyond the tips of the husks, which usually occurred between sixty-five or seventy days from time of planting.

**Development of the spikelet.** Sequence in the development of the parts of the spikelet was found to occur as described by Weatherwax (22, 26) and Miller (13). Each of the small protuberances on the terminal pistillate primordium divides to form two lobes, each of which is a primordium of a spikelet. Each spikelet primordium develops two flowers.

The first development of the spikelet is the appearance of a small protuberance on the lower side of the primordium which forms the lower glume. The appearance of the lower glume is followed immediately by the upper glume and lemmas. The primordium
of the sterile flower is next differentiated on the side next the lower glume. The remaining meristematic portion of the spikelet forms the fertile flower. The palet of the fertile flower and rudimentary stamens are differentiated and the remaining portion of the primordium forms the pistil. The cells at the edge of the rounded tip of the pistil primordium grow rapidly forming a cup-shaped ovary wall about the central portion or ovule. The ovary wall next the lemma develops more rapidly than on the palet side. This causes the ovary wall on the lemma side to bend over the top of the ovule before coming in contact with the ovary wall adjacent to the palet. The ovary wall above the ovule increases in thickness and elongates to form the silk, composed of the style and stigma (5, 26). As the silk elongated numerous epidermal cells on its surface divided and elongated to form the hairs of the silk. Miller and Weatherwax (13, 26) found that pollen tubes gain entrance to the interior of the silk through these hairs.

Simultaneously with the development of the silk further differentiation of the ovule occurs, forming the inner integument and nucellus. Soon afterwards the outer integument arises on the surface of the inner integument. Meanwhile an arche-sporial cell is formed by a subepidermal cell of the nucellus, and the ovule begins to curve in toward the cob.

By the time the silks appear the nucellus has become large and the embryo sac is mature, having several antipodal cells, two large polar nuclei and egg apparatus. Following fertiliza-
tion the endosperm and embryo were observed to undergo rapid
development. Five days after the silks appeared the endo-
sperm had absorbed about one-half of the nucellus. The embryo
at this time consisted of an oval group of cells terminating the
slender suspensor (Fig. 33). The beginning of the disorganiza-
tion of the cells of the ovary wall also occurred at this period.
Five days later the scutellum was distinct and first formation
of the plumule was apparent (Fig. 34). Within fifteen days follow-
ing the appearance of the silks, the embryo consisted of a scute-
lum and a plumule, the latter having an apical meristem and three
or four leaf primordia (Fig. 35). The radicle, however, was not
completely differentiated until five days later. Twenty days
after the appearance of the silks the nucellus was practically
absorbed by the endosperm as described by Poindexter (16) and
the pericarp was observed to be formed in the manner described
by True (20). A hundred and twenty days after planting the
kernels were mature and the top ear usually averaged nine to
twelve inches in length.

Axillary shoots below top ear.

The axillary shoots of the nodes differed only in the de-
gree of development attained. About fifty days after planting
the emphasis in development of the axillary shoots was trans-
ferred to the tenth shoot, the one that produced the main ear.
(Fig. 22). This shoot soon attained the lead in development
while at the same time the rate of development of the axillary
shoots below was diminished. These lower shoots of different plants often showed considerable variation in the ultimate size and development attained.

In the variety studied in 1930 the ninth shoot reached its average maximum size (two to four inches in length) when the plants were about ninety days of age (Fig. 29). The spikelets were well developed and embryo sacs produced (Fig. 26), but kernels were not formed. (This same variety of corn grown in 1932 often produced small ears with few grains at the ninth node). The eighth axillary shoot attained its average maximum length of about one or two inches between seventy and eighty days from planting (Fig. 27), but its spikelets varied in development ranging from formation of the megasporangium to development of the embryo sac. The seventh shoot was smaller in size than the eighth shoot and seldom produced megasporangia (Figs. 26, 27). The shoots at the sixth and fifth nodes seldom exceeded the differentiation of the empty glumes of the basal spikelets of the ear (Fig. 26), and usually attained their maximum size when the plants were about sixty-five days of age (Fig. 27). The fourth and third buds seldom showed any development after about the sixty-fifth day (Figs. 24, 26). Their maximum development was usually attained before the spikelet primordia showed any differentiation (Fig. 26). The second and first buds usually attained their maximum size and development before the fifty-fifth day (Figs. 20-24).

Sometimes, however, one or more of these lower shoots elon-
gated into suckers (Fig. 17) bearing a terminal inflorescence of perfect flowers which often produced seed (Fig. 30), and small axillary buds at the nodes of its stem. Suckers in sweet corn have the same origin (Fig. 18).

In general the four lower buds are below or near the surface of the ground (Fig. 17) and showed signs of being reabsorbed by the plant or disintegrated by action of organisms soon after the plants were seventy to eighty days of age.
DISCUSSION

The ontogeny of the corn plant consists of three rather distinct phases. The first of these phases is confined almost entirely to the first forty days of the plant's development reckoning from the beginning of germination and has to do with the following: further development of nodes, internodes, and internal anatomy of the embryonic stem axis; the further differentiation of leaves, roots and axillary buds; and, finally, the transformation of the apical meristem into a tassel primordium.

The second phase, covering the period from about 40 to 80 days has to do with the elongation and enlargement of structures differentiated during the first forty days.

The third phase which covers the period from 70 to 80 days after the beginning of germination to the maturity of the plant is concerned with fertilization and development of the kernels.

The ultimate achievement of the corn plant depends upon the differentiation, during the first 40 days, of the structures required for the optimum development of the plant during the remaining phases of growth.

Environmental factors, such as crowding, shading, drought, which prevent the formation of the normal number of vascular bundles and leaf primordia during this period of differentiation have a stunting effect which the plant cannot later overcome.
This condition in corn is due to the inability of the plant to develop more leaves or form more vascular tissues after the period of differentiation for the tip meristem has been transformed into a tassel primordium and there is no provision for the further formation of vascular tissues.

The close association in time of the cessation in the formation of axillary primordia and the appearance of the tassel primordium raises the question as to whether or not the tassel exercises a controlling influence on the formation and development of lateral buds. The development of the lateral shoots already present when the tassel primordium appears is held in check until the tassel has nearly attained its maximum elongation. After the tassel has attained approximately its maximum length, the growth emphasis shifts to the top ear which develops rapidly and apparently at the expense of the axillary shoots below.

A feature noted in connection with the development of the axillary shoots may afford an explanation of the greater susceptibility of the corn plant to smut infection at certain periods in its development. When the plant is 12 to 20 inches high, or about twenty to twenty-four days of age (Fig. 10) the primordia of the axillary shoots are present as exposed protuberances of meristematic tissue. The leaf primordia have not developed far enough at this stage to afford protection for the meristem. At this time smut spores can come in contact with the tender tissues of the meristem and leaf primordia, as suggested by Platz (15) in his study of corn smut.
SUMMARY

The first forty days of the growth of corn was characterized by the formation of the primordia of leaves, roots, vascular bundles, axillary buds, and tassel. The stem seldom exceeded three or five inches in height at this age.

The first primordia of the axillary buds appeared about twenty days after planting, and all axillary buds were usually differentiated before the plants were thirty days of age.

About thirty days after planting the apical meristem of the stem was transformed into the primordia of the staminate inflorescence which developed spikelet primordia within the next ten days. The formation of the tassel and cessation in the differentiation of axillary buds occurred simultaneously.

The permanent root system originated entirely from the stem. Usually seven to nine whorls of roots were produced during the first sixty days of the plant's growth.

Leaves were differentiated acropetally from the apical meristem during the first thirty days after planting. Each leaf was supplied with numerous large leaf traces (twenty or more) and smaller, alternating, vascular bundles at the time the leaf was separated from the young stem.

In the varieties studied the primordia of over ninety percent of the vascular bundles in the lower internodes were differentiated at forty-five days of age. When plants are grown more
than three in a hill they had fewer bundles in the lower internodes than when grown with three or less in a hill.

Maximum length and maximum diameter of internodes were attained simultaneously. Increase in length was due to the elongation of cells produced by the intercalary meristem just above each node. Increase in diameter was due to enlargement of cells and vascular primordia formed by a peripheral meristematic layer in the stem of young plants.

The primordia of vascular bundles were differentiated in nodes and internodes. Primordia first appeared as striated provascular strands which soon differentiated protoxylem and protophloem. Annular vessels were formed centrifugally and were the first to appear in the vascular primordium. Pitted vessels were formed on the lateral sides of the vascular primordia simultaneously with the differentiation of the phloem. A distinct cambium-like tissue was commonly found in the vascular bundles just above the nodes, but it was not so prominent in the bundles in the upper region of the internodes. The differentiation of phloem elements usually occurred with the formation of the pitted vessels. The bundle sheath was the last to mature.

The vascular bundles were smaller and more numerous towards the periphery, but the conducting elements of each bundle were reduced in number and size.

Some bundles branched as they passed through the node. These branches anastomosed with the bundles of the node, forming
a complex vascular region at each node. Annular vessels were persistent in bundles passing through the node.

Each of the lower nodes below the top ear bore an axillary bud. The development of these lateral buds was very similar to the development of the stem. The similarity of the morphological development of the staminate and pistillate inflorescences indicate that these structures are morphologically homologous, while differences at maturity are due to suppression of different essential organs of the flowers.

The primordium of an axillary shoot carries the potentials for the development of a shank bearing husks, axillary buds, and a terminal pistillate inflorescence. About fifty days from date of planting the upper ear attained the lead in the development of the axillary shoots and apparently decreased the rate of development of the lower axillary shoot.

The upper shoot which produces the main ear attains complete development with the maturity of the plant. The ninth shoot may also produce seed, under favorable conditions. The ninth shoot did not produce grain during the summer of 1930 and reached its maximum development when the plants were ninety days of age. The eighth and seventh shoots attained their maximum development by the eightieth day; the spikelets often formed embryo sacs but did not develop grain. The axillary shoots of the sixth and fifth nodes seldom exceeded the differentiation of the glumes of the basal spikelets. The four basal shoots of
the plant attained their maximum size before the fifty-fifth day and were usually reabsorbed or disintegrated before the plants reached maturity. Suckers were commonly produced by these basal shoots near the ground.

The embryo is differentiated soon after fertilization and its parts were developed twenty days after the silks appeared. The parts of the embryo appeared in the following order: scutellum, coleoptile, apical meristem, leaf primordia, and radicle.
ACKNOWLEDGMENT

The writer is especially indebted to Dr. J.N. Martin for his advice in directing this investigation and assistance in preparation of the thesis.
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Figure 7. Longitudinal section of the plumule of an embryo removed from the seed before germination.
Figure 8. Longitudinal section of a corn seedling 17 days after planting. Note the differentiation of leaf primordia from the apical meristem.
Figure 9. Corn plants twenty-four days after planting. The third whorl of roots is just appearing.
Figure 10. Longitudinal section of a young corn seedling 24 days after planting. Note variation in development of the axillary buds from base to apex of young stem.
Figure 11. Longitudinal section of a corn seedling 31 days after planting. The apical meristem has been transformed into the tassel primordium.
Figure 12. Longitudinal section of a corn seedling 34 days after planting. Note the elongation and development of the tassel primordium.
Figure 13. Corn plants 36 days after planting. The dark band indicates the soil surface. The plant to right has the basal portion of plant removed to show length of the young stem.
Figure 14. Longitudinal sections of corn seedlings 37 days after planting. Note differentiation of axillary buds and nodes and elongation of the tassel.
Figure 15. Corn plants 42 days after planting. The stem is just extending above the soil surface.
Figure 16. Corn plants 48 days after planting. Note increase in length of the stem as shown by the plant to the right.
Figure 17. The stem of a corn plant 48 days after planting. The stem is about 15 inches in length. Note the first axillary bud on left covered by the roots. The third axillary shoot is elongating to form a sucker.
Figure 18. Sweet corn plants 45 days after planting showing the origin of suckers from the basal shoots.
Figure 19. Axillary shoots removed from corn plants 52 days after planting.
Figure 20. Drawings of the axillary buds removed from corn plants 52 days after planting. The eighth and ninth shoots show the greatest degree of development. The shoots are numbered in order from base of stem to top ear.
Figure 21. Tassel and axillary shoots removed from corn plants 57 days after planting.
Figure 22. Drawings of the axillary shoots removed from corn plants 57 days after planting. Note the advancement in development of the tenth or top ear.
Figure 23. Axillary shoots removed from corn plants 61 days after planting.
Figure 24. Drawings of axillary shoots removed from corn plants 61 days after planting.
Figure 25. Axillary shoots removed from corn plants 66 days after planting. Small ears are removed to show relative sizes.
Figure 26. Drawings of axillary shoots removed from corn plants 56 days after planting.
Figure 27. Axillary shoots removed from a corn plant 70 days after planting. First appearance of the silks.
Figure 29. Axillary shoots removed from corn plants 90 days after planting, showing maximum development of the upper shoots.
Figure 30. Terminal inflorescences produced on suckers growing from the basal shoots of yellow dent corn.
Figure 31. Longitudinal section of an axillary shoot showing leaf primordia, axillary buds, and ear primordium.
Figure 32. Spikelet showing the large fertile flower (A) and small infertile flower (B).
Figures 33-36. Longitudinal sections of maturing ovules showing the development of the embryo.

Figure 33. Five days after appearance of silks.
Figure 34. Ten days after appearance of silks.
Figure 35. Fifteen days after appearance of silks.
Figure 36. Twenty days after appearance of silks.