A DROUGHT-RESISTING ADAPTATION IN SEEDLINGS OF HOPI MAIZE

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INTRODUCTION

A study of the maize grown by the Hopi, Zuni, and Navajo Indians of New Mexico and Arizona has brought to light an adaptive character that promises to be of economic importance in dry regions where germination is uncertain.

These southwestern Indians have preserved from pre-Columbian times a type of maize able to produce fair crops in regions where the better known varieties of the East fail for lack of sufficient water. An important factor in the drought resistance of this type of corn is its ability to force the growing shoot of the seedling to the surface of the soil when planted at a depth of a foot or more. At such depths less specialized varieties die before reaching the surface.

The literature of corn contains reports of many experiments conducted to determine the proper depth of planting, but the results are confusing and contradictory. It has generally been realized that the optimum depth is influenced by differences in soil and climate, but that the proper depth might vary with different varieties seems not to have been appreciated. The experiments referred to later, as well as many unpublished data showing the varying behavior of types when planted at different depths, indicate that it is unsafe and unscientific to generalize with respect to cultural factors without taking type, varietal, and even individual differences into account.

MORPHOLOGY OF THE MAIZE SEEDLING

To explain this drought-resistant character, it will be necessary to discuss briefly the different parts of a maize seedling. (See fig. 1.) The primary root, or radicle, which is the first organ to emerge from the germinating seed, is soon followed by the shoot or plumule. Inclosing the shoot is the cotyledonary sheath, or coleoptyle, a tubular organ which is closed and pointed at the upper end. Between the base of the coleoptyle and the seed the axis is somewhat elongated. With seeds germinated in the laboratory this elongation is so slight that it might easily be overlooked. Nevertheless, this small organ has not escaped the notice of morphologists, and its nature has been the subject of much discussion. It has been variously called "hypocotyl," "mesocotyl," and "epicotyl." By some it is held to be an internode, by others merely an elongated node.

The choice of a name for the organ depends on the interpretation of the homologies of the other parts of the embryo, particularly as to what is considered as constituting the cotyledon. If the sheath, or coleoptyle, be thought of as the cotyledon, the most appropriate name would be hypocotyl. Although this interpretation was accepted by Richard (1811),[1] Hofmeister (1858), and Sachs (1875), there seems to be little evidence in its favor and it is summarily dismissed by other morphologists.

The two remaining views are as follows:

(1) The scutellum alone is the cotyledon, the epiblast (absent in maize) representing a second leaf and the coleoptyle a third. The elongated axis between the coleoptyle and scutellum is thus considered an internode and is then given the name "epicotyl." Among the supporters of this hypothesis are the following: Warming (1879–80), Hackel (1887), Bruns (1892), Van Tieghem (1897), and Holm (1908–9).

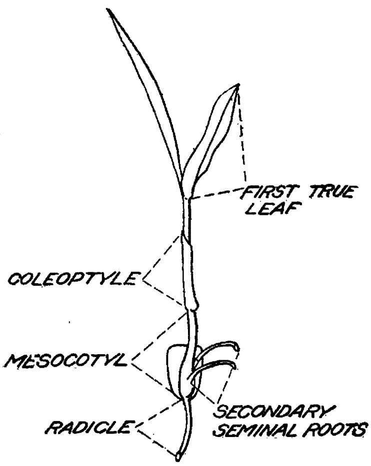

FIG. 1.—Diagram of seedling maize plant, giving terminology of parts.

(2) All these organs, scutellum, epiblast, and coleoptyle, are viewed as parts of a more highly specialized cotyledon, in which case the term "mesocotyl" is applied to the portion between the coleoptyle and scutellum. With various modifications this last interpretation is adopted by Van Tieghem (1872), Hagelmaier (1874), Klebs (1881), Schlickum (1896), Čelakovský (1897), and Goebel (1905).

Van Tieghem originally subscribed to the view that the coleoptyle was a part of the cotyledon, but as a result of further investigations abandoned that position and adopted a modification of the views of Warming to the effect that the mesocotyl and coleoptyle represent a metamer distinct from the scutellum. The epiblast he held to be a rudimentary second cotyledon. Van Tieghem carried this interpretation to its logical conclusion and adopted the view that the apparent similarity between the grasses and other monocotyledons did not represent homologies, but that the two groups were phylogenetically distinct. He further held, on the strength of anatomical differences, that the portion of the axis between the scutellum and the coleoptyle is in some grasses an internode and in others an enlongated node. The evidence regarding the morphology of the mesocotyl appears so conflicting that a definite interpreta-

[1] For "Literature cited" see p. 301.

tion satisfactory to all morphologists seems very remote. With organs that pertain to the very beginnings of the plant, even the primary differentiation into root, stem, and leaves may not be complete, and to insist on a definite classification of these primitive organs may be idle.

Studies of seedlings of Hopi maize show that the mesocotyl may frequently develop up to lengths of 36 cm.,[1] and it has been possible to note a fact which appears thus far to have escaped notice—namely, that the mesocotyl may give rise to roots at any point on its surface—but these roots are threadlike and do not resemble the roots that arise from the nodes of the culm. They do, however, closely resemble the roots that arise from the radicle immediately below the seed. (See Pl. XXIX, fig. 1.) In grasses roots usually arise from nodes, not from internodes, and the presence of roots on this organ in maize distinguishes it sharply from subsequent internodes and is an argument in support of the interpretation that this intercalary growth, long though it is, is really a part of the cotyledon and may properly be termed a mesocotyl. A further reason for retaining the term "mesocotyl" is because the interpretation implied by its use permits more direct comparisons with other groups of monocotyledonous plants, where the organ sheathing the plumule seems undoubtedly to be a part of the cotyledon.

From observations upon many varieties of maize it has become apparent that when a grain of corn germinates in the ground this usually insignificant organ is of vital importance to the life of the plant, for it is through the elongation of the mesocotyl that the shoot is enabled to reach the surface. So long as the seedling remains below ground, away from light, the mesocotyl will continue to elongate until it reaches a maximum length, which we have found to differ in different varieties, but which seems reasonably constant within the variety. As the mesocotyl elongates, the coleoptyle, with its firm, sharp point, is pushed upward through the soil. As soon as the coleoptyle emerges from the soil, the elongation of the mescotyl ceases, and elongation of the internode bearing the first true leaf begins, forcing open the coleoptyle.

If the seed is planted so deep that the maximum elongation of the mesocotyl, which in anatomical structure shows a striking relation to the radicle, fails to bring the coleoptyle to the surface, the task of penetrating the soil and reaching light devolves upon the first true leaves. In comparison with the sharp coleoptyle, these leaves are but poorly adapted for forcing their way through the soil, and if the tip of the coleoptyle stops more than a few centimeters below the surface these leaves usually crumple and never reach the light.

In the varieties of maize commonly grown we have been unable to force the mesocotyl to a length greater than 10 cm., while in the Hopi and Navajo varieties this usually minute organ has in our experiments frequently reached the enormous length of 25 or even 30 cm.

[1] In Euchlaena also the mesocotyl may reach a length of 28 cm. Van Tieghem gives 3 cm. as the maximum length of this organ in grasses.

GERMINATION OF NAVAJO MAIZE

It has been frequently stated that the Navajos, like their neighbors, the Hopi and Zunis, plant maize at unusual depths, 15, 30, and even 45 cm. having been reported. Since planting at such depths is known to be impracticable with other varieties, experiments were planned to test the ability of the Navajo maize [1] to pierce the soil. A representative experiment is here reported. A box 70 cm. long, 33 cm. wide, and 34 cm. deep was sunk in the ground. A quantity of sandy-loam soil sufficient to fill the box was slightly moistened and carefully sifted. At one end the box was filled to within 1 cm. of the top, the soil sloping in a straight line to within 1 cm. of the bottom at the other end.

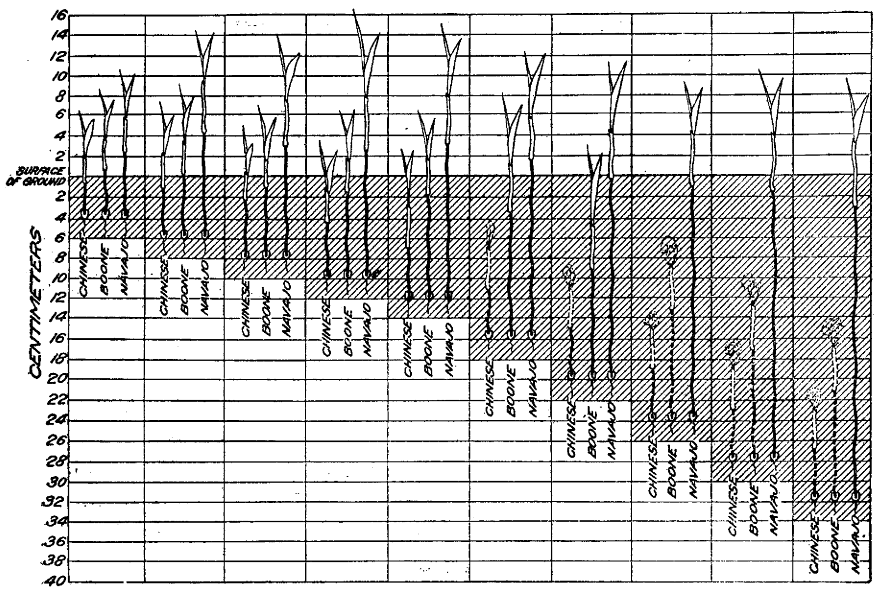

FIG. 2.—Diagram showing the average size of seedlings of Chinese, Boone County White, and Navajo maize planted at different depths.

Five seeds each of Navajo, Boone County White, and Chinese maize were placed in a row transverse to the inclined surface of the soil, 2 cm. from the top of the box. A similar row was planted at a depth of 4 cm. from the top, and so on at the following depths: 6, 8, 10, 12, 16, 20, 24, 28, and 32 cm. The box was then filled with the soil and struck off level with the top. The seeds germinated promptly, and when the most advanced seedlings had reached a total height of about 60 cm. the plants which appeared above the surface were dug up, and the mesocotyl and coleoptyle were measured. (See Table I and fig. 2.)

[1] In the fall of 1912 Messrs. Walter T. Swingle and Karl F. Kellerman visited the region about Shiprock, N. Mex., in the Navajo Reservation and secured specimen ears of the maize grown by the Navajos. This collection was kindly placed at the disposal of the writer. Additional seed was later secured through the courtesy of Mr. William T. Shelton, Indian agent at Shiprock.

TABLE I.—*Average measurements of seedlings of Chinese, Boone County White, and Navajo maize planted at different depths.*

Depth.	Chinese.			Boone County White.			Navajo.		
	Cole-optyle.	Meso-cotyl.	Coleoptyle and meso-cotyl.	Cole-optyle.	Meso-cotyl.	Coleoptyle and meso-cotyl.	Cole-optyle.	Meso-cotyl.	Coleoptyle and meso-cotyl.
Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
2	2.3	2.3	4.6	3.7	3.2	6.9	5.5	5.0	10.5
4	2.5	3.5	6.0	3.1	4.9	8.0	4.3	6.5	10.8
6	2.8	5.0	7.8	3.4	6.1	9.5	5.2	10.2	15.4
8	2.5	5.8	8.3	2.8	7.4	10.2	4.9	11.0	15.9
10	3.2	5.8	8.9	3.1	8.6	11.7	5.6	12.2	17.8
12	4.0	5.2	9.2	3.4	10.4	13.8	5.0	15.1	20.1
16	......	......	....	4.6	12.4	17.0	4.3	17.5	21.8
20	......	......	....	4.5	10.9	15.4	4.7	19.7	24.4
24	......	......	....	......	....	....	5.2	23.0	28.2
28	......	......	....	......	....	....	5.6	26.5	32.1
32	......	......	....	......	....	....	6.5	29.0	35.5

Twelve cm. was the greatest depth from which seedlings of the Chinese variety appeared at the surface. Seedlings of Boone County White appeared from all depths up to 20 cm., while plants of Navajo maize appeared from all plantings, including the very deepest, 32 cm.

There were numerous instances in which the combined length of the mesocotyl and coleoptyle was less than the depth at which the seed was planted. This, of course, means that the upper layers of the soil were penetrated by the true leaves. The maximum depth of soil thus penetrated by the true leaves of the plants of the Chinese variety was 5 cm. One plant of Boone County White maize forced its leaves through 8 cm. of soil. In all of the Navajo plants the coleoptyle reached the surface.

The extent to which the seedlings of the Chinese and Boone County White varieties were able to penetrate the soil by means of the true leaves was doubtless much greater in the carefully prepared soil of the experiment than it would be under field conditions, where any slightly compacted lump of soil would deflect the tender leaves and cause them to crumple. On the other hand, many seedlings failed to come up where there was less than 2 cm. between the top of the coleoptyle and the surface of the ground. The results clearly show that the coleoptyle is the proper organ for penetrating the soil, and where this office devolves upon the leaves there will be many plants that fail to reach the surface.

It has been observed in many field plantings that the spatulate first leaf, formerly called the cotyledon, is the first evidence of the germinating plant. When this occurs in any considerable proportion of the plants, it is safe to assume that the seed has been planted too deep for the best results.

The three types of maize used in the box experiment were also planted in the field. Four seeds of each of the varieties were planted as follows: At the surface and at 5, 10, 20, 30, and 40 cm. below the surface. The greatest depth from which plants of the Chinese variety reached the surface was 10 cm., that of the Boone County White was 20 cm., while that of the Navajo was 30 cm.

The seeds planted at the surface were naturally the first to appear, but on June 17, one month after planting, the largest of the Chinese variety were those from a depth of 5 cm., while the largest plants of both the Boone County White and the Navajo maize were from the 10-cm. depth. On July 11 the plants that came up from a depth of 10 cm. were the tallest in all the varieties, including the Chinese, and to the end of the season this appeared the most favorable depth for the Chinese and Boone County White varieties. With the Navajo, however, the plants from a depth of 20 cm. had equaled those from the 10-cm. depth before the end of July, and from that time the plants from the 20-cm. planting continued to make the most rapid growth, as though this depth represented the most favorable condition for the Navajo variety.

DESCRIPTION OF ROOT SYSTEM

We have observed further that the root systems of the Navajo, Hopi, and Zuni varieties differ from those of the other varieties; the roots of their seedlings extend to a greater depth, and there is only a single root arising from each seed, while in the seedlings of the Chinese and Boone County White varieties the roots are shorter and more numerous.

The roots of maize are of two kinds: Those that arise from the embryo or seed, called "seminal roots," and those produced from the nodes of the plant. Of the latter class those that arise from the nodes above the ground are often called "brace roots" or "aerial roots." In the varieties commonly grown in the United States there are, in addition to the primary root, or radicle, from two to six additional roots that arise from the base of the cotyledon. These secondary seminal roots, though appearing somewhat later, usually equal or exceed the radicle in size. In the Pueblo varieties of maize these secondary seminal roots have been absent in all seedlings thus far examined, the radicle being the only root arising from the seed. (See Pls. XXIX and XXX, fig. 2.)

FIELD STUDIES OF PUEBLO VARIETIES OF MAIZE

In September, 1913, opportunity was afforded for a visit to the Zuni, Navajo, and Hopi Indian Reservations of Arizona and New Mexico. It was thus possible to form some idea of the agricultural significance of the peculiar habits of germination of this type of maize.

The value of deep planting made possible by the greatly elongated mesocotyl was obvious. In the localities selected by the Indians for planting maize the soil is sandy, and in the absence of spring rains the surface layers are, of course, very dry. (See Pl. XXXI, figs. 1 and 2.) The seed, to germinate at all, must be planted deep enough to be in contact with the moist soil. In Navajo fields near Tohatchi, N. Mex., plants were dug up, and the remains of seeds were found at depths ranging from 13 to 18 cm. below the surface. Similar depths were found in a Zuni field near Black Rock, Ariz. (See Pl. XXXI, fig. 1.) In a Hopi field at Polacca, Ariz., near the First Mesa, where the conditions are extreme, the seed had been planted at a depth of 25 cm. (See Pl. XXX, fig. 1.) It thus appears that there is no fixed depth for planting, the custom being to plant deep enough to place the seed in moist soil. If the seed were planted at ordinary depths, germination might be delayed until the latter part of June or the first of July, at which time the rains usually occur; or if the seeds germinated as a result of one of the occasional showers occurring in May, the plants would die from subsequent desiccation.

Like the long mesocotyl, the simple radicle of the Pueblo varieties of maize may be looked upon as an adaptation to the extreme conditions that exist where these types are grown. For six or eight weeks after planting, no rain can reasonably be expected, and during this time the moisture is constantly receding from the surface. By concentrating the energy of the seedling into a single root the latter is forced to greater depths and consequently kept in moister soil than would be the case were a number of seminal roots developed.

Under ordinary conditions, where moisture is distributed through the entire seed bed, the seminal roots become of little importance as soon as the seedling is established and nodal roots have developed. If a half-grown or nearly mature corn plant is carefully dug up, the seminal roots and traces of the seed can still be found, but they are usually dry and shrunken and are obviously of little use to the plant. This was also the condition found in Navajo and Zuni maize fields, though the seminal root was more strongly developed than in the eastern varieties. (See Pl. XXIX, fig. 2.) But in the more extreme conditions existing in the fields near the Hopi villages, where the seeds were planted deeper, it was found that the seminal roots were relatively much larger and were still alive and fresh, making it apparent that they retain their function of supplying moisture and are able to play an important part during the entire life of the plant.

In one Hopi field at the base of the First Mesa the hills of maize were planted about 20 feet apart, with from 10 to 20 plants in a hill. The soil was apparently pure sand washed down by the winter rains and entirely destitute of vegetation other than the planted maize. An average hill dug up in the field was found to contain 15 plants ranging from 60 to 90 cm. in height. (See Pl. XXX, fig. 1.) The remains of the seeds were found at 25 cm. from the surface, and from each seed there descended a single large seminal root. (See Pl. XXX, fig. 2.) These seminal roots were traced to a depth of 35 cm. and extended even farther down. They were still fresh and densely covered with fine branches. This mass of 15 seminal roots, while less in volume than the nodal roots arising near the surface, was apparently playing an important part in the support of the plants. The mesocotyls connecting the seminal roots with the plants above, while dry on the outside, were filled with live tissue quite unlike the dry and shrunken mesocotyls found in plants of similar age grown under more favorable conditions.

When planted by the Indian methods, the Hopi and Navajo varieties of maize have been found superior to the more improved eastern varieties for these very dry regions. At the time of our visit there was a small field near Keams Canyon that had been planted by eastern methods. The plants were in rows and thinned to one stalk to the hill. There had evidently been a fair germination, but the plants had died without reaching maturity and had produced no seed. At the same time, in the nearest Indian fields at Polacca the plants were dark green and maturing a fair crop, though the season was said to have been unusually dry. (See Pl. XXXI, fig. 3.)

Even under irrigation the somewhat larger strains grown by the Navajos have been found to compare very favorably with eastern types. Several acres of Navajo maize were seen at Shiprock, N. Mex., under irrigation. The fields were very uneven, apparently the result of alkali, but in the better portions the yield was good. The plants were standing about 2 feet apart in the row, the rows 4 feet apart, and nearly every plant was bearing from two to four fair-sized ears. (See Pl. XXXII.)

The ears from 36 plants, representing a number of distinct types, were collected. The 36 plants bore in all 94 ears, weighing 37.6 pounds, an average of 15.2 ounces per plant. The plants producing these ears averaged only a little over 5 feet in length.

CONCLUSIONS

Throughout the western part of the Great Plains area the difficulty of securing uniform germination is a serious obstacle to the growing of maize. With the varieties commonly grown, if the seed is planted at the customary depth, many seeds fail to germinate from insufficient moisture; if planted deep enough to come in contact with moist soil, the plants may fail to reach the surface.

The agricultural Indians of the Southwest have continued from prehistoric times to grow maize successfully in regions where drought, and especially the absence of spring rains, makes it much more difficult to start the crop than in the Great Plains. A study of the varieties grown by the Hopis and other agricultural Indians shows that these varieties possess two special adaptations: (1) A greatly elongated mesocotyl that permits deep planting and (2) the development of a single large radicle that rapidly descends to the moist subsoil and supplies water during the critical seedling stage.

This indigenous type of maize seems to have attracted little attention, perhaps because it has been included in the popular mind with a series of inferior varieties commonly known as "squaw corn." But the Pueblo Indians of Arizona and New Mexico have strains sufficiently productive to compare favorably with improved varieties even when grown under irrigation. The peculiar adaptations of this type definitely indicate its value for the semiarid regions and warrant experiments to determine the possibility of its utilization.

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DESCRIPTION OF PLATES

PLATE XXIX. Fig. 1.—A seedling of Hopi maize with mesocotyl 18 cm. long. The seed was planted in sand 20 cm. below the surface. There is a single seminal root with threadlike branches similar to those arising from the mesocotyl. The first nodal roots have begun to form at the base of the coleoptyle. One-half natural size.

Fig. 2.—The root system of a plant of Zuni maize dug from a field near Zuni, N. Mex., showing the well-developed, single seminal root and the comparatively feeble nodal roots. Natural size. The field from which this plant was dug is shown in Plate XXXI, figure 1.

XXX. Fig. 1.—A hill of Hopi maize containing 15 plants grown under conditions of extreme drought at the base of the First Mesa near Polacca, Ariz. The ears can be seen borne at the surface of the ground.

Fig. 2.—A plant of Hopi maize. One of the smaller plants from the hill shown in figure 1. The remains of the seed are scarcely visible at the sharp bend of the mesocotyl, 25 cm. below the surface of the ground.

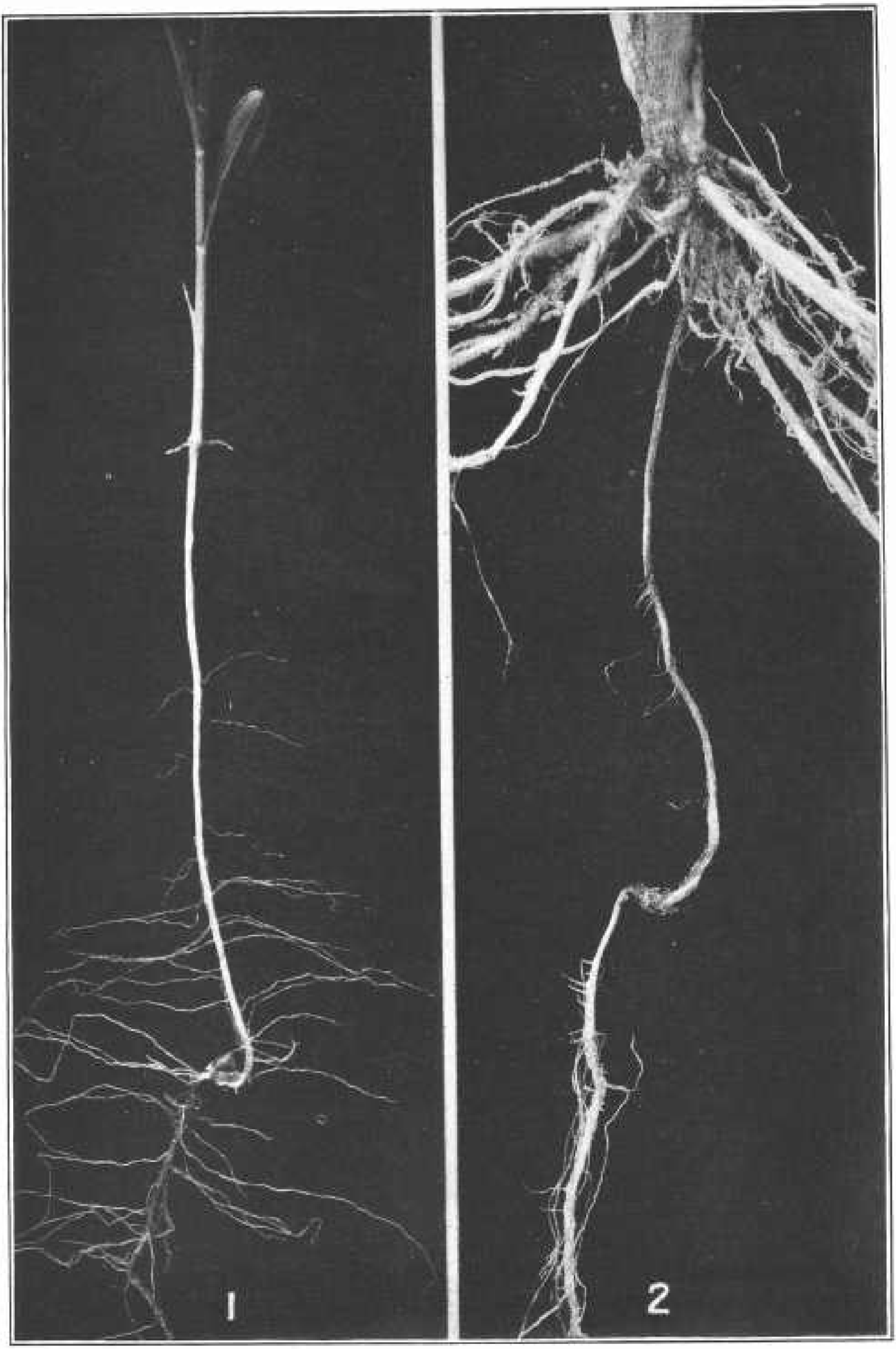
XXXI. Fig. 1.—A field of Zuni maize near Zuni, N. Mex. One of the hills near the center containing but a single plant shows a relatively large ear borne at the surface of the ground.

Fig. 2.—A hill of Zuni maize in the field shown in figure 1. Note the large ears borne near the surface of the ground.

Fig. 3.—A hill of Hopi maize making luxuriant growth under conditions of extreme drought. Note the manner in which the low-spreading plants shade the ground. Polacca, Ariz.

XXXII. Fig. 1.—A single plant of Navajo maize grown under irrigation at Shiprock, N. Mex.

Fig. 2.—The basal portion of the plant of Navajo maize shown in figure 1, with leaves and husks removed. The ears from this plant after drying weighed 2 pounds.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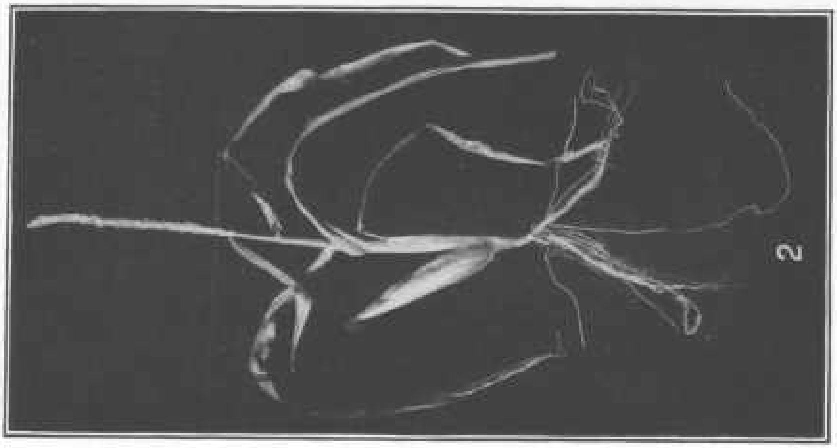

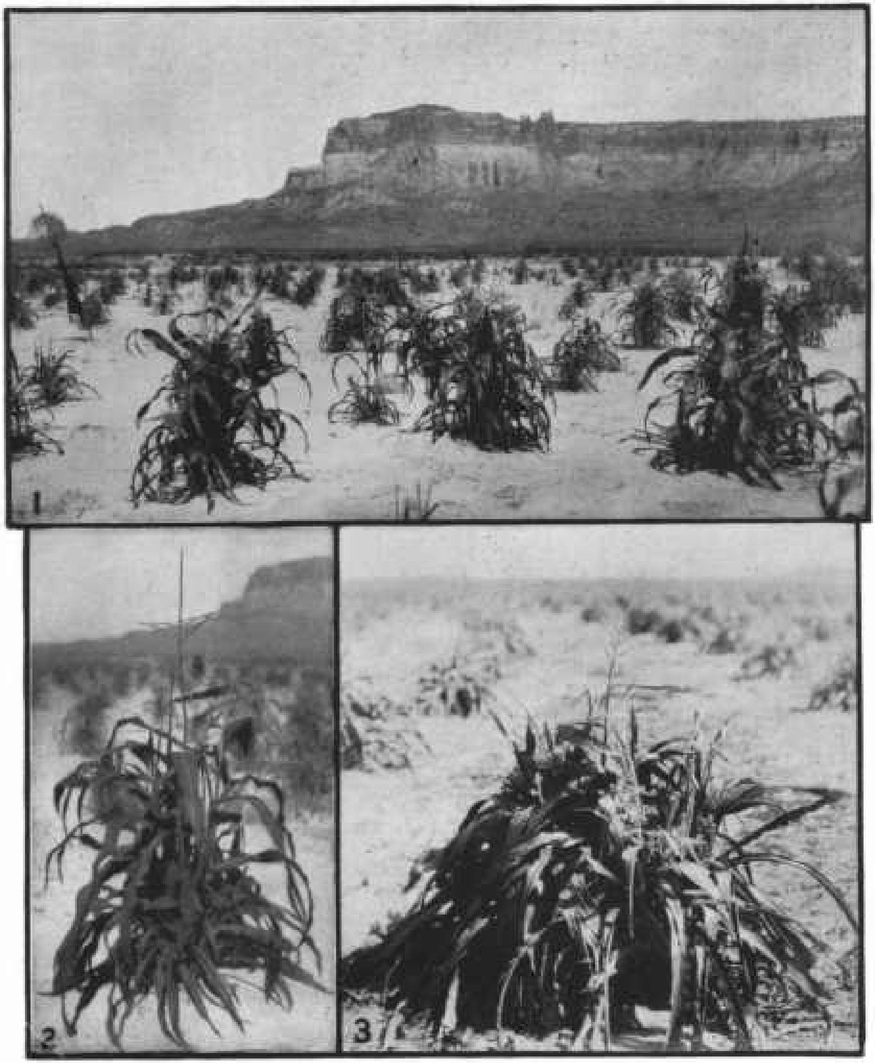
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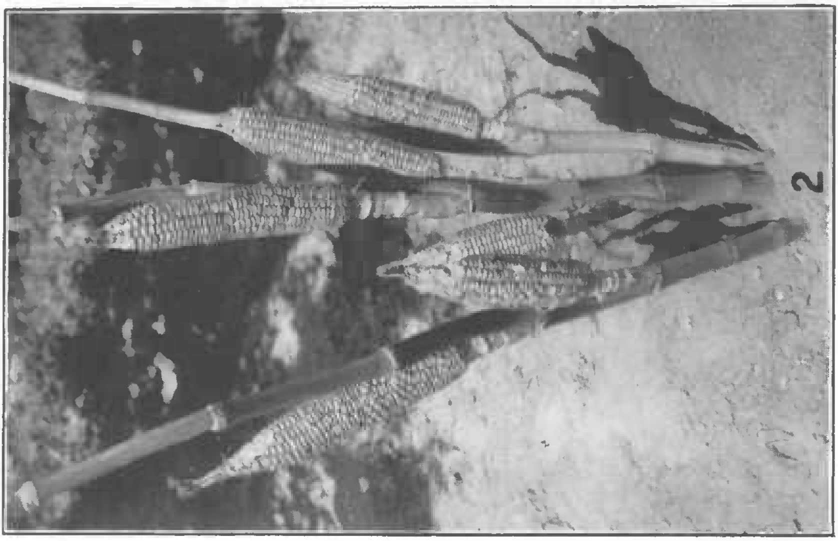
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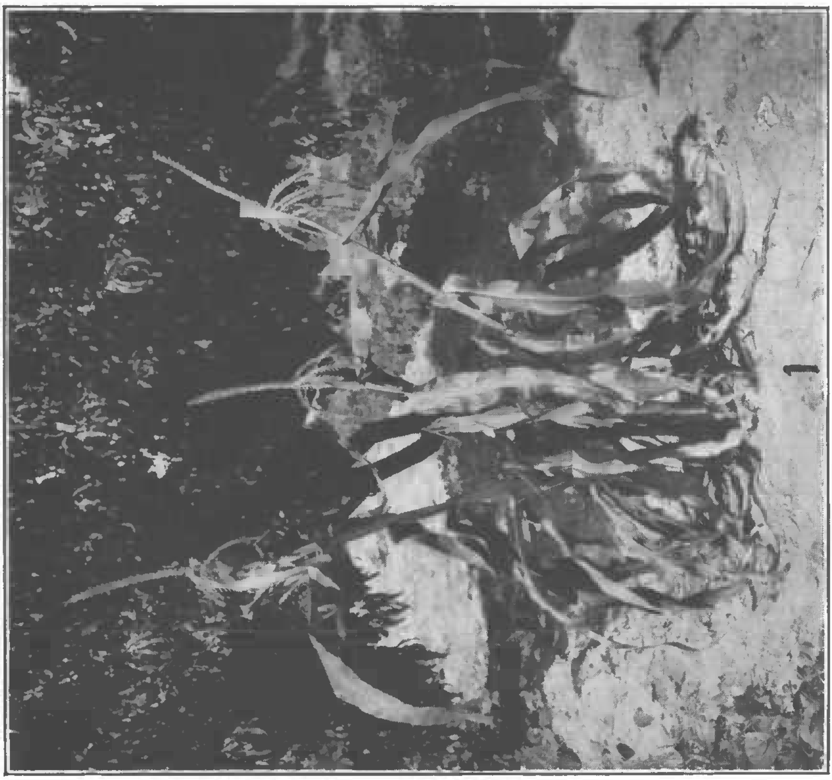
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