

formation used by regulatory agencies, such as the U.S. EPA, are generally limited in their predictive power by relying on experiments that give parameterized aerosol yields from reacting precursor compounds. Incorporation of the chemical mechanisms derived experimentally by Paulot *et al.* into deterministic models of gas-aerosol chemistry should help to improve their predictive capabilities.

#### References

1. F. Paulot *et al.*, *Science* **325**, 730 (2009).
2. A. Guenther *et al.*, *J. Geophys. Res.* **100**, 8873 (1995).
3. B. J. Finlayson-Pitts, J. N. Pitts Jr., *Science* **276**, 1045 (1997).
4. C. E. Reeves, S. A. Penkett, *Chem. Rev.* **103**, 5199 (2003).
5. M. Claeys *et al.*, *Science* **303**, 1173 (2004).
6. E. O. Edney *et al.*, *Atmos. Environ.* **39**, 5281 (2005).
7. J. H. Kroll *et al.*, *Environ. Sci. Technol.* **40**, 1869 (2006).
8. D. K. Henze, J. H. Seinfeld, *Geophys. Res. Lett.* **33**, (2006).
9. M. Kalberer *et al.*, *Science* **303**, 1659 (2004).
10. J. Lelieveld *et al.*, *Nature* **452**, 737 (2008).
11. A. Hofzumahaus *et al.*, *Science* **324**, 1702 (2009).
12. T. J. Dillon, J. N. Crowley, *Atmos. Chem. Phys.* **8**, 4877 (2008).
13. M. E. Jenkin *et al.*, *Phys. Chem. Chem. Phys.* **10**, 4274 (2008).
14. J. Peeters *et al.*, *Phys. Chem. Chem. Phys.* **11**, (2009).
15. J. A. Thornton *et al.*, *J. Geophys. Res.* **107**, 4146 (2002).
16. X. Ren *et al.*, *J. Geophys. Res.* **113**, D05310 (2008).

10.1126/science.1178324

## GENETICS

# A-maize-ing Diversity

Trudy F. C. Mackay

**M**aize (*Zea mays*)—corn—is a staple food source in much of the world, as well as a source of cooking oil, grain alcohol, livestock feed, and biofuel. There is enormous quantitative variation among maize strains for traits of agronomic importance, due to allelic variation at multiple quantitative trait loci (QTLs) with effects that are sensitive to the environment. Knowledge of the genetic basis of this variation (see the figure) would be a major boon to selective breeding programs, but has been hindered by the difficulty of mapping the underlying QTLs. On pages 714 and 737 of this issue (1, 2), Buckler and colleagues describe the genetic properties of a new resource for mapping maize quantitative traits (3), and discuss the genetic architecture of a key trait—flowering time—derived from it.

The molecular basis of quantitative genetic variation remains unclear because accurate phenotypes and high-density molecular marker genotypes for tens of thousands of individuals are needed to map QTLs whose effects are not large. In addition, the resolution of DNA recombination—the exchange of genetic material between homologous chromosomes—must be high enough to identify the genes involved. Linkage mapping can readily detect chromosomal regions containing one or more QTLs that affect a trait, with samples of several hundred individuals and molecular markers, but it is difficult to precisely localize the QTLs (4). This approach usually relies on crosses between two strains, thus capturing only a tiny fraction of genetic diversity in the population. By contrast, association mapping widely samples genetic diversity and requires fewer

individuals (4), but has less power to detect QTLs when alleles are not common. Thus, precision of localization comes at the expense of high-resolution genotyping. Association mapping is also highly sensitive to spurious false positives that result from recent mixing of populations with different allele frequencies and values of the quantitative trait.

Buckler and colleagues combine the benefits of linkage and association mapping in a single population through a nested association mapping (NAM) approach. The maize NAM population was derived by crossing a common reference sequence strain to 25 different maize lines. Individuals resulting from each of the 25 crosses (families) were self-fertilized for four further generations, to produce 5000 NAM recombinant inbred lines. This NAM population can be used for initial QTL detection using linkage mapping with moderate numbers of markers, followed by a second stage of high-resolution association mapping in QTL regions that capitalizes on a high-density marker map within each diverse strain. Because all individuals within a given recombinant inbred line are nearly genetically identical, the phenotype of the same quantitative trait can be scored for multiple individuals of the same genotype, increasing the accuracy of estimating the true genotypic value of each line. The same lines can also be evaluated for many quantitative traits and in multiple environments, providing a valuable resource for

understanding the genetic basis of pleiotropy (single gene effects on multiple traits) and genotype-environment interactions.

McMullen *et al.* (1) genotyped 4699 lines of the NAM population for 1106 single-nucleotide polymorphisms (SNPs), giving a composite genetic map with an average marker density of one SNP per 1.3 cM and a total of 136,000 recombination events. From 63 to 74% of the SNPs were polymorphic in any given family. Substantial variation in recombination was not attributable to QTLs with general effects on recombination, but rather to numerous and localized regions of variation in recombination that are specific to each family. Unfortunately, variation in recombination confounds combining linkage and association mapping of QTLs—the intention of the NAM design—which assumes constant recombination frequencies across populations. Otherwise, the NAM population is an excellent resource for QTL mapping, with nearly equal representation of genetic material from both founder lines in all of the 25 families in the NAM population.

Buckler *et al.* (2) used the NAM population to map QTLs affecting flowering time in nearly 1 million plants representing all the NAM lines, and also in a separate set of 282 strains that represent maize diversity, in each of four different environments and in two different years. Depending on the analysis performed, a range of 29 to 56 QTLs were found to affect flowering time. Most were shared among multiple families; however, the effects varied among families, which suggests that common QTLs with different low-frequency alleles affect



**Diverse corn.** The genetic diversity of maize can explain the vast phenotypic variation observed across strains.

Department of Genetics, Campus Box 7614, North Carolina State University, Raleigh, NC 27695, USA. E-mail: trudy\_mackay@ncsu.edu

variation in flowering time. The effects of all QTLs were, however, small. Tests for epistasis and genotype-environment interactions revealed very little contribution of context-dependent effects to the genetic architecture of flowering time.

Using the NAM population for high-resolution recombination mapping will not be possible until the parent strains are genotyped for a dense panel of molecular markers. The large numbers of QTLs, small effects, and likelihood of identifying novel genes affecting quantitative traits from dissection of natural genetic variation pose a challenge for functional validation.

The observation of large numbers of QTLs with small effects on flowering time is consistent with results from mice, flies (*Drosophila melanogaster*), and humans for many different quantitative traits (5). However, the lack of QTLs with large effects is in contrast to the genetic architecture of flowering time in rice, barley, sorghum, and the model flowering plant *Arabidopsis thaliana*, where large-effect QTLs account for most of the observed

variance (6–9). The trivial contribution of epistasis is also in contrast to epistatic interactions affecting flowering time in *Arabidopsis* (10) and rice (11), as well as the common occurrence of epistasis affecting quantitative traits in *Drosophila* and mice (5). Genotype-environment interaction is also a typical feature of the genetic architecture of quantitative traits in *Drosophila* and mice (5). The extent to which mating system, demography, sampling, experimental design, and relationship to fitness contribute to the genetic architecture of quantitative traits is an open question.

Genetic variation for most quantitative traits in most organisms may well be attributable to large numbers of loci with small effects. What, then, is the future of genetic dissection of complex traits? Rather than analyzing one gene at a time, we will need to understand how molecular variants affect quantitative traits through correlated networks of transcripts, proteins, and metabolites. The NAM population joins the mouse Collaborative Cross (12), the *Drosophila* Genetic Reference Panel (13), and the *Arabi-*

*opsis* 1001 Genomes Project (14) projects as a community resource population suitable for such systems' genetics analysis (15, 16).

#### References and Notes

1. M. D. McMullen *et al.*, *Science* **325**, 737 (2009).
2. E. S. Buckler *et al.*, *Science* **325**, 714 (2009).
3. J. Yu *et al.*, *Genetics* **178**, 539 (2008).
4. T. F. C. Mackay, *Annu. Rev. Genet.* **35**, 303 (2001).
5. J. Flint, T. F. C. Mackay, *Genome Res.* **19**, 723 (2009).
6. C. Alonso-Blanco, S. E. El-Assal, G. Coupland, M. Koornneef, *Genetics* **149**, 749 (1998).
7. M. Yano *et al.*, *Theor. Appl. Genet.* **95**, 1025 (1997).
8. A. Turner, J. Beales, S. Faure, R. P. Dunford, D. A. Laurie, *Science* **310**, 1031 (2005).
9. Y. R. Lin, K. F. Schertz, A. H. Paterson, *Genetics* **141**, 391 (1995).
10. M. E. El-Lithy *et al.*, *Genetics* **172**, 1867 (2006).
11. N. Uwatoko *et al.*, *Euphytica* **163**, 167 (2008).
12. G. A. Churchill *et al.*, *Nat. Genet.* **36**, 1133 (2004).
13. [www.hgsc.bcm.tmc.edu/project-species-i-Drosophila\\_genRefPanel.hgsc?pageLocation=Drosophila\\_s.Medline](http://www.hgsc.bcm.tmc.edu/project-species-i-Drosophila_genRefPanel.hgsc?pageLocation=Drosophila_s.Medline)
14. D. Weigel, R. Mott, *Genome Biol.* **10**, 107 (2009).
15. S. K. Sieberts, E. E. Schadt, *Mamm. Genome* **18**, 389 (2007).
16. M. V. Rockman, *Nature* **456**, 738 (2008).
17. Supported by NIH research grant GM45146.

10.1126/science.1178420

## PHYSICS

# Quantum Football

Franco Nori

Quantum information processing is usually based on two-level quantum systems, called quantum bits or qubits, but the use of additional quantum levels can simplify some quantum computations. It can also allow the emulation of other quantum systems, in which one quantum system acts as an analog of another and allows it to be better understood by reproducing its dynamics in a more controllable manner. On page 722 of this issue, Neeley *et al.* (1) demonstrate the operation of a superconducting circuit with five quantum levels, and show how to manipulate and measure its quantum states. They used this circuit to emulate the dynamics of single spins with various quantum numbers, including the measurement of their geometric phases that result from spin rotations. This extension of the two-level qubit to a multi-level “qudit” opens possibilities for richer quantum computing architectures and better emulations of other quantum systems.

Superconducting circuits can behave like atoms, in that both systems have discrete

energy levels, and coherent quantum oscillations can occur between those levels. Such circuits can perform microscopic quantum mechanics at macroscopic scales and can be used to conduct atomic-physics experiments on a silicon chip (2–4). However, whereas transitions between electronic energy levels in atoms are controlled with visible or microwave photons, transitions in the artificial atoms are driven by currents, voltages, and microwave photons.

Quantum circuits can be lithographically designed to have specific characteristics, such as a large dipole moment (2–5) or particular transition frequencies. This tunability is an important advantage over natural atoms for several applications. For example, quantum circuits can produce photons (6–8), can be cooled (9–11) like natural atoms, can form molecules (12), and can be used for quantum memories (13, 14).

For applications in quantum computing, quantum circuits have been designed to store and manipulate information as two-level quantum systems, called qubits (2, 3). The greater complexity and flexibility of a many-level quantum system can be illustrated by making analogies with a

A superconducting circuit passes a quantum state between several energy levels like a football is passed between players.

classical system, that of a game of football (soccer). The main characters in standard quantum information processing are two players (two energy levels that form a qubit) with player numbers  $|0\rangle$  and  $|1\rangle$ . The state of the quantum system—the football—can be written as the sum of  $a\cdot|0\rangle + b\cdot|1\rangle$ , where  $a$  and  $b$  are complex numbers that can vary in time but always satisfy the normalization condition  $|a|^2 + |b|^2 = 1$ . For instance, when ball state =  $|0\rangle$ , the ball is with player  $|0\rangle$ . In general, the quantum ball is in a superposition state: It is shared between both players.

Now, consider quantum information with several states. In the experiment by Neeley *et al.*, the states in their quantum circuits can emulate a particle with spin  $s$ , which can be described as a vector rotating on a sphere. When a spin rotates as it moves around a closed path, the spin state that describes it is multiplied by a phase factor, often referred to as Berry's phase. This phase factor depends on the solid angle enclosed by the path. For a  $2\pi$  rotation, integer spins are unchanged, whereas half-integer spins are multiplied by  $-1$ . This parity difference leads to the symmetric statistics

Advanced Science Institute, RIKEN, Wako-shi, Saitama 351-0198, Japan, and Department of Physics, University of Michigan, Ann Arbor, MI 48109, USA. E-mail: fnori@riken.jp