Different seismic probes of the core-mantle boundary have different abilities and limitations in resolving thin boundary layers containing super low seismic velocities. For example, seismic waves that travel down into the mantle and bounce off the boundary back toward the surface inherit additional small seismic arrivals due to energy that reflects off the top surface of the ULVZ. If the transition from the ULVZ to the overlying mantle is not sharp, these reflections are significantly subdued. On the other hand, the SPdKS seismic wave has small segments of energy that diffract along the core-mantle interface (see upper left panel in the figure). SPdKS is more sensitive to lowered wave speeds in the boundary layer than to the sharpness of the top of the ULVZ. Recent efforts (*11*) point to regions lacking highly anomalous ULVZ structure, suggesting instead that complex CMB boundary layer structure is intermittent in the lateral direction.

One conclusion is constant among all models. However the ULVZ signature observed in the seismological waveforms is interpreted, it appears to require strong physical and chemical interactions between Earth's mantle and its core. As more high-quality seismic data are collected and analyzed, with multiple types of seismic waves sampling specific spots of the core-mantle boundary, we will be in a better position to resolve this apparently exotic boundary deep within our planet.

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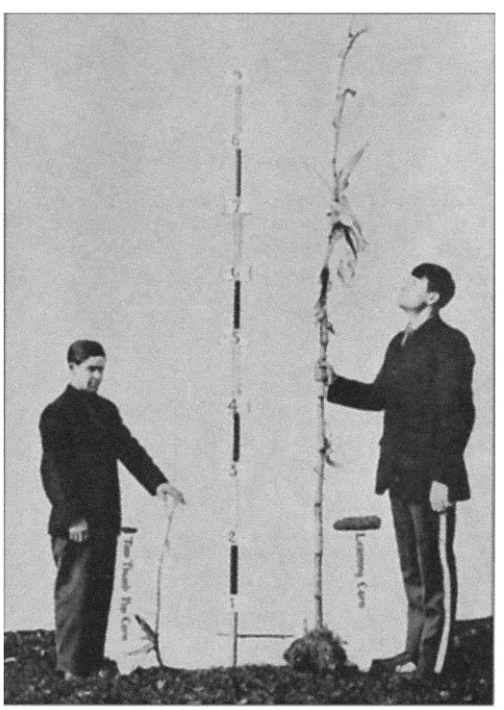
PERSPECTIVES: PLANT GENETICS

A Tomato Gene Weighs In

John Doebley

Look at any group of people and you will see that they differ from one another in a continuous or quantitative fashion. Short to tall or slender to stout, the variations are continuous. Such quantitative variation has been the raw material for both Darwinian evolution under natural selection and crop improvement under human selection (see the figure, this page). As such, quantitative variation has occupied the interest of geneticists for nearly a century (*1*). Yet, progress in understanding how genes control quantitative traits has been slow, and the field of quantitative genetics has been largely occupied with making statistical descriptions of the underlying genes, never really knowing what genes are involved. On page 85 of this issue, Frary, Tanksley, and their colleagues (*2*) break through this impasse with their report of the molecular cloning of one of the genes (*fw2.2*) responsible for the quantitative difference between the small-fruited wild tomatoes of Mexico and their monstrous cultivated counterparts arrayed on the grocer's shelf (see the figure, next page).

The journey to clone *fw2.2* began in the late 1980s when Tanksley's laboratory at Cornell University reported the first genome-wide scan for quantitative trait loci (QTLs), the genes that control quantitative traits (*3*). Conceptually, QTL scans or mapping experiments are straightforward. For tomato, simply cross the wild (*w*) and cultivated (*c*) types and then self-pollinate their hybrid to make an F_2 generation that will have a continuous range from small- to large-fruited plants. By having "markers" throughout the genome, one can observe whether a particular F_2 plant has two cultivated variants or alleles (*cc*), two wild alleles (*ww*), or one of each (*cw*) at various points (markers) along the chromosomes. If a QTL for fruit weight lies near a particular marker, then F_2 plants with two *w* alleles at that marker will have, on average, smaller fruits than plants with two *c* alleles. By this method, the Cornell team identified at least 28 QTLs controlling the difference in fruit weight between wild and cultivated tomato, one of which is *fw2.2* (*4*). By refined mapping studies over the past decade, they localized *fw2.2* to a narrow chromosomal region (1/10,000th of the genome) (*5*), setting the stage for cloning of this gene.



The long and short of it. Photograph from a 1914 article by geneticist Albert Blakeslee showing extremes in quantitative variation for height in corn and students at Connecticut Agricultural College. [Source: (*9*)]

To fully appreciate this feat, one needs to understand the complexities of quantitative inheritance. If fruit size were controlled by a single gene with alleles *S* for small and *s* for large, then the progeny of crosses between wild and domesticated tomato would segregate in nice 3:1 ratios of small- to large-fruited plants. For such discrete traits, one can infer the "genotype" (*SS* or *Ss* versus *ss*) by observing the "phenotype" (large or small). Under these circumstances, geneticists have an impressive arsenal of tools that can make gene cloning a summer project for an undergraduate student. For quantitative traits, the situation is more complex. First, quantitative traits are controlled by multiple QTLs, and plants with the same phenotype can carry different alleles at each of many QTLs. Second, plants with identical QTL genotypes can show different phenotypes when raised under different environments. Finally, the effect of one QTL can depend on the allelic constitution of the plant at other QTLs. For these reasons, one cannot infer the genotype from the phenotype, and one must construct specialized genetic stocks and grow them in precisely controlled environments as a prelude to cloning.

Many previous reports have implicated specific genes in the control of quantitative traits. For example, several studies point to an association between *ApoE* in humans and coronary heart disease (*6*); another report links *scabrous* to the number of cuticular bristles in fruit flies (*7*). These studies used a statistical ap-

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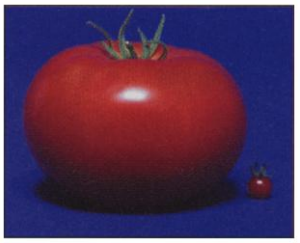
proach called "association analysis" that, while offering compelling evidence, falls short of giving absolute proof that a particular gene influences a given trait. This is where Tanksley and co-workers break new ground. Having cloned *fw2.2*, they transformed the wild version of the gene into a cultivated tomato, and the transformed plants showed the expected decrease in fruit weight. Remarkably, the observed decrease in the fruit weight of transformed plants was of the expected magnitude, demonstrating that there are no additional fruit weight QTLs nearby on the chromosome. The use of transformation to confirm the cloning of a gene has been the "gold standard" in most areas of genetics, but prior to this, quantitative geneticists relied almost exclusively on statistical or correlative evidence.



You like tomato, and I like tomah-to. Fruits from the wild tomato species *Lycopersicon pimpinellifolium* **(right)** and the cultivar Giant Red (*L. esculentum* cv), bred to produce very large tomatoes **(left)**. [Source: (*2*)]

The difficulties associated with the analysis of quantitative traits have left many questions unanswered. For example, how many QTLs typically control quantitative traits, and how large are their effects? One viewpoint has been that the number of QTLs for each trait is so large (100 or more) and their individual effects so small that there is no hope of studying QTLs individually (*8*). Given the nature of the experimental evidence, this is a reasonable position. However, in the case of *fw2.2*, this view does not apply. The effects of *fw2.2* are sufficiently large (adding 17 grams to a tomato) that one can easily see the difference [see Fig. 1B in (*2*)]. Again, because Tanksley and colleagues have used transformation, skeptics will not be able to dismiss their results as correlative. As additional QTLs are cloned and transformation experiments performed, the genetic control of quantitative traits will come more sharply into focus.

The cloning of *fw2.2* is a remarkable achievement, but from beginning to end it has taken a decade to accomplish. One might expect that cloning of the next 27 QTLs for fruit weight will require a couple of centuries. Happily, advances in genomics will greatly expedite QTL cloning in the future. Publicly available high-density marker maps will enable researchers to zero in on QTLs rapidly, eliminating the need for each lab to pioneer the development of markers around their QTLs. Once the mapping is done, the complete sequence of the genome will enable researchers to order their genes from clone banks, eliminating the tedious process of constructing and screening genomic libraries.

Unlocking the secrets of quantitative variation is probably the greatest challenge facing geneticists in the 21st century. For even after genomes have been sequenced and the functions of most genes revealed, we will have no better understanding of the naturally occurring variation that determines why one person is more disease prone than another, or why one variety of tomato yields more fruit than the next. Identifying genes like *fw2.2* is a critical first step toward attaining this understanding.

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PERSPECTIVES: CHEMISTRY

Superacids—It's a Lot About Anions

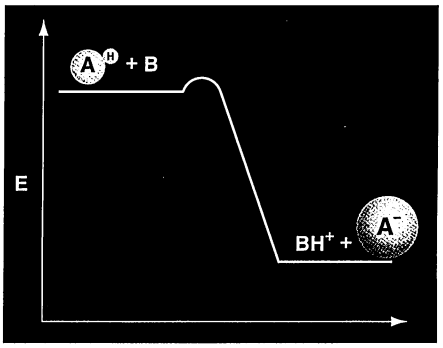
Darryl D. DesMarteau

The term superacid was first proposed in 1923 by Conant to describe acid systems stronger than conventional mineral acids (*1*). Much later, Olah popularized the term in the study of stable carbocations in highly acidic media (*2*). According to Gillespie's arbitrary but now widely accepted definition, a superacid is an acid system stronger than 100% sulfuric acid (*3*). On page 101 of this issue, Reed *et al.* (*4*) report the synthesis of a new superacid that is not only strong, but also gentle. This remarkable acid can protonate and stabilize HC_{60}^+, and its conjugate base can stabilize C_{60}^+.

The ideal superacid, HA, should be capable of protonating a weak base, B, in a variety of solvents, and the resulting A^- should not interact with the BH^+ formed. One can envisage HA as a large ball with a small proton attached (see the figure), soluble in an unreactive solvent and able to donate a proton to a weak receptor (see the figure). Upon loss of the proton, the negative charge is delocalized over the entire sphere, thus stabilizing it and providing little if any interaction with BH^+. Reed *et al.* (*4*) report the discovery of such an ideal superacid in the carborane species $H(CB_{11}H_6X_6)$, with X = Cl, Br. The large stable sphere is the $(CB_{11}H_6X_6)^-$ icosahedral cluster. The use of this novel superacid has already led to exciting new insights into the chemistry of the C_{60} fullerene.

Well-known examples of superacids include the oxyacids FSO_3H, CF_3SO_3H, and ClO_4H. The conjugate bases of these acids are the resonance-stabilized anions FSO_3^-, $CF_3SO_3^-$, and ClO_4^-. But in the presence of strong electrophiles, these small anions exhibit important interactions through their oxygen atoms and, in case of FSO_3^-, also the fluorine atom. These interactions can lead to a number of undesirable effects, such as oxidation and fluoride ion transfer.

The acidity of many Bronsted acids (proton donors) can be greatly enhanced by the addition of a strong Lewis acid (an electrophilic substance) (*5*), because the Lewis acid increases the concentration of solvated protons in the acid medium by forming a complex with the conjugate base of the acid. Antimony pentafluoride is the most powerful Lewis acid; when added, for example, to FSO_3H, the acidity is increased by many orders of magnitude over the pure FSO_3H. Also, the larger $FSO_3SbF_5^-$ anion (and other more complex anions formed) is a weaker nucleophile than FSO_3^- alone. These factors combine to allow the study of much stronger



The role of the anion in superacids. Efficient delocalization over the anion is important to avoid strong interactions with the protonated base.

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