

Plant evolution: **The dominance of maize**

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The gene *teosinte branched 1* controls major differences in architecture between cultivated maize and its wild ancestor. The differences correlate with different amounts of gene product.

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Maize was domesticated in Mexico, from a wild grass known as teosinte. Six thousand years later, the story of that event (or events) has both evolutionary biologists and geneticists excited. It is unquestionably the best example of how major morphological changes might occur in response to selection. The maize ear, or corn cob, is a monstrosity. There is no other structure quite like it in the plant kingdom, so its origin has been, if not quite an abominable mystery, at least obscure. Classical taxonomic data showed clearly that the origin of maize had to involve grasses either in the genus *Tripsacum* (gamagrass) or in what is now the genus *Zea* (teosinte and maize). But which species? The literature was long on verbiage and short on data, until the late 1970s, when John Doebley and his advisor Hugh Iltis (at the University of Wisconsin) decided that the solution would be to look at a part of the plant not affected by human selection.

The ear is actually an inflorescence made up entirely of female flowers (Fig. 1a). The male flowers are at the top of the plant in a separate, branched inflorescence, the tassel. Because human selection has apparently had its greatest effect on the ear, Doebley and Iltis turned their attention to the male flowers in the tassel, which they compared to the male flowers in teosinte and gamagrass. The result of this study was a revision of the taxonomy, and a suggestion that maize (*Zea mays* ssp. *mays*) was very similar to *Zea mays* ssp. *mexicana* and *Zea mays* ssp. *parviglumis*, both known as teosinte [1,2]. In subsequent work, Doebley (now at University of Minnesota) followed up on his morphological work and found that the subspecies of *Zea mays* were also similar in isozyme profiles, chloroplast genomes and shared polymorphisms in nuclear genes [3]. This apparently laid to rest the question of the ancestor of maize.

The evolutionary pattern, though, is only part of the story. The process was still unknown. How could something like teosinte give rise to an oddity like maize? In the case of other domesticated species, the genetic basis of the domestication process is fairly easy to see. In wheat, for instance, early agriculturalists selected for floral stalks that did not break apart when the seed was ripe, and later selected for plants with seeds that were easily separated from their surrounding floral bracts. But a domesticated wheat plant looks quite similar to a wild wheat plant. This is not the case with teosinte and maize.

Figure 1

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The genetic basis of the distinction was far from obvious. The teosinte plant branches from its base and then produces branches on those branches, so that at maturity it looks like a candelabra, quite different from the pole-like architecture of maize (Fig. 1b) [4]. Each major branch in teosinte ends in a tassel of male flowers. Only the secondary branches produce ears of female flowers. Furthermore, the ear of teosinte looks nothing like the ear of maize. The female flowers of teosinte, and therefore its seeds, are enclosed in outgrowths of the floral stalk plus a floral bract (glume), which surround the developing fruit (Fig. 1a). At maturity, these become extremely hard, and look like small shiny pebbles. In the maize ear, on the other hand, the fruits (kernels) are exposed; the floral stalk does not grow out, and the bracts are small and soft.

Fortunately, teosinte and maize can be crossed to produce fertile progeny. The cross was made by Mangelsdorf and Reeves [5] in the 1930s, to test their theory that maize was a hybrid between teosinte and gamagrass. (There is no current evidence for this theory, although recent data show that the entire genus *Zea* may be a segmental allotetraploid formed by a much more ancient cross of disparate ancestors about 11 million years ago — long before the divergence of teosinte and maize [6].) In looking at the progeny of the teosinte–maize cross, George Beadle recognized that only a few genes differentiated the parents, perhaps no more than five [7]. Doebley and his colleague Adrian Stec repeated Beadle's experiment, but with the added help of the tools of quantitative trait locus mapping, and the tremendous power of maize genetics. Doebley and Stec crossed maize with *Zea mays* ssp. *mexicana* [8], and later with *Zea mays* ssp. *parviglumis* [9], and found that Beadle had been correct: there were five regions, perhaps corresponding to single genes, with major effects on the characteristics that differentiate maize and teosinte.

The next challenge was to characterize, and perhaps clone, those loci. In a recent issue of *Nature*, Doebley, Stec and Lauren Hubbard [10] describe the gene *teosinte branched 1* (*tb1*), which corresponds to one of the five loci of major effect. They have introgressed the chromosome segment containing the maize allele into teosinte and find that it changes the plant architecture from the candelabra-like teosinte into the pole-like maize. From this, they infer that *tb1* affects apical dominance, which is the hormonal control exerted by the apical bud of a stem on all lower buds [11]. With strong apical dominance, lower buds on the stem fail to grow out and produce branches; when the apical bud is removed, however, the buds are then permitted to grow out. (This is the principle behind trimming a hedge, in which the removal of apical buds allows additional branching.)

Doebley, Stec and Hubbard cloned *tb1* by transposon-tagging with a *Mutator* element. Amino acid sequences of

tb1 from four maize lines and four teosinte collections showed that there were no fixed differences between the wild grasses and the cultigen. Transcripts of the genes in maize and teosinte were the same size, but the amount of *tb1* RNA was greater in maize. This suggests that the evolution of maize involved changing the regulation of *tb1* such that it was expressed at higher levels and in different parts of the plant.

The DNA sequence of *tb1* is similar to that of the snapdragon gene *cycloidea* (*cyc*). Like *cyc*, *tb1* affects development of perianth parts (called lodicules in the grasses) and stamens [12], but unlike *cyc*, *tb1* also affects development of branches. The difference in expression pattern between the two genes could be caused by modifications in the millions of years since the divergence of dicots (leading to snapdragon) and monocots (leading to maize). Alternatively, there may be other genes yet to be found in the *cyc/tb1* class. If this is the case, the maize orthologue of *cyc* may be more similar to it in sequence and expression pattern than *tb1* is.

The other four loci are also under study. One, which maps close to the known maize loci *terminal ear1* or *tassel replaces upper-ear1*, interacts with *tb1*. A second, *teosinte glume architecture* (*tga*) affects the peculiar outgrowth of the floral stalk and bract [13]. As with *tb1*, the maize allele of *tga* has been introgressed into teosinte, and *vice versa*. This showed that the gene affects the outgrowth of the stalk, the orientation of the floral bract, the development of lignin (which affects how soft the bract will become) and the shininess of the surfaces. The remaining two loci have yet to be identified, but are known to lie on chromosomes 2 and 5. The former affects the number of rows of kernels, and the latter affects not only number of rows, but also number of female inflorescences [9].

The identification and description of *tb1* is thus another chapter in the story of maize domestication. But the results have broader implications, because the control and modification of plant architecture are agronomically important. In many crops, the domesticated varieties are less branched than their wild relatives, allowing closer planting and less self-shading. In forestry as well, trees with strong apical dominance (less branching) are often preferred because these give the longest straight stretches of trunk from which to make logs. In addition, many plants modify their degree of branching in response to environmental conditions. (In the second growth forests of the northeastern United States, for example, it is easy to spot a tree that grew up when the area was in pasture — it is far more extensively branched than the trees around it.) The analysis of the *tb1* gene seems likely to provide a window on this process.

Equally important, evolution by artificial selection (domestication) is a model for evolution by natural selection, an

analogy used effectively by Darwin in *The Origin of Species*. If we can understand the genetic changes that occurred to create maize from teosinte, then we may understand more about how organisms change form in evolutionary time. The data on *tb1* and *tga* reinforce the idea that much morphological change can be attributed to only a few loci of relatively large effect. Other studies of quantitative trait loci suggest that this result may be general, even for traits that appear superficially to be quantitative and continuously varying [14].

It is sometimes tempting to equate ‘genes of large effect’ with ‘macromutations’. In terms of the phenotype, ‘large effect’ is easily defined as some large percentage of the variance of trait. In the case of maize, ‘large effect’ also has an anthropocentric definition — the mutant (cultivated maize) is of enormous economic importance. It is less clear what constitutes a large (macro) mutation. A point mutation probably does not count, whereas a genome rearrangement probably does. As genes like *tb1* are cloned and the ancestral and descendant alleles compared, we will learn the nature of the molecular change that led to the phenotype. Doebley, Stec and Hubbard [9] have shown that the maize and teosinte alleles of *tb1* differ in amount of the gene product, but do not reflect a major disruption or alteration of the gene sequence. In this case, therefore, a large effect on the phenotype — a substantial difference in plant architecture — apparently comes from a modest change in the regulation of a single gene. Ongoing work by Doebley and his colleagues will soon tell us what the change is. It seems likely that one small step for the genome was truly a giant leap for mankind.

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