

organ. Thus the pronounced induration of modern teosinte may be a character derived from modern maize, a view opposite to that generally held. A given level of sink capacity which would allow induration in a tiny spike of teosinte with its 6 to 10 kernels might not be sufficiently high to provide for induration in even a primitive ear of maize bearing about 50 kernels.

While the morphological evidence of teosinte introgression in both archaeological and modern maize is generally accepted, it is possible that in some cases, the high induration on which the evidence is partly based may be independent of the introgression and due rather to a combination of genes for a small ear together with a high sink capacity.

One of the methods which we are using to investigate the maize-teosinte relationship is to compare the effects of teosinte germplasm, especially that of chromosome 4, upon the spikes in the  $F_2$  progeny from parallel crosses of teosinte by primitive maize versus teosinte by modern maize.

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#### 6. Ontogeny and phylogeny of the cupule.

In the early stages of floral ontogeny in maize, the orientation of the primordia of the pistillate spikelets is vertical or parallel to the rachis as it is in the other American Maydeae and most closely related Andropogoneae. In the American Maydeae, the primordia are embedded within cupules in the rachis. In teosinte and tripsacum, the young pistillate spikelets remain within the confines of their individual cupules while these structures expand and differentiate simultaneously. Eventually the developing outer glume of the embedded spikelet completes the enclosure of a unique protective device, the cupulate fruit case. As the fruit case matures, it becomes indurated (hardened) and an abscission layer develops at each node (underface of the trace).

Although the lining of the cupule is derived from tissue homologous to that of the hairy pulvinus, it is glabrous within the tight confines of the fruit case, except where it surrounds the pulvinus notch on either side of the spikelet. A dense tuft of hair fills the pore so that it is

nearly impenetrable except by the primary root during germination and by water to initiate this germination.

In teosinte, mechanical support and protection to the spike as a whole during its final stages of maturation comes from a single enveloping husk leaf. After maturation, the disarticulated fruit cases usually sift out through the open top of the husk after the dead plant bends toward the ground or, if shredded by storms and/or birds, they may escape through tattered husks.

In modern maize, however, the young pistillate spikelets elongate outward and bend away from their individual cupules in coordination with an arrest in further cupule development. The timing of this spikelet inclination and its associated control over cupule development varies with the degree of teosinte introgression as shown experimentally with the A158 derivatives of teosinte. Also, fortuitous changes to either single spikelets or to multiplications above two result in cupule widths which match precisely those of the associated spikelets.

The oldest archaeological maize from Mexico, especially the Chapalote related material, has deep, triangular cupules which approach those of teosinte except for a general pubescence over the surface. Apparently the hairy nature of the pulvinar tissue has been reasserted after the protective function of the cupule was lost. The specialized hairy pulvinus notch remains in maize, also without function.

That the maize cupule is not merely an artifact of ontogeny is shown by its ready response to genetic selection and by the presence of the specialized pore, the pulvinus notch. In a relatively small breeding project for reduced cupule development, a non-cupulate cob was selected in my cultures through recombining certain genes derived from Confite Morocho of Peru and a sweet corn inbred (Ia. 5125) which appears to be related to Chullpi (Chuspillu) also from Peru. This non-cupulate rachis, which is also known archaeologically from Peru, is probably a derived condition following drift away from teosinte rather than a primitive one because the cupulate state and the associated tendency for vertically-oriented spikelets provides a better sequential connection to all of the known relatives of maize.

My interpretation of the cupule in maize as a vestige of the cupulate fruit case of teosinte and tripsacum does not invalidate my earlier views on the homologies of the cupule within the framework of the phytomer, as previously described (Galinat, 1963).

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7. The role of the cupule in the modern maize cob.

While the cupule has a functional role in the relatives of maize, at first glance it does not appear to have a function in the maize cob. Yet, cupules are always present in the cobs of modern maize. Despite this, selection for smaller cupules is possible and the ultimate non-cupulate rachis may be controlled by as few as two recessive genes.

If the cupule is now vestigial in maize and yet genetically controlled, why does it persist in the cobs of all the modern races? Some observations presented here suggest an answer.

In studying the cupules of the various races of maize, I have observed that the flour corns tend to have the widest cupules while the flints, the popcorns, the dents and some of the dent-related sweet corn varieties have progressively smaller cupules in the order listed. Derivatives from crosses between these variants, in which kernels of different sizes and endosperm types are combined with a cupule smaller than that of the original parental stock, tend to have two types of difficulties. (1) The kernels may develop mold in the field which usually results from a splitting of the pericarp and an accompanying release of sugar from endosperm tissue. Sudden changes in the moisture level of both cob and kernels may cause this pericarp splitting through unequal stresses. (2) The second difficulty is shattering which occurs later during drying of the mature ears. The kernels shrink to a fixed minimal size before the cob shrinks. If the cob subsequently contracts more than that attained by the kernels, some of the kernels are mechanically pushed out and off from the cob. In the case of the flour corns, which have excessively large kernels that do not shrink appreciably on drying, selection is strong for a wide and indurated cupule which provides the necessary dimensional stability (hardness) to the drying cob.