Plant Breeding Reviews

VOLUME 42

Edited by
IRWIN GOLDMAN

Wiley

PLANT BREEDING REVIEWS
Volume 42

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WILEY

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Mark E. Sorrells: Plant Breeder, Geneticist, Innovator, Mentor

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ABBREVIATIONS

AMMI	Additive Main Effects and Multiplicative Interactions
CIMMYT	International Maize and Wheat Improvement Center
CSSA	Crop Science Society of America
DArT	Diversity Arrays Technology
EST	Expressed sequence tag
FHB	Fusarium head blight
GBS	Genotyping by sequencing
G×E	Genotype by environment
GEBV	Genomic estimated breeding value
GOBii	Genomic Open-source Breeding Informatics Initiative

GOM Award	Gerald O. Mott Award
GS	Genomic selection
GWAS	Genome-wide association study
ICARDA	International Center for Agricultural Research in the Dry Areas
ITMI	International Triticeae Mapping Initiative
IWWIP	International Winter Wheat Improvement Program
MAS	Marker-assisted selection
PCR	Polymerase chain reaction
PHS	Preharvest sprouting
QTL	Quantitative trait loci
PS	Population structure
RF	Random forest
RFLP	Restriction fragment length polymorphism
SDRF	Single-dose restriction fragment
SIU	Southern Illinois University
SNP	Single-nucleotide polymorphism
SSR	Simple sequence repeat
USDA	United States Department of Agriculture
wBSR	weighted Bayesian shrinkage regression

Mark E. Sorrells is a plant breeder, geneticist, mentor, and professor who has dedicated more than 40 years to the field. Mark's major contributions have been in the development of breeding methodologies for wheat improvement, including the use of a dominant male-sterile gene, marker development, genomic selection theory, and application in small grains and variety development. He has also been very engaged in graduate student education. The success of his students in both academia and industry reflects his ability as an instructor and mentor, which is perhaps his biggest contribution to plant breeding. Mark always provides outstanding scientific training, and continually emphasizes the value of excellence in the research process, the value of hard work, and the importance of an open mind to new technologies. One of the most remarkable of his skills is the ability to combine plant breeding theory and practice. His work has focused mainly on wheat, but he has also published on maize, rice, oat, barley, tef, and sugarcane, which has given him a wide perspective. These assets have contributed to a career marked by more than 270 scientific papers, many national and international collaborations and conferences, and outstanding student training and mentoring. As his colleagues and former students, we dedicate this chapter to Mark's outstanding career in plant breeding and genetics, his leadership, and his positive influence on students and colleagues over the years.

I. BIOGRAPHICAL SKETCH AND BACKGROUND

Dr. Mark Sorrells' love for scientific knowledge was grounded in his childhood spent on a diverse central Illinois farm that included both field crops and livestock. Dr. Sorrells began his scientific career at Southern Illinois University (SIU)-Carbondale, majoring in electrical engineering. SIU had a tropical plant conservatory that Sorrells frequented on his way to classes. He became acquainted with the conservatory manager, Mr. Mayberry, who would often give Sorrells plants or cuttings to take home. Because of his growing interest in plants, he changed his major to botany in his sophomore year, earning a bachelor's degree in that subject in 1973. He achieved his master's in plant and soil science two years later, under the watchful eye of Dr. Oval Myers, Jr., a maize and soybean breeder. As part of this program, he spent a year in Brazil's Federal University of Santa Maria with a team of scientists conducting breeding, genetics, and physiology research on maize, sorghum, and soybean.

Sorrells received his Ph.D. in plant genetics and breeding from the University of Wisconsin–Madison in 1977, working on maize under the supervision of Dr. John Lonnquist, whose program was focused on population improvement. Subsequently, he joined Edwin T. Bingham's lab to work on cytogenetics of the *ms1* mutant in soybean. Within a year of acquiring his doctorate degree, Sorrells joined the faculty of the Department of Plant Breeding and Biometry at Cornell University. Six years later, he became associate professor, and then a full professor in 1991. After joining the faculty at Cornell, Sorrells took advantage of his training in population improvement and cytogenetics to initiate related projects. For example, he introgressed the dominant male-sterile gene into locally adapted wheat germplasm and initiated recurrent selection in several populations. He used tetraploid and diploid oat species to create novel amphidiploids, which he crossed to cultivated oat for introgression of genes from other species.

Innovative research, important assignments, and travel to many countries distinguish Dr. Sorrells' career. He served as Chair of the Department of Plant Breeding and Genetics from 2006 to 2014. He is a Fellow of the American Association for the Advancement of Science (since 1998), the Crop Science Society of America (CSSA) (1993), the American Society of Agronomy (2003), and the Atkinson Center for a Sustainable Future (2014). Additionally, he was named Outstanding Alumnus by the SIU College of Agriculture in 1997 and recognized by the Cornell College of Agriculture and Life Sciences for Outstanding Accomplishments in Applied Research in 2012. In 2015, he received

the State University of New York Chancellor's Award for Excellence in Faculty Service. He won the CSSA Outstanding Research Award in 2016. Recently, he was identified by Thomson Reuters as one of the world's most influential scientific minds, based on literature citations over the past 11 years. He has had the honor of serving in various capacities for numerous college, national, and international organizations, including the editorial boards of *Crop Science*, *Theoretical and Applied Genetics*, *Genome*, the *Australian Journal of Agricultural Science*, and *The Plant Genome*. As of 2017, Dr. Sorrells has published more than 270 scientific articles in peer-reviewed journals and given 254 presentations at national and international venues. As an example of the breadth of his invited talks, during 2015 alone, he gave 13 presentations in the U.S., India, Thailand, France, Poland, Germany, and Australia.

Working with or being a student of Dr. Sorrells means being exposed to contagious enthusiasm for science and plant breeding. His mentoring philosophy is to give students the freedom to direct their own program and to provide guidance as needed. He has had a positive influence on students he has directly mentored and taught, as well as on countless other students with whom he has interacted during scientific meetings, plant breeding functions, and spirited discussions at the Big Red Barn, a weekly social activity that takes place at Cornell. He has directly mentored 33 undergraduates, 55 graduates as major advisor, 23 graduates as minor advisor, 22 post-doctoral associates, and 35 visiting scientists, many of whom have gone on to influential careers in academia, industry, and government. His graduates are spread over 18 countries, with half of them being international students from the Americas, Europe, Asia, and Africa. In the classroom, his primary course responsibilities at Cornell are "Introductory Plant Breeding Laboratory" and "Perspectives in Plant Breeding Strategies," both taught since the early 1980s. The laboratory is team-taught by plant breeding faculty and includes field tours to breeding nurseries, hands-on selection, statistical exercises, and demonstrations. "Perspectives in Plant Breeding Strategies" is a higher-level graduate course with a focus on advanced plant breeding methods, including classic scientific papers and state-of-the-art molecular genetics methodology. His teaching style uses the Socratic method of engaging students in relevant discussions that ignite creative thinking in assignments that extend, combine, or challenge the approaches of presented papers. This method is a two-way street structured to galvanize students' inherent intellectual abilities and to serve as a source for Sorrells' own continued learning and stimulation of ideas. Through careful facilitation during course discussion,

he helps students open new vistas to original thought, chisel their scientific minds, and develop critical-thinking skills, all of which prepare them for careers in academia and industry. Many students reflect on "Perspectives in Plant Breeding Strategies" as the course that really taught them plant breeding, developed the skills they needed to make steady and thoughtful contributions throughout a scientific career, and solidified the network of Cornell plant breeding alumni, forging lifelong ties among colleagues even across generations.

Dr. Sorrells is not only an effective mentor to his students in both research and career development, but also promotes propagation of new knowledge and international cooperation (Fig. 1.1). He has conducted courses internationally on genomic selection (GS), including a week-long course at Kasetsart University in Kamphaeng Sean, Thailand and a workshop on plant breeding and seed production in Uberlandia, Brazil. He has visited many institutions in China, including Nanjing Agricultural University, China Agricultural University, Northwest A&F University, Shandong Agricultural University, and the Chinese Academy of Agricultural Sciences. Many students and young scientists have benefited from his talks and lectures on various topics of genome research, comparative genomics, and GS. Dr. Sorrells was one

Fig. 1.1. Sorrells presents small grains variety characteristics at a seed growers' field day.

of the invited outstanding scientists for research and education innovation at Nanjing Agricultural University's "111 Project," supported by the Education Ministry of China. During his various visits to Nanjing Agricultural University, he would discuss research projects with the graduate students and give valuable suggestions and advice.

The innovative and productive research program Dr. Sorrells has led for nearly 40 years is proof of the purpose and dedication of this outstanding scientist. Focusing on the development of new tools, methods, and breeding strategies for crop improvement, his career path is marked by several "firsts" in knowledge generation and modern technologies, underpinning the broad discipline of plant breeding. He purchased the first personal computer in the Department of Plant Breeding and Biometry at Cornell, an Apple II, in 1979. He regularly adopts new technology, mechanizes his research program, and incorporates new methodologies, including whole-genome genotyping, high-throughput phenotyping, and gene editing.

Dr. Sorrells' pioneering work has led him to become a major thought leader in the plant breeding community, with a remarkable ability to promote the adoption of new technologies and to bring scientists together as a community.

II. RESEARCH

A. Breeding, Preharvest Sprouting, and Mapping Populations

1. Variety Development. Combining theory and practice is one of Dr. Sorrells' differentials. In fact, during his career, he released or co-released 13 winter wheat varieties, four spring oat varieties, and one winter barley variety. Cayuga was the first soft white winter wheat variety with a high level of resistance to preharvest sprouting (PHS), a major problem in the northeastern United States. When Caledonia was released, it set new grain yield standards for soft white winter wheat in New York, Michigan, and parts of Ontario, Canada. Since the release of Jensen in 2007, all released wheat varieties have had at least moderate resistance to PHS and Fusarium head blight (FHB), the two most serious production problems in Upstate New York.

2. Innovative Methodologies in Applied Plant Breeding
a. Pioneered Recurrent Selection for Wheat Improvement Using a Dominant Male-Sterile Gene. Recurrent selection is rarely practiced in self-pollinated crops. Dominant male-sterility genes, which have

been found in cotton, wheat, and rice, can facilitate cyclical methods. Mass selection, half-sib selection, S_1 selection, combinations of these schemes, and backcrossing can all be greatly expedited using the dominant male-sterile allele (Sorrells and Fritz 1982). Dr. Sorrells introgressed a dominant male-sterility gene from 'Chris' spring wheat and developed 20 different populations, which have been under selection for various traits since 1983. This is possibly one of the longest-running recurrent selection programs for wheat in the world. It is currently used as a student-training tool and for the development of novel germplasm. Heffner et al. (2008) showed that these recurrent selection populations increased the opportunity for genetic recombination between exotic and cultivated genomes, facilitating the fine mapping of segregating loci. The population that was selected for good anther extrusion and large anthers has been licensed to companies interested in using those traits for the development of hybrid wheat.

b. Landmark Papers Published on Genotype by Environment (G×E) Interactions. Brown et al. (1983) presented a methodology to improve the efficiency of cultivar testing programs by first clustering nursery environments based on environmental variables and then identifying optimum selection environments within clusters through linear regression on a genotypic index. Gauch et al. (2011) devised two new strategies for detecting quantitative trait loci (QTL) and for understanding them through environment interactions. One method uses a parsimonious Additive Main Effects and Multiplicative Interactions (AMMI) model to improve the accuracy of the phenotypic data used in QTL scans, thereby improving QTL results. The other uses Interaction Principal Component environment scores to order the environments in a manner that reveals consistent patterns and systematic trends that may have an ecological or biological interpretation. Using some of the same biological materials employed in Gauch et al. (2011), the Sorrells lab investigated the impact of different growing environments on gene expression networks. It identified distinct gene expression networks that were influenced by the environment, and demonstrated that these networks were related to traits that exhibit high gene by environment (G×E) interactions (Munkvold et al. 2013).

Dr. Sorrells has coauthored several other papers on G×E, culminating in a groundbreaking approach by Heslot et al. (2014) that incorporates a crop model in the GS framework using environmental stress covariates. These authors proposed new solutions for integrating environmental data in GS in order to predict G×E, by extending factorial regression to the GS context, developing a new machine-learning approach

that captures the response of QTL to stresses nonparametrically. This approach uses a crop model to enable the use of daily weather data in prediction models that characterize G×E through genotypes in order to predict phenotypes in untested environments.

3. Seed Dormancy and Preharvest Sprouting Research. The premature germination of seeds before harvest, known as PHS, is a serious problem in most wheat-growing regions of the world. Dr. Sorrells' predecessor, Neal Jensen, challenged him to develop a PHS-resistant soft white winter wheat variety. Sorrells initiated PHS research shortly after arriving at Cornell and published his first paper on PHS in 1981, in collaboration with Dr. Imre Tamas. Later, Paterson et al. (1989) determined the relative contributions of genotypic and environmental factors to PHS of wheat lines, ranging from highly resistant to highly susceptible, and evaluated a technique for extending the testing period by preserving dormancy. Their data proved to be useful in planning basic investigations of PHS resistance and incorporating sprouting resistance testing procedures into wheat breeding programs. Paterson and Sorrells (1990a) also evaluated the utility of spike- and seed-based mass selection techniques for improving PHS resistance in wheat populations. Their results have been useful for the improvement of PHS resistance in large, heterogeneous wheat populations (Paterson and Sorrells 1990b).

Resistance to PHS is difficult to incorporate into new varieties because heritability is low and selection is limited to one generation per year. To overcome this, Anderson et al. (1993) identified eight genomic regions containing QTL associated with resistance to PHS using restriction fragment length polymorphism (RFLP) markers, which explained 44–51% of the genetic variance for PHS in wheat populations. The wheat community later utilized these markers as indirect selection criteria for the improvement of PHS resistance.

Munkvold et al. (2009) undertook a study to determine genetic control of PHS resistance in wheat. A total of 15 different PHS QTL were detected, including a major QTL that was significant in all of the 16 tested environments and which explained 5–31% of the trait variation in a given environment. These comprehensive results provided valuable information for future PHS haplotyping studies, marker-assisted selection (MAS) for PHS within and between wheat breeding programs, and research into mechanisms governing seed dormancy in wheat (Somyong et al. 2011, 2014). Kulwal et al. (2012) validated some of the earlier known QTLs for PHS in wheat and extended this knowledge by using association mapping to identify QTLs with

Diversity Arrays Technology (DArT) and simple sequence repeat (SSR) markers linked to PHS resistance.

4. Established Important Wheat Reference Mapping Populations. Reference populations are valuable resources in genetic studies for determining loci order, marker selection, trait mapping, construction of large-insert libraries, cross-referencing of marker platforms, and genome sequencing. Good reference populations can be propagated indefinitely, are highly polymorphic, and present a normal distribution of quantitative traits. In 1988, Tanksley and Sorrells traveled to the International Maize and Wheat Improvement Center (CIMMYT) to craft a proposal for the United States Department of Agriculture (USDA) regarding mapping RFLPs in wheat. During that visit, they discussed the appropriate germplasm and activities. A number of studies grew out of these modest beginnings, including a survey of very diverse wheat germplasm and a methodology for constructing mapping populations (Anderson et al. 1993). The original International Triticeae Mapping Initiative (ITMI) population was developed by Autrique and Sorrells in the early 1990s (pers. comm.). Later, Sorrells et al. (2011) developed two new reference populations using the same parents as the original ITMI population: an F1-derived doubled haploid population (SynOpDH) of 215 inbred lines and a recombinant inbred population (SynOpRIL) of 2039 F6 lines derived by single-seed descent. Initially, a low-density linkage map was constructed for the SynOpDH population using 1446 markers, but Saintenac et al. (2013) added more than 400 000 further markers from various platforms to the map. These populations have been used globally to map genes in wheat, and are still used as reference sets to anchor new molecular markers, linking each new technology to our previous knowledge.

5. A Global Team for Developing Durable Rust Resistance in Wheat (DRRW) by the Bill & Melinda Gates Foundation. The recent emergence of wheat stem rust Ug99 and evolution of new races within the lineage threatens global wheat production. In susceptible wheat cultivars, new races of rust may cause 80% yield loss. Breeding for stem rust-resistant wheat is urgently required. However, little is known about the resistance genotypes of widely used wheat germplasm. In a project funded by the Bill & Melinda Gates Foundation, Dr. Sorrells and a team composed of scientists from international centers, government agencies, and universities assembled a diverse set of nearly 1000 global wheat genotypes and conducted haplotype analysis for the stem rust-resistance genes *Sr2, Sr22, Sr24, Sr25, Sr26, Sr36, Sr40*, and 1A.1R in

the germplasm panel (Yu et al. 2010). To identify loci conferring adult plant resistance to race Ug99, they employed genome-wide association mapping to current global wheat breeding lines, identifying 15 and 11 marker loci significantly associated with stem rust resistance in spring and winter wheats, respectively (Yu et al. 2011, 2012). Sorrells' group validated markers linked to the resistance genes and optimized protocols for MAS in wheat breeding for the rust-resistance genes *Sr22, Sr25, and Sr26*; they published the protocols on the GlobalRust (http://www.globalrust.org/knowledge) and MASwheat (http://maswheat.ucdavis.edu/protocols) websites, making them available to national and international wheat breeders and research scientists. Additionally, in collaboration with wheat scientists from USDA, CIMMYT, and a number of universities, Sorrells' group constructed the first consensus map of QTLs associated with Ug99 stem rust resistance (Yu et al. 2014). This map includes 75 stem rust-resistance loci identified in different populations and can be used to develop molecular markers for selecting stem rust-resistant wheat lines. It contains DArT, SSR, and single-nucleotide polymorphism (SNP) markers linked to stem rust-resistant QTLs, and thus provides a useful tool for developing stem rust-resistant wheat. It has been used in gene pyramiding by international wheat breeding programs in CIMMYT, the International Winter Wheat Improvement Program (IWWIP), and the International Center for Agricultural Research in the Dry Areas (ICARDA) to improve wheat resistance to stem rust Ug99.

B. Molecular Marker-Assisted Breeding

1. Innovated Theory and Analysis of Linkage for Molecular Mapping in Polyploids.
In the early 1990s, Coppersucar (now CTC), a sugarcane company located in Piracicaba, Brazil, was interested in initiating molecular mapping studies. It collaborated with the Hawaiian Sugar Planters Association to support RFLP mapping research in the United States; this led to a long and productive partnership that has continued intermittently up to the present date. Wu et al. (1992) devised a method for detecting and estimating linkage in polyploids using single-dose restriction fragments (SDRFs). RFLP linkage maps for several major diploid crops had already been constructed, but the construction of such maps directly in autopolyploids lagged as a result of several complicating issues. To overcome these problems, a general method for mapping in autopolyploids based on segregation of SDRFs was proposed. Hypothetical allopolyploid and autopolyploid species with four ploidy levels were used to illustrate the procedures for identifying SDRFs,

detecting linkage among them, and distinguishing allopolyploids versus autotetraploids for accessions with unknown genome constitutions. In addition, it was shown that multiple-dose markers could be used to identify chromosomes belonging to the same homoeologous groups (Ripol et al. 1999).

Dr. Sorrells' group contributed to the study of inheritance of multiple-dose markers by segregation ratio, an important new method for studying autopolyploid genetics. Da Silva and Sorrells (1996) compared methods of linkage analysis in polyploids facilitated by the use of molecular markers and illustrated their application in understanding chromosome relationships and pairing behavior in those polyploids with regular bivalent pairing and polysomic inheritance. Because the dosage of each marker is obtained from the segregation data, one cannot know *a priori* the dosage of each polymorphic marker obtained at the first step of a mapping project. Mapping studies of species involving populations obtained from crosses between heterozygous tetraploids, such as potato, alfalfa, and apple, benefited the most from this methodology, given their greater expected proportion of multiple-dose markers.

2. Application of Molecular Marker Technologies in Wheat Gene Mapping. The advent of molecular markers in the 1980s offered new methods for tagging wheat genes for MAS and map-based cloning. Sorrells' lab was one of the first to apply these marker tools in wheat. Minella and Sorrells (1992) pioneered the study of the inheritance, chromosome location, and relationships among diverse sources of tolerance to aluminum toxicity in barley, an important trait for adaptation to acid soils. Through collaboration with Dr. Bikram Gill of Kansas State University, Ma et al. (1993) mapped two hessian fly-resistance genes with RFLP markers. Ma et al. (1994) continued their work on the powdery mildew-resistance genes *Pm1–Pm4*. The RFLP markers identified were closely linked to these genes, and some were converted to polymerase chain reaction (PCR)-based markers and served as the starting point for fine mapping (Liang et al. 2016). Interest in cytoplasmic male sterility led Ma et al. (1995a) to apply the marker technology to the investigation of fertility-restoration loci in wheat and to map the fertility-restoration genes *Rf1*, *Rf3*, and *Rf4* and a few minor-effect loci through marker-trait regression analysis. Moreover, they identified *Rf6,* transferred from chromosome 6U of *Aegilops umbella* (Ma et al. 1995), which was a small translocation almost undetectable using conventional cytogenetics tools. Autrique et al. (1995) evaluated leaf rust resistance in an RFLP-mapping population of wheat inbred lines. Map locations were assigned for seedling resistance genes *Lr10*, *Lr23*, *Lr27*,

and *Lr31* and the adult plant resistance gene *Lr34*. The Sorrells lab continues to define and develop tools for introgressing traits in cereals.

3. DNA Sequence Comparative Map for Wheat/Rice. The era of comparative mapping with low-density molecular marker maps provided a broad picture of the state of conservation of genome structure between the major grass species, with many labs around the world making incremental contributions using RFLPs throughout the 1990s. However, as mapped expressed sequence tags (ESTs) became available, it became possible to directly compare sequences across species. When Sorrells et al. (2003) constructed *in silico* comparative maps between rice and wheat using the DNA sequence of thousands of mapped wheat ESTs and the available sequence of the rice genome, the resulting analysis substantiated much of the "macroscopic" gene content and order established in earlier comparative maps, but at the same time provided a much finer resolution. The high-resolution, sequence-based maps could be used to transfer information from model species to related organisms, integrate information on gene location at a more localized level (micro-synteny), and infer evolutionary processes across related species. The surprising result was that the micro colinearity of DNA sequences between rice and wheat was not as conserved as previously thought, with substantial localized structural divergence between them. Later, La Rota and Sorrells (2004) updated the comparative sequence analysis utilizing the first draft of the rice genome sequence and all available wheat cDNA clones mapped on the cytogenetically based chromosome bin map. Munkvold et al. (2004) further extended the sequence-based comparison to detail the chromosomal-level maintenance and breakdown of synteny between rice chromosome 1 and wheat group 3 chromosomes. These sequence-based maps significantly enhanced the understanding of the structural genome relationships between the rice and wheat genomes. The availability of sequence data facilitated the development of SSRs for conserved gene sequences, leading to the construction of an EST-SSR marker-based comparative map for wheat and rice (Yu et al. 2004a,b).

4. Comparative Molecular Maps and Traits Among *Poaceae* Species.
Comparative mapping among the grasses in the early 1990s occurred shortly following the release of RFLP maps. Dr. Sorrells and his group worked closely with collaborators to use wheat aneuploids to associate chromosomes with diploid rice and maize genetic maps (Ahn et al. 1993). This work was extended to genetic maps of wheat with the work of Van Deynze et al. (1995a), who assessed the degree of genome

conservation among *Triticeae* species, oat, and rice, indicating that certain regions have been conserved in all four species. These authors showed that the relative positions of major genes governing traits such as seed storage proteins and resistance to leaf rusts have been conserved between cultivated oat and *Triticeae* species. Van Deynze et al. (1995b,c) demonstrated that there is a high degree of conservation (71–84%) at the macro level between the genomes of oat and *Triticeae*, rice, maize, sorghum, and sugarcane. Species that are not as well studied genetically, such as oat, have the most to gain from map comparisons with species such as wheat, rice, and maize.

Van Deynze et al. (1998) defined the concept and implementation of "anchor probes" selected from cDNA libraries developed from rice, oat, and barley for comparative mapping of grass genera. They focused on mapping and end-sequencing a set of cDNA probes that could be used by a wide range of researchers to detect anchor loci for comparative genome analysis among several members of the grass family. Wilson et al. (1999) mapped loci detected by maize cDNA probes in both rice and maize to extend and refine the comparison of these genomes and used this information to make inferences about the genome structure of a progenitor from which modern maize may have evolved. This helped facilitate alignments and genomic cross-referencing of genes and phenotypes and clarify the interpretation of interclade map comparisons.

5. Molecular Marker Maps for Oat, Barley, and Wheat. In the late 1980s, scientists were beginning to apply RFLP technology to crops. Dr. Sorrells recognized early on the potential of marker-assisted selection and genomics in plant breeding, especially in a crop with complex genetics like wheat. Being a scholar and practitioner, he immediately put to work the developments of his predecessors, taking advantage of nulli-tetrasomic stocks developed by Sears (1954), by defining the chromosomal locations of markers using RFLPs, the latest technology at the time (Anderson et al. 1993; Nelson et al. 1995a,b,c; Van Deynze et al. 1995a). This study laid the foundation for a consortium to develop the first high-density genetic maps in wheat in the cross Synthetic W7984 × Opata M85, a wheat reference population that he developed and distributed. He was among the group of 13 scientists who founded the ITMI in 1989. The development of genetic maps in wheat established the foundation required to apply this technology directly in breeding in order to find QTL and understand the inheritance of complex traits.

Oat and barley researchers likewise began RFLP mapping in the late 1980s. Heun et al. (1991) developed one of the first RFLP maps

for barley, which was immediately useful in mapping QTL for different traits. This barley RFLP map also aided in the construction of saturated linkage maps for hexaploid wheat and oat. O'Donoughue et al. (1995) published the first molecular marker map for oat using a population developed from a cross between *Avena hirtula* and *A. atlantica*. Anderson et al. (1992) developed the first chromosomal arm map for wheat based on RFLP markers. They located a large number of DNA restriction fragments corresponding to single or low-copy clones of chromosome arms in wheat using aneuploid genetic stocks developed by Dr. Ernie Sears, which could be applied to gene tagging, linkage mapping, fine mapping of QTL, cytogenetic manipulations, and genetic studies. This also contributed to our knowledge of the comparative organization of homoeologous chromosomes in wheat (Anderson et al. 1992).

6. Molecular Marker Map of Tef. The McKnight Foundation was very active in funding joint U.S. and developing country research in the early 2000's and was involved in supporting tef (*Eragrostis tef*) research in Ethiopia. At the request of Dr. Robert Goodman, Sorrells and colleagues submitted a proposal to construct a molecular marker map of tef. This was the beginning of a collaboration with Ethiopian colleagues at Debre Zeit, Ethiopia that lasted for more than 10 years. Yu et al. (2006a) constructed the first comprehensive molecular linkage map of tef, an important staple crop in Ethiopia, using various types of molecular markers derived from tef ESTs and transferrable markers from other cereal crops such as wheat, rice, and barley (La Rota et al. 2005). This map proved to be useful for further genetic studies in tef, including germplasm characterization, mapping of QTL for various agronomic traits, and comparative analysis with other cereal crops (Yu et al. 2007). It is still used as a reference map to anchor new molecular markers and QTL for tef breeding. In addition, the Sorrells lab was the first to generate publicly available DNA and RNA sequences from tef, which are still utilized in academia and public institutes (Yu et al. 2006b).

7. Molecular Marker Map of *Saccharum*. Using the SDRF method, the first RFLP linkage map of the wild sugarcane species *Saccharum spontaneum* L. was developed; this was particularly useful for the complex, highly polyploid genome of sugarcane, which could not otherwise be mapped by contemporary tools. With 86% genome coverage, the map allowed the first analysis of polysomic segregation based on the genome for *Saccharum* spp. The SDRF method was used to