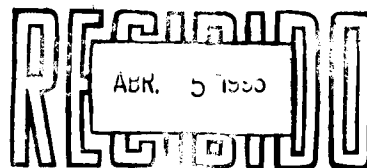


This document is supplied on the condition that it will be used solely for research. Further reproduction may be prohibited by copyright law.



EL ORIGEN DEL MAIZ: EL GRANO DE LA HUMANIDAD THE ORIGIN OF MAIZE: GRAIN OF HUMANITY^{1,2}

WALTON C. GALINAT

Galinat, Walton C. (University of Massachusetts, Waltham, MA 02154) USA. THE ORIGIN OF MAIZE: GRAIN OF HUMANITY. *Economic Botany* 49:(1)3-12. 1995.

Key Words: co-evolution; maize; maize genetics; plant breeding; *Tripsacum*; teosinte; transposition.

Queridos amigos, me da gran placer a hablar con ustedes, aquí en México, acerca del maíz. Es un placer, pues, porque son ustedes la noble gente cuyos antepasados de hace ocho mil años crearon el maíz aquí en este sagrado lugar. Ellos desarrollaron el maíz de una planta silvestre nativa, llamada teosinte, lo que significa el grano de Dios.

Estos antepasados de ustedes tuvieron la inteligencia, la visión y la maravillosa bendición de seleccionar de entre mutaciones de grupos silvestres, dos tipos de plantas de teosinte con cuatro hileras de granos en cada mazorca, y de cultivar estos dos tipos juntos y aisladamente. El híbrido derivado de ellos llegó a ser el primer maíz, nombre que significa el grano de la humanidad.

Yo no hablo español, and so please allow me to continue in my native tongue.

MAIZE AND HUMAN CULTURE

Many scientists recognize that there is a co-evolutionary relationship between food crops, discussed here with maize and human cultures. The consequences of this interrelationship, as a distant mirror of the present and possible future status of civilization, have not been fully appreciated and applied to the present. The evolving sophistication of a once simple dependency may be diagrammed as a wheel with breeding at the hub, support systems as spokes and civilization

as the consequence at the rim. A circle or wheel symbolizes civilization because it has no beginning or end. It can enlarge from progress by wisdom and crisis or it can collapse from warfare and starvation. It turns through time from plant breeding power at the hub. At first breeding was combined with hunting and gathering and a small simple wheel of cultural development evolved (Fig. 1A). Many of civilization's traits at the rim were to increase the efficiency of the agricultural process. As breeding and improved farming greatly increased the food supply, people became more settled and the wheel of coevolution between breeding and culture expanded (Fig. 1B).

Ten thousand years ago, the unreliability and limitation of wild food together with increases in human populations probably stimulated a decision to gradually try farming along with hunting and gathering in various areas as a means to supplement the wild food supply. The rudiments of farming technique had already been surmised from observing accidents involving their food plants. These plants grew from seed disposed in garbage heaps. They grew better in full sunshine and moist soil. While no single factor actually triggered a farming lifestyle, an accidental fire may have set the stage when it burned trees and brush and, thereby, opened the land to sunshine and to growth by annuals and herbaceous perennials that sprouted from seeds and rhizomes. Grasses that provided food such as teosinte were especially important. The obvious lesson was that fire could serve as a management practice to bring forth the growth of food plants and spread of grazing animals. This could be the first step along a new pathway of agricultural evolution. Later

¹ Received 24 June 1994; accepted 24 July 1994.

² Distinguished Economic Botanist Address. June 24, 1994, 35th Annual Meeting of the Society for Economic Botany Mexico City, Mexico).

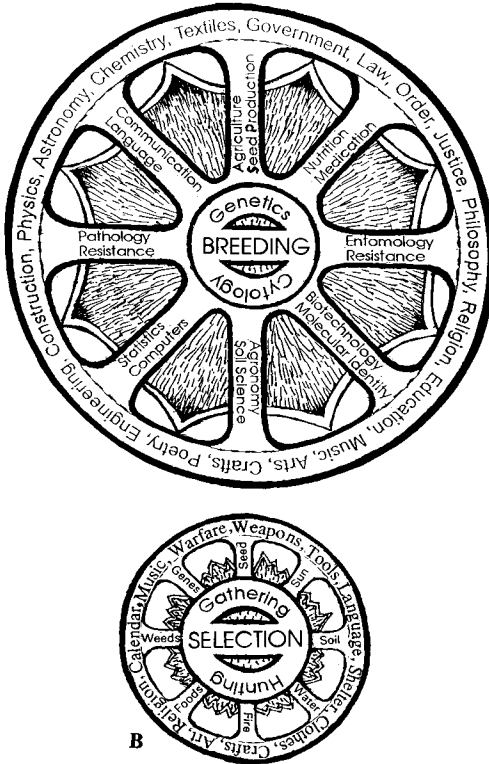


Fig. 1 (A, B). Two wheel diagrams showing the coevolution of food supply and civilization. The small wheel (A) represents the primitive condition under which starvation played a role. Accordingly, a hungry man knows not compassion, comprehension or civilization. He understands only violence, anger and humiliation. The advent of scientific breeding in (B) produced an abundance of food and greatly expanded the wheel of civilization (rim) and its support systems (spokes). The evolved wheel represents a possible future version of the modern wheel because many aspects of the primitive wheel still exist today such as warfare, but now with weapons made more deadly by high technology.

additional ideas for agricultural improvement were intercommunicated involving irrigation, planting, cultivation, fertilization and domestication of the most useful food plants and animals. To paraphrase Kaufman (1993) on the evolution of ideas, "Ideas, like genes, once set free by communication, harbor their own lives, follow their own unsuspected paths, mature in unforeseen ways, and mingle with their own logic. If useful, they have progeny." Thus, there came to be a co-evolution between crops and culture. Increases in the productivity of the food crop allowed more time and energy to settle down, to improve health with better nutrition and medi-

cation and to build a more complex society based on an immortal accumulation of wisdom from all of humanity. The consequences of this co-evolution are represented here in some of their aspects out at the rim of civilization's wheel (Fig. 1B).

The wheel of civilization, like that of most life, is either directly or indirectly dependent upon the ability of chlorophyll to chemically capture solar energy.

The greatest plant breeding achievement of all times at the hub of the wheel took place here in Mexico some 8000 years ago. These first Mexicans transformed a wild native grass called teosinte, meaning the grain of God, into the first maize, meaning the grain of humanity (Fig. 2, see poem in caption).

The only other human achievement comparable to the origin of maize and other domesticated food plants was the much older invention of spoken language, a technology still evolving with the silicon microchip. The consequence of language and communication is the power which turns the wheel of civilization. In addition to the thousands of cultural languages, there are special scientific languages which tend to be universal or intercultural.

GENETICS AND MAIZE DOMESTICATION

A description of the origin, evolution and improvement of maize involves the genetic language. Unfortunately some of the genetic symbols for key traits separating maize from teosinte were coined without consideration of the fact that because teosinte is the wild ancestor of maize, the teosinte key trait alleles are the wild type alleles and the maize alleles are the divergent or mutant alleles. An example is the use of the symbol *tr* for two-ranked ear (Tavcar 1935; Langham 1940) that is the wild type of teosinte and most other grasses. The divergent type in maize represents an increase in ranking. In all cases, the gene action involves ranking and so it is more logical to use the symbol *Rk* for rank. The location of the major *Rk* gene is on the short arm of the chromosome 2, as shown with the genetic data for the *tr* synonym used (Rogers 1950), with maize-*Tripsacum* interchange chromosomes by Galinat (1973) and with molecular markers by Doebley et al. (1990). There may be at least three alleles at this locus: *Rk-t* (two-ranks, bilateral), *Rk-f* (four-ranks, decussate or in two alternate

yokes) and *Rk-s* (six-ranks, tricussate or in two alternate whorls, each tripartite). The expression of *Rk-f* and *Rk-s* is enhanced into higher orders of ranking by interaction with genes elsewhere for increased condensation and/or fasciation. The flattening effect of fasciation occurs when the surface area of a slender rachis is insufficient to accommodate the ranking. Edgar Anderson (unpub.) described it as an unsuccessful attempt at branching or Siamese twinning.

The selection by teosinte seed gatherers of the *Rk-f* gene in wild populations produced a decussate type of four-rowed ear which was obviously more productive than the original wild type and worthy of growing in their experimental gardens. Perhaps at least one of these first farmers was famous for his garden of strange teosinte and he may have offered a reward to those gatherers who brought him seed of new strange types.

One of these new introductions to the isolated teosinte gene pool was also four-rowed but it was a morphologically and genetically different type of four-rowing. Instead of four-rows from four ranks of single spikelets controlled by the *Rk-f* gene, it had four rows from two ranks of paired spikelets because of female expression of the *Pd* gene, probably resulting from the excision of a transposon from the *Pd* locus on chromosome 3, as documented later. Normally in teosinte, only the male spikelets are paired as if this transposon will not bind with and inhibit *Pd* in a male internal environment.

The power of language as a means of communication has been mentioned. The significance of words seems to increase in the form of poetry. Although poetry loses both rhyme and rhythm in translation, it reflects the beauty of art work with words *combined here with my actual drawing* (Fig. 3)—as follows:

Here you see,
How two kinds of teosinte,
Became the key,
To corn's pedigree,
When one morn, the first corn was born,
An amazing creation, from recombination.

The development of the eight-rowed condition in teosinte was a remarkable plant breeding achievement. However, one more step was necessary to produce a tiny version of the modern ear. The glumes still had the teosinte architecture of an erect orientation with a texture of hard induration. A major gene controlling both the orientation and partly the texture is located close

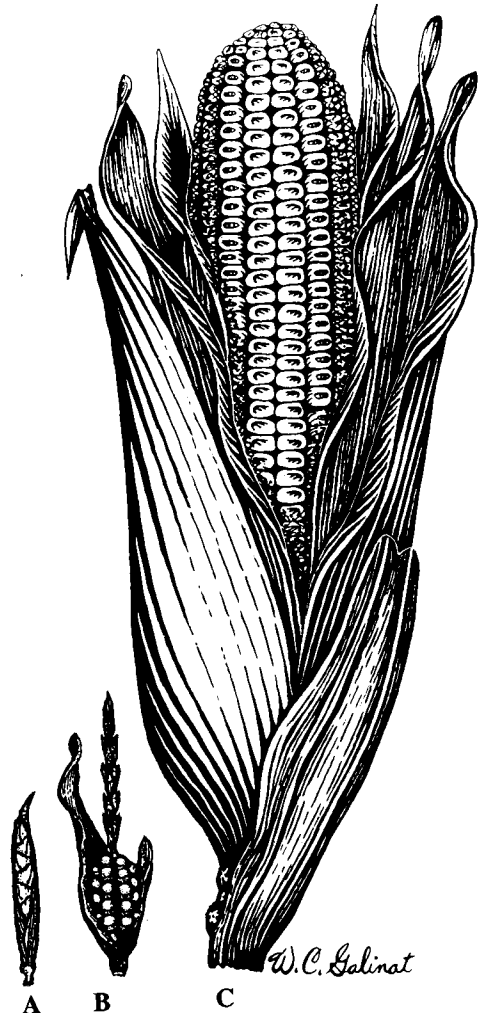


Fig. 2 (A-C). The origin of maize from teosinte, the greatest plant breeding accomplishment known to human kind. (A) Teosinte, the wild ancestor. (B) The oldest known archaeological ear of maize of ca 5500 years ago (Long, et al 1989). (C) The modern ear of maize. (Adapted from Galinat 1992). The importance of the origin of maize may be powerfully expressed in poetry as follows:

Origin of Maize

Of all creations
by all civilizations,
the highest praise
belongs to maize.

Ablaze in phase
with admiring craze,
we forever raise
this amazing maize.

W. C. G.

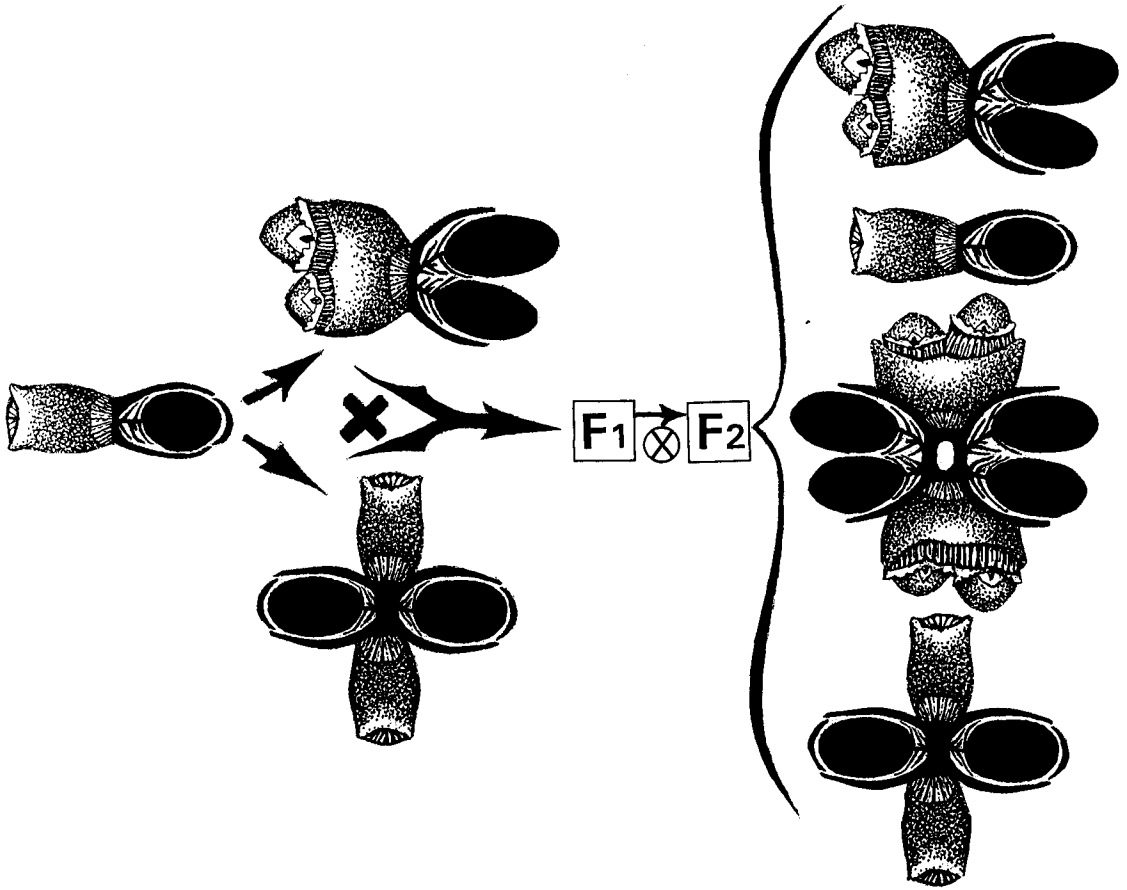


Fig. 3. The origin of maize in the F_2 from a hybrid between two kinds of four-rowed teosinte.

to the sugary-1 locus on the short arm of chromosome 4 (Rogers 1950; and others) and recently symbolized as *Tga* (Teosinte glume architecture) by Dorweiler et al. (1993) (Fig. 4). The *Tga* allele is the wild type from the wild ancestor. The divergent mutant allele to the typical condition of maize has been symbolized as *mga* for maize glume architecture (Galinat 1994). The fourth tunicate allele (*tu-f*) occurs in primitive corn such as Chapalote. The various allelic components of the strongest allele (*Tu*) are separable by mutation or crossing over and reconstructible by recombination (Mangelsdorf and Galinat 1964).

MAIZE BREEDING IN THE 20TH CENTURY

Maize has a great ability to adapt to almost any environment, perhaps more so than any other food plant. At the time Columbus arrived here

in the western hemisphere about 502 years ago, maize had already diverged into more than 300 races adapted to thousands of niches ranging from Canada to southern South America, from sea level to 12 000 feet high in the Andes, and from swamps to deserts. Maize was already the staff of life for three great New World cultures, the Aztec, the Maya and the Inca, approaching in complexity the European culture that Columbus represented.

The most important maize breeding achievement since that time was the development of hybrid corn about the time of World War I stemming from the pioneering efforts of G. H. Shull, E. M. East and D. F. Jones, all from northeastern United States where I come from. Since the advent of hybrid corn and now its almost universal use in the more developed parts of the world, corn yields have quadrupled, allowing fewer farmers to produce more food. The use of hybrid

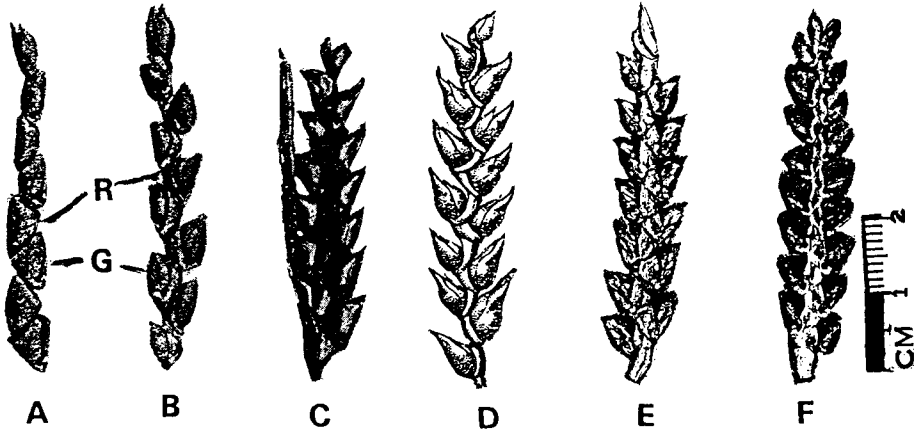


Fig. 4. Ear of teosinte (A) with its teosinte glume architecture (*Tga*) compared with tunicate (B to E) and non-tunicate derivatives (F). Ears (A) and (B) are adapted from Dorweiler, et al. (1993) in which the rachis segment (R) of teosinte (A) is fully developed with the cupule sealed by the outer glume (G) in forming a fruitcase type of protective device about the kernel. Ear (B) is claimed by Dorweiler, et al. (1993) to be *tga* teosinte. On the basis of comparison with the other teosinte derivatives (C to F), it is suggested here that it may be *mga tu*⁴. Ears (C) and (D) are *mga tu*⁴ teosinte adapted from Beadle in 1972 and 1980 respectively. The 1980 line drawing may be made from the 1972 photograph. Ears (E) and (F) are from my large collection of connecting like stocks that I have developed for my studies still underway on the origin of maize. Ear (E) is believed to be *mga tu*⁵ and similar to ear (B). Ear (F) has a combination of the modern maize genes *mga* and *tu*. All ears appear to be stable for single female spikelets.

corn together with advances in agricultural technology have so greatly increased food production in the United States that the number of people actually working on farms has declined to less than four percent now as compared with eighty percent in 1800. Yet the yield of maize in United States continues along a pathway of ever higher yields because of the skill of American corn breeders in the conventional art of breeding. In 1942 the U.S. corn crop was 3 billion bushels, 1959—4 billion, 1970—5 billion, 1992—9 billion or about one-half of the total world production. Most of the U.S. corn is used for livestock feed with about a quarter of it—two billion bushels—being exported to other parts of the world including use as feed corn here in Mexico. In using other animals to inefficiently convert our corn crop into other food forms, poultry, pork and beef, we admit that there is much yet to be done on the food quality of corn.

MAIZE AND THE HUMAN POPULATION

Domestication, agriculture, and the migration of most people into cities have all tended to increase the rate of population growth with our world numbers now reaching over six billion and increasing at a rate of a quarter million each day

or about 3 more people every second. The world population is forecast to double or grow to 12 billion by the year 2050, according to UNESCO dossier 3 de Catalunya, *All of Us* (Nov. 1993), which includes a dramatic cartoon representing a future world exploding with people.

Despite the seemingly unlimited supply of food provided by domestication and technological agriculture under present conditions, it may be very difficult to double the food supply when the population doubles. The amount of arable land and irrigation water is finite. The ancient problem from 10 000 years ago of finding a reliable sustainable food supply for humans could revisit us again with hunger falling upon billions of people this time around. But don't forget, we are the innovative, creative, and intelligent species that solved that problem of food supply once before and now it has taken us 10 000 years to get into the same problem of food once again. It is both the communication of understanding and the team effort between hub and spokes that enlarges and rotates the wheel of civilization. It is time now to take another leap forward. When the breeding power of genetics is increased with support from biotechnology, the potential will be there to solve the challenges of a world ecosystem which we have disrupted with our run-away pop-

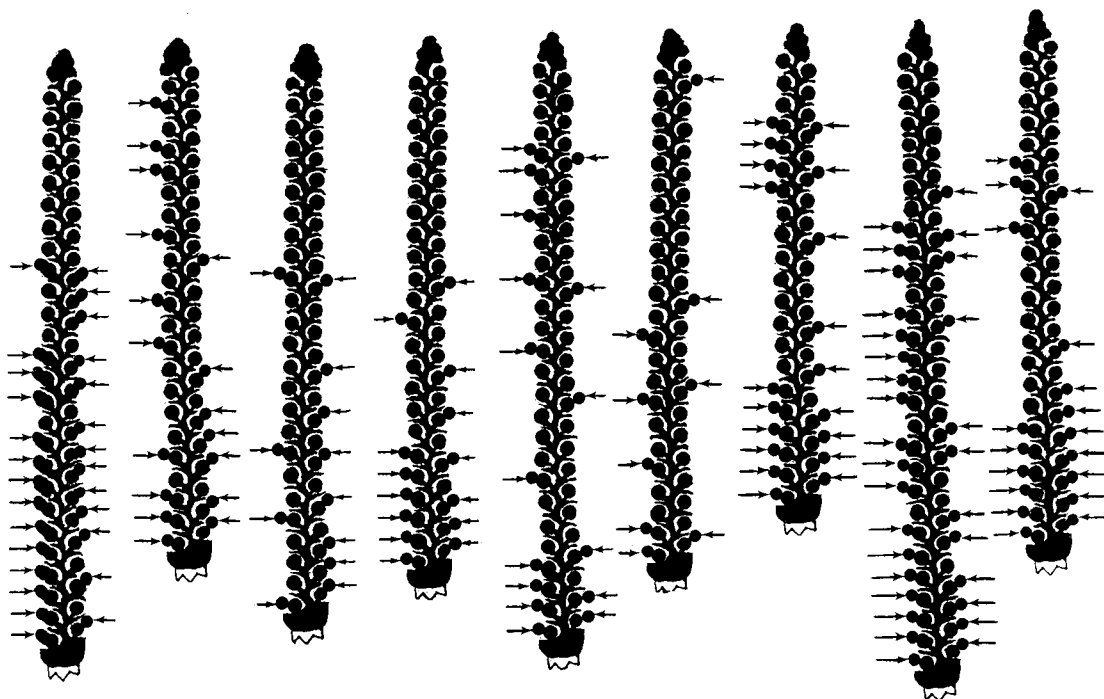


Fig. 5. Paired and single spikelets in lines intermediate between teosinte and maize.

ulation growth while we have extinguished other species. With all of our wisdom and optimism, we will keep that expanding wheel of civilization rolling along into what we have determined must become a beautiful place that we call our heaven on earth rather than the hell of just another extinct species.

THE FUTURE OF MAIZE BREEDING

The leap forward into the future for maize will come from genetics just as its origin from teosinte and its evolution to the present depended on human selection. But the new diversity for the leap will come from alien sources transferred to maize with the tools of biotechnology. The new leap genes will have a problem of expression within an old background of more than 40 000 genes that are already organized to serve other functions involving gene complexes, regulators and transposons. Likewise the alien genes will have been extracted from their own gene complexes, regulators and support systems that may not be available in the new host.

The attempted union, addition, or substitution between any two systems may or may not be congruous. A knowledge of the evolutionary his-

tory of maize during its origin from teosinte should be helpful in reorganizing the plant's structure with potential altering mutations that allow divergence into new pathways of quality rather than the traditional high yield pathway of dent corn. Present specialty types involving changes in endosperm quality result from certain key switch genes interacting with adaptive complexes. These include flint, flour, meal, pop, waxy, several sweet types (*su*, *sh2*, *se*), and a high oil complex, as well as a high lysine (opaque-2) type still under adaptive development. All of these types involve breeding with the natural diversity within maize. Biotechnology derived switch genes, perhaps from legumes, may lead to protein breeding beyond high lysine, and other nutritional and medicinal substances of value to human health. This new dimension may allow a more efficient production of food plants necessary for larger populations of people tending to be vegetarians. The maize plant will still be designed to capture solar energy by photosynthesis although perhaps with a radial phyllotaxy rather than the present bilateral one, or perhaps a return to the more primitive branching habit of the teosinte ancestors of maize with the *tsb* (teosinte branched, chr.1S-Burnham) or *gt* (grassy-tiller,

TABLE 1. NUMBER OF PROGENY EARS WITH SINGLE (S) OR PAIRED (P) SPIKELETS IN TWO POPULATIONS GROWN FROM S AND P PARENTAL SEED BORNE IN VARIATION BY 24 PARENTAL EARS.

Parent ear	Total seed	Progeny from S			Progeny from P		
		Total	S	P	Total	S	P
2004	14	3	0	3	11	0	11
2006-4	22	14	1	13	8	1	7
2012	19	8	3	5	11	2	9
2013-1	25	11	4	7	14	0	14
2025-1	44	12	3	9	32	3	29
2028-5	18	2	1	1	16	4	14
2030-1	29	9	4	5	20	9	11
2030-4	13	8	2	6	5	0	5
2033	21	14	8	6	7	2	5
2035	19	6	3	3	13	4	9
2046-1	18	7	0	7	11	4	7
2046-2	46	21	7	14	25	9	16
2062-1	34	14	2	12	20	2	18
2088-1	29	7	3	4	22	2	20
2089	14	4	2	2	10	8	2
2091-2	24	13	4	9	11	4	7
2093	20	7	1	6	13	4	9
2097-2	16	6	0	6	10	2	8
2103-1	17	5	1	4	12	2	10
2124-1	28	8	3	5	20	4	16
2125-1	32	7	0	7	25	2	23
2127-1	10	4	0	4	6	4	2
2132	16	7	4	3	9	8	1
2192-2	64	40	13	27	24	11	13
Totals	592	237	69	168	355	91	264
% of totals		40%	12%	28%	60%	15%	45%
% within treatment			29%	71%		26%	74%

The above data was analyzed as a completely random design. The analysis of variance, one-way classification with unequal replication, was conducted according to the methods described by Steel and Torrie (1980).

unplaced-Shaver) or *tru* (tassel replaces upper ear, chr.3L-Sheridan) genes.

THE TRANSPOSON PROCESS

By looking into the genesis of maize, we not only see a distant mirror of the past, present, and possible future of maize, but we also, for the first time, substantiate the predication of McClintock that a transposon process regulates morphogenesis and evolution. This regulation is apparent with the *pd* gene that pairs the female spikelets, a condition that normally occurs in just the male spikelets of teosinte. Normally, the female spikelets of teosinte are solitary in adapting for the protective function of grain enclosure within a cupulate fruitcase. In breeding with intermediate lines between teosinte and maize, several stocks appeared in which the expression of paired and single spikelets variegated or fluctuated back and forth in an unstable manner similar to that ex-

pected for the incision and excision of a transposon (Fig. 5).

Progeny tests for the heritability of the differences between the single and paired condition on 24 ears were conducted. The data flow sheet is shown in Table 1.

The progeny ears classified as being paired (*Pd*) carried only paired spikelets while those classified as being single (*pd*) were actually variegated for both *Pd* and *pd* expression similar to the original mutant ear. In all 592 ears, only two were stable (100%) single spikelets. The results reveal a highly significant heritability for both paired spikelets (Table 2) and single spikelets (Table 3).

Because both the single and paired conditions on these variegated ears are inherited and because a pair of spikelets produces twice as many kernels as the single ones, the population would of its own accord shift to the paired condition without human help.

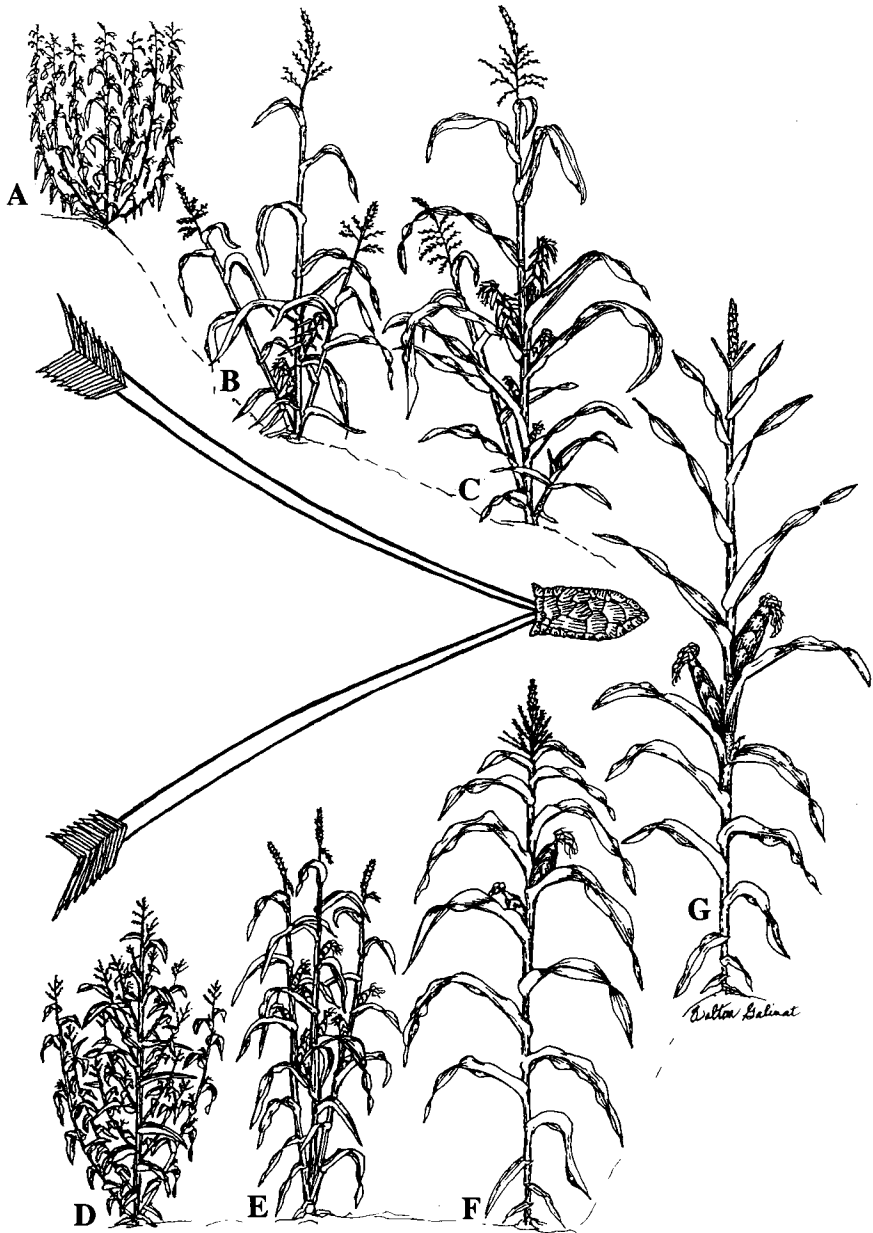


Fig. 6 (A-G). The evidence from plant habit corresponds to that from cob morphology in supporting two pathways of maize races tracing back to a double origin from two different teosintes (Galinat 1992). The two series of plant habits that may be termed the basal branching type and lateral branching type, both lead to the intermediate hybrid type, Corn Belt (G).

In the upper pathway, teosinte subspecies *parviglumis*, race Balsas (A) develops basal tillers under the most favorable growing conditions. When stunted, even at its center of origin, it may be tillerless. Next (B), the eight rowed flour corn indigenous to the upper Missouri area is similar to the proto-Chapalote of the Southwest, especially the Rio Grande Valley of New Mexico. Its ear appears to terminate an elevated, condensed tiller. Advancing to the Northern Flint (C), the ear node elevates to a more central position but its trail of ascent remains down to basal tillers. The Northern Flint of New England, New York and Canada appears to trace primarily to the Southwest although some early eight-rowed corn of the Nal Tel type came up the east coast after spreading across from Texas and Mexico. This basal branching habit is manifest by the grassy tiller (*gt*) mutant in advanced maize.

TABLE 2. NUMBER OF PAIRED SPIKELET EARS FROM SINGLE (S) SPIKELET SEED AND PAIRED SPIKELET EARS FROM PAIRED (P) SPIKELET SEED BORNE IN VARIEGATED EARS.

Trt	ri	Yij	Mean Yi	Y ² ij	Y ² i/ri	(Yij - mean Yi) ²
S	237	168	0.71	1846	119.1	1619.54
P	355	264	0.74	3970	196.3	3592.42
Sum	592	432		5816	315.4	5211.96

Analysis of variance for data summarized above.

Source of variation	df	SS	MS	F
Among treatments	1	288.84	288.84	32.71**
Within treatments	590	5211.96	8.83	
Total	591	5500.8		

The analysis of variance given above is significant; tabulated $F(0.005) = 7.88$ for 1 and 590 degrees of freedom. Therefore sufficient evidence exists to suggest that the mean number of paired spikelet types produced from single (0.71) and paired (0.74) spikelet type parent plants are different from reasons other than chance.

The data demonstrate an inherited component possibly of TE-like nature that is regulating *pd-Pd* expression and is passed on to the next generation. The random distribution of paired and single spikelets is mostly in the central third of the ear as shown in the figure, with increased pairing in the lower third and increased singles in the upper third. Two explanations for the gradient in pairing assume TE activity along the ear are suggested.

THE ENERGY DIFFERENCE

A gradient in energy (glucose) along the ear that is highest at the basal input, may under certain assumptions control pairing; assuming it requires more energy to proliferate a pair of spikelet primordia than solitary ones; assuming a relationship involving an increased energy (glucose) level that triggers TE movement away from the *Pd* locus in an excision reactivation of the second member of the pair. The same high energy environment that triggered TE movement

TABLE 3. NUMBER OF SINGLE SPIKELET EARS FROM SINGLE (S) SPIKELET SEED AND SINGLE SPIKELET EARS FROM PAIRED (P) SPIKELET SEED BORNE IN VARIEGATED EARS.

Trt	ri	Yij	Mean Yi	Y ² ij	Y ² i/ri	(Yij - mean Yi) ²
S	237	69	0.29	407	20.09	369
P	355	91	0.26	561	23.33	515.36
Sum	592	160		968	43.42	884.36

Analysis of variance for data summarized above.

Source of variation	df	SS	MS	F
Among treatments	1	40.4	40.4	26.93**
Within treatments	590	884.36	1.5	
Total	591	924.76		

The analysis of variance given above is significant; tabulated $F(0.005) = 7.88$ for 1 and 590 degrees of freedom. Therefore sufficient evidence exists to suggest that the mean number of single spikelet types produced from single (0.29) and paired (0.26) spikelet type parent plants are different from reasons other than chance.

also adapted the maize ear into becoming a larger energy sink. This is consistent with known energy transfers during enzyme activation and other important biological reactions (Wills 1989:174).

THE TEMPERATURE DIFFERENCE

It is known that transposition in bacteria and yeast is greatly stimulated by low temperatures and the enzyme responsible (Wills 1989: 132). At first glance, the patterns of *pd* variegation in the maize ear do not seem to fit the patterns that might be expected on a basis of temperature sensitivity by bacteria and yeast. In maize, the heat of the sun is applied externally and not necessarily synchronized with the start of ear development. The thicker layer of husk leaves over the lower third of the ear probably serves better to keep heat out rather than retain possible internal heat. While temperature does *not* seem to be the controlling factor in a structurally complicated and highly evolved organism such as maize, the fact that it does play a transposition role in primitive forms of life only lends support

← In the lower pathway, starting with teosinte subspecies *mexicana*, race Chalco (D), the first evolutionary advance is to a multi-eared popcorn such as Palomero Toloqueno (E). There is no trail of ears down to the tillers. The next and last step before hybridization is the Southern Dent represented by 'Gourd Seed' (F). Note its ramosa-like tassel. The lateral branching habit is manifest by the *tb* (teosinte branched) mutant and the *tru* (tassel replaces upper ear) mutant in advanced maize.

At the focal point, the Corn Belt Dent (G) unites the two pathways by hybridization between the Southern Dent and Northern Flint. Figure 6 is adapted from Galinat (1992).

to the possibility that energy such as glucose could serve a similar function in maize.

THE FUTURE

What the future holds for corn after the somewhat reluctant merger of traditional corn breeding with biotechnology is difficult to guess. In 500 years there may be as much difference between biotech corn and today's corn as there is between today's corn and teosinte. When biotech corn is used as a factory to manufacture drugs, hormones, enzymes, and proteins, we may reorganize the plant's structure with potential altering mutations that allow it to diverge along new pathways. The capturing of solar energy by photosynthesis and its storage as food and other products useful to humans has been, and will probably always be, the chief function of maize.

The deadly warfare between Indian tribes over attempts to gain agricultural land, food, slaves, and sacrificial victims to please their ancient gods must have impacted the origin and evolution of maize. There is evidence for at least two independent origins from different teosintes based on evidence from both cob morphology and plant habit (Galinat 1992) and possibly as many as five origins based on homologous complexes of chromosome knobs in maize and teosinte (Kato 1984). The two-origins hypothesis is illustrated with plant habit in the final figure (Fig. 6).

The great and powerful story of how modern Mexico emerged after freedom from tyranny and suffering is movingly portrayed in the murals painted by Diego Rivera in the Chapel of Chapingo (Rodriguez 1986). During the struggle, the seeds of new ideas of equality, justice, and ample food were planted and grew within brains. The ideas nourished a coevolution between maize and culture. Because the people won freedom and ample food, they became free at least to convert nature and society into a new paradise.

Like many others before me, perhaps I too have planted some seeds in your brains which you have the power to grow and nourish into more productive cornfields together with the beauty of a noble society, as represented by the advanced wheel of civilization devoid of warfare and starvation (Fig. 1B).

ACKNOWLEDGMENT AND DEDICATION

This paper is dedicated to my son, David, one of evolution's finest products and best observers. My own thinking and understanding of the

origin and evolution of maize has always been harmonized with his keen perceptions.

LITERATURE CITED

- Beadle, G. W.** 1972. The mystery of maize. *Field Mus. Nat. Hist. Bull.* 43(10):2-11.
- . 1980. The ancestry of corn. *Sci. Am.* 242(1): 112-119.
- Doebley, J. F., A. Stec, J. F. Wendel and M. Edwards.** 1990. Genetic and morphological analysis of a maize-teosinte F2 population: implications for the origin of maize. *Proc. National Academy of Science, USA* 87:9888-9892.
- Dorweiler, J., A. Stec, J., Kermicle and J. Doebley.** 1993. Teostinte glume architecture-1-a genetic locus controlling a key step in maize evolution. *Science* 262:233-235.
- Galinat, W. C.** 1973. Intergenomic mapping of maize, teosinte and *Tripsacum*. *Evolution* 27:644-655.
- . 1992. Evolution of corn. Pages 203-231 in D. L. Sparks ed., *Advances in Agronomy* 47. Academic Press, Inc., New York.
- . 1994. The identity of *Mga* (maize glume architecture) on 4S confused with a multiple allelic series at the *Tu* (tunicate) locus. *Maize Genetics Cooperative Newsletter*. 68:109.
- Kato-Y, T. A.** 1984. Chromosome morphology and the origin of maize and its races. *Evol. Biol.* 17: 219-253.
- Kaufmann, S. A.** 1993. *The origins of order*. Oxford University Press, New York, NY.
- Langham, D. G.** 1940. The inheritance of intergeneric differences in *Zea-Euchlaena* hybrids. *Genetics* 25: 88-108.
- Long, A., B. F. Benz, D. J. Donahue, A.J.T. Jull, and L. J. Toolin.** 1989. First Direct AMS dates on Early Maize from Tehuacán, Mexico. *Radiocarbon* 31: 1035-1040.
- Mangelsdorf, P. C. and W. C. Galinat.** 1964. The tunicate locus in maize dissected and reconstituted. *Proc. National Academy of Science. USA* 51:147-150.
- Rodriguez, A.** 1986. Canto a la tierra, Los murales de Diego Rivera en la Capilla de Chapingo, Universidad Autonoma Chapingo, Mexico.
- Rogers, J. S.** 1950. The inheritance of inflorescence characters in maize-teosinte hybrid. *Genetics* 35: 541-558.
- Steel, R.G.D. and J. H. Torrie.** 1980. *Principles and Procedures of Statistics A Biometrical Approach*. 2nd Edition. McGraw-Hill Book Company.
- Tavcar, A.** 1935. Beitrag zur Vererbung der Kornreihenanzahl on Mais-Kolben. *Zeits f. Zuchtung. Reige A. Pflanzenzuchig.* 20:364-376.
- Wills, C.** 1989. *The wisdom of the genes*. Basic Books. Dunmore, PA.