

The Hot and the Classic

Because cereal grains account for more than one-half of all agricultural crop production, they have always been at the forefront of applied and basic plant research. A citation analysis of the literature confirms the general theme of this Special Issue: The cereal plants are, in their own right, an experimental model system of great merit. In the analyses presented here and in the inaugural version of *The Hot and the Classic* (December 2000 issue), reviews and technique papers, although of obvious importance to the progress of science, were excluded because they tend to be cited disproportionately more often than do experimental papers. Also excluded from consideration in the present case were those papers in which a grass species was studied only secondarily. Presented below are summaries of the most cited cereal grain articles for each year of the 1990s.

1990: Maize opaque-2 (o2) Gene Is a Transcription Factor

The o2 mutation of maize (*Zea mays*) effects a phenotypic change from hard glassy kernels to seeds with soft powdery endosperm that are opaque to light. This change is correlated with a reduction in the transcription and quantity of zein storage proteins. Schmidt et al. (1990) report that the O2 protein shares sequence similarity with the Leu zipper DNA-binding domain characteristic of mammalian oncogenes and fungal transcription activation factors. The Leu zipper domain of O2 apparently interacts directly with one or more zein promoter elements.

1991: Maize viviparous-1 (vp1) Is a Transcriptional Activator

Viviparous mutants of maize do not enter dormancy during seed maturation. Most viviparous mutants are caused by dysfunctions in the synthesis of abscisic acid or its precursors, but the vp1 mutant is exceptional. Mc-

Carty et al. (1991) demonstrate that the maize vp1 gene encodes for a protein with no detectable homology to any known proteins but which contains an acidic transcriptional activation sequence. These results indicated that VP1 is a novel transcription factor possibly involved in the potentiation of a seed-specific abscisic acid response.

1992: Quantitative Trait Loci (QTL) in Maize

To explore heterosis (hybrid vigor) and genotype-by-environment interaction in maize, Stuber et al. (1992) mapped QTLs associated with seven major traits (including grain yield) in a cross between two maize inbred lines. Whenever a QTL for grain yield was detected, the heterozygote had a higher phenotype than the respective homozygote (with only one exception), suggesting not only overdominance but also that these detected QTLs play a significant role in heterosis. This conclusion was reinforced by a high correlation between grain yield and proportion of heterozygous markers. Although plant materials were grown and measured in six diverse environments, there was little evidence for genotype-by-environment interaction for most QTLs.

1993: Bt Toxin Genetically Engineered into Maize

Koziel et al. (1993) introduced a synthetic gene encoding a truncated version of the CryIA(b) protein derived from *Bacillus thuringiensis* (*Bt*) into immature maize embryos. Plants expressing high levels of the insecticidal *Bt* protein exhibited excellent resistance to heavy infestations of European corn borer (*Ostrinia nubilalis*) under field conditions.

1994: KNOTTED1-Related Homeobox Genes Predict Patterns of Morphogenesis

Mutations of the *KNOTTED1* gene of maize perturb specific aspects of

maize leaf development. Jackson et al. (1994) describe the expression patterns of a family of homeobox genes related to *KNOTTED1* in maize. Four members of this gene family are expressed in shoot meristems and the developing stem, but not in determinate lateral organs such as leaves or floral organs. The genes show distinct expression patterns in the vegetative shoot apical meristem that together predict the site of leaf initiation and the basal limit of the vegetative "phytomer" or segmentation unit of the shoot.

1995: Cloning of a Disease Resistance Gene in Rice

Song et al. (1995), in the first successful use of positional cloning in cereals, isolate the rice (*Oryza sativa*) *Xa21* gene, which confers resistance to *Xanthomonas oryzae*. Fifty transgenic rice plants carrying the cloned *Xa21* gene displayed high levels of resistance to the pathogen. The sequence of the predicted protein, which carries both a Leu-rich repeat motif and a Ser-Thr kinase-like domain, suggest that it may play a role in the recognition of a pathogen-derived ligand at the cell surface and the subsequent activation of an intracellular defense response.

1996: Nested Retrotransposons in Maize

Plant genomes consist of repetitive DNA sequences intermixed with genes. The maize genome, for example, contains about 60% to 80% repetitive DNA. Diagnostic sequencing by SanMiguel et al. (1996) indicated that a 280-kb region containing the maize *Adh1-F* and *u22* genes is composed primarily of retrotransposons inserted within each other. Ten retroelement families were discovered, with reiteration frequencies ranging from 10 to 30,000 copies per haploid genome. These retrotransposons accounted for more than 60% of the *Adh1-F* region and at least one-half of the nDNA of maize. These elements were largely in-

tact and are dispersed throughout the gene-containing regions of the maize genome.

1997: Barley *mlo* Disease Resistance Gene Isolated

Barley (*Hordeum vulgare*) that is homozygous recessive at the *Mlo* locus exhibits spontaneous formation of leaf lesions as well as broad-spectrum resistance to the fungal pathogen *Erysiphe graminis*. Buschges et al. (1997) isolated the *mlo* gene using positional cloning. The deduced protein was homologous to other functionally unidentified amino acid sequences in plants, but showed no homology to any known proteins outside the kingdom Plantae. The *mlo* protein appears to be membrane anchored by at least six membrane-spanning helices. Functional *mlo* proteins may play a role in slowing or preventing leaf cell death, and their absence may prime the defense systems of the plant to respond more quickly to pathogen attack.

1998: Rapid Reorganization of R-Gene Homologs

Plant resistance to particular pathogens involves recognition events that are race specific and triggered by corresponding resistance (*R*) genes in the host and avirulence (*Avr*) genes in the pathogen. Leister et al. (1998) took advantage of conserved domains in the major class of dicot resistance *R* genes to isolate related gene fragments via PCR from rice and barley. Interspecific analyses of *R*-like genes frequently revealed non-syntenic map locations between the cereal species rice, barley, and foxtail millet (*Setaria italica*), although tight collinear gene

order is a hallmark of monocot genomes. These data suggest a dramatic rearrangement of *R*-gene loci between related species and imply a different mechanism for nucleotide binding site plus Leu-rich repeat gene evolution compared with the rest of the monocot genome.

1999: Molecular Biology of Maize Domestication

Maize and teosinte (*Z. mays* subsp. *meticana*) display profound morphological differences, the major one being that teosinte has long branches with tassels at the tip, whereas maize has short branches tipped by an ear. The *teosinte branched-1* (*tb1*) gene is thought to be a major determinant of these morphological differences. Wang et al. (1999) examined nucleotide polymorphism in *tb1* in a wide variety of accessions of teosinte and maize, and determined that the effects of selection were limited to the gene's regulatory region and could not be detected in the protein-coding region. These results help to explain why maize is such a variable crop, and confirm previous evidence that maize was domesticated from teosinte indigenous to southwestern Mexico.

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