

involve a nutrition-induced signal that would render each individual primordia cell insensitive to juvenile hormone–induced growth inhibition. This would not explain, however, why the same primordia cells are sensitive to juvenile hormone in early-stage feeding larvae but become resistant in the last instar. Alternatively, a signal that is dominant over juvenile hormone and that is triggered by nutrition at this specific stage could do the job. The existence of such a “metamorphosis initiating factor” is suggested both by Truman *et al.* and by another recent study (7). Its nature and the mechanisms leading to its specific activation by nutrition at the start of the last-instar larva remain to be identified.

Finally, the sustained presence of juvenile hormone in starved animals suggests that the endocrine tissue that produces this hormone might respond to nutrition and modulate its pro-

duction or secretion accordingly. During food deprivation and in the absence of a metamorphosis initiating factor, juvenile hormone would prevent disc formation. Another possibility comes from recent studies in *Manduca*'s cousin, the fruit fly *Drosophila melanogaster*, that implicate a larval tissue called the fat body (the equivalent of both vertebrate liver and fat tissue) in orchestrating nutritional responses (8, 9). The larval fat body is an important source of juvenile hormone esterase, an enzyme that degrades the hormone to control its circulating levels. One possible scenario is that the fat body, acting as a nutrition sensor, modulates circulating amounts of juvenile hormone by producing the esterase and thereby directs imaginal disc development. The temporal control of this process is an intriguing issue that also needs to be addressed. Possible answers to these questions may come by extending these

results to the genetically amenable *Drosophila* model, where new roles for juvenile hormone in development, growth, and morphogenesis are prime for exploration.

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PLANT SCIENCE

Unfallen Grains: How Ancient Farmers Turned Weeds into Crops

John Doebley

Some 10,000 years ago during the agricultural revolution, ancient farmers bred hundreds of wild species into the domesticated crops on which humans are dependent today. During this process, these ancient peoples saved seeds from plants with favored traits to form each subsequent generation, and over time they converted slender and unpromising wild species into reliable, bountiful crops. Variants or mutants of genes that conferred favorable phenotypes rose in frequency over time, while variants that best adapted plants to life in the wild were removed by selection from the domesticated population.

Foremost among the creations of ancient plant breeders are the cereals—rice, wheat, and maize, a triumvirate that provides more than 50% of the calories consumed by humans. As compared to their progenitors, these cereals have more and larger grains, thicker stalks, seed that thresh freely from the chaff, and improved flavor. The cereals, and most other crops, share one additional feature that is central to domestication: Their grains remain attached to the plant for harvest by humans rather than falling (shattering) from the plant, as required for wild species to produce their next generation. Although quantitative trait locus (QTL) mapping (1) has convincingly shown that the evolution of domestication traits



Gathering grain. Two agricultural workers harvesting rice in Yangshuo, Guangxi Province, China.

such as the loss of shattering arose through a relatively small number of gene changes, the nature of these genes and the molecular changes within them is not well understood.

In research published in *Science* earlier this year (2) and on page 1392 of this issue (3), groups in the United States and Japan take two

Cereals are the world's primary food, but if they are to be harvested grains must remain on the plant. Two of the genetic changes responsible for this essential trait for domestication have been identified.

big steps toward bridging the gap between domestication QTLs and domestication genes. Li *et al.* (2) cloned *shattering4* (*sh4*), a gene first identified by this group as a major QTL controlling 69% of the variance for shattering in crosses of wild and cultivated *indica* rice. This team was able to localize the causative difference to a 1700–base pair region, and then to demonstrate that a single amino acid change is principally responsible for the loss of shattering. An extraordinary feature of the cultivated allele of *sh4* is that it severely weakens but does not eliminate shattering. Thus, the grains are retained on the plants long enough for harvest, but then they can be removed easily by threshing.

Konishi *et al.* (3) identified a second major shattering QTL (*qSH1*) in a cross of the two independently domesticated forms of rice, *indica* and *japonica*. This QTL controls 68% of the variation for shattering in this hybrid population, and the authors cloned the gene and mapped the causative difference to a single nucleotide change. An absolutely exquisite result is that this single nucleotide change in cultivated rice obliterates a cis-regulatory element required for the expression of *qSH1* in the abscission layer, which is needed for the grain to break away from the plant. Other cis-regulatory elements in *qSH1* are conserved between wild and cultivated rice, and thus *qSH1* still fulfills its other functions in the inflorescence of cultivated rice.

These two rice genes join the growing number of plant domestication QTLs cloned to date.

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In 1997, the maize gene *tb1* was reported as the first domestication QTL to be cloned (4). *tb1* controls the complex differences in plant architecture between maize and its progenitor, teosinte. In 2000, a major QTL (*fw2.2*) contributing to the massive increase in fruit size that was a central feature of tomato domestication was cloned (5). In 2005, the maize domestication QTL *tga1*, which provides naked grains to maize (as opposed to the covered grains of teosinte), was cloned (6). And thus far in 2006, in addition to the two rice shattering genes, cloning of the wheat *Q* gene was reported (7). *Q* controls the compaction and fragility of the ear of wheat and also the ease with which the grain can be separated from the chaff.

A notable feature of this list of six domestication genes is that five of the six encode transcription factors that regulate other (target) genes by directly binding to their DNA. Transcription factors represent only about 5% of genes in plant genomes (8, 9) but 83% of the domestication genes listed above. Interestingly, the five domestication transcription factors belong to five separate families: TCP (*tb1*), SBP (*tga1*), AP2 (*Q*), MYB3 (*sh4*), and HOX (*qSH1*). This suggests that the exaggerated proportion of transcription factors among domestication genes is the product of some general feature of transcription fac-

tors and not of one particular class of transcription factors. The predominant role of transcription factors in domestication mirrors their equally large role in controlling plant development (10), which supports the view that they have properties that predispose them to become the major genes contributing to morphological evolution in plants (11).

Another remarkable feature of this list is that the domesticated alleles of all six genes are functional. If domestication involved the crippling of precisely tuned wild species, one might have expected domestication genes to have null or loss-of-function alleles. Rather, domestication has involved a mix of changes in protein function and gene expression. As a consequence of domestication, *sh4* shows changes in protein function and expression level (2), *qSH1* shows a change in the spatial pattern of its expression (3), *tb1* shows increased expression (4), *tga1* shows a change in protein stability or protein function (6), *fw2.2* shows a heterochronic shift in its expression (5), and *Q* shows changes in protein function and gene expression (7). Given that the cultivated allele of not one of these six domestication genes is a null, a more appropriate model than “crippling” seems to be adaptation to a novel ecological niche—the cultivated field. Tinkering and not disassembling is the order of

the day in domestication as in natural evolution, and Darwin’s use of domestication as a proxy for evolution under natural selection was, not surprisingly, right on the mark.

A consequential question now is whether modern plant breeders might borrow from the playbook of their Neolithic predecessors. Might one tinker with the expression patterns or protein functions of known domestication genes to create superior alleles? Can every transcription factor in the genome be manipulated in a systematic manner to generate a pool of new trait variation? Knowledge of past successes should help to intelligently guide future crop improvement.

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PLANETARY SCIENCE

Exploring Other Worlds to Learn More About Our Own

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The exploration of our solar system was originally driven primarily by curiosity and the search for answers to the eternal question: Are we alone? As the first spacecraft began to visit our neighboring planets in the solar system, hopes of finding life quickly faded and instead the focus began to shift toward gaining a more scientific understanding of their nature and history. After a generation of exploratory robotic spacecraft missions from the 1960s through the 1980s, it became clear that most planets—except Mercury—and some moons had permanent and substantial atmospheres. These atmospheres can be subdivided into three large families: those composed primarily of nitrogen (Earth, Titan, Triton, Pluto), carbon dioxide (Venus, Mars), and hydrogen/helium (Jupiter, Saturn, Uranus, Neptune). On page 1366 of this issue, Forbes et

al. (1) provide fresh insights into the effects of variations in solar radiation intensity on the upper atmospheres of Mars and Earth, which have now been simultaneously observed.

Numerous space missions, along with Earth-based observations and theoretical models, have given us an unprecedented understanding of planetary atmospheres. Yet some of their fundamental prop-

Energy flow on Mars. Solar ultraviolet radiation heats the dayside to 300 K; winds transport some of this energy toward the nightside, where temperatures are typically lower by 100 K. On the dayside, vertical conduction and adiabatic cooling offset solar heating, whereas the nightside temperatures are raised by adiabatic heating. A portion of the solar energy is radiated back into space through infrared cooling by CO₂.

Simultaneous observations of the drag of satellites through the upper atmospheres of Mars and Earth reveal how carbon dioxide is differentially cooling their upper atmospheres.

erties are still poorly understood, including the atmospheric energy balance (see the figure). What are the sources of energy incident upon an atmosphere, how is this energy redistributed

