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ROBERT WAYNE ALLARD
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A Biographical Memoir by

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Biographical Memoirs

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BY MICHAEL T. CLEGG

ROBERT ("BOB") WAYNE ALLARD made wide-ranging contributions to both basic and applied plant genetics. He began as a plant breeder and wrote one of the most successful plant-breeding texts of his era, but his most important contributions were in evolutionary genetics. He was a founder of experimental plant population genetics and he infused the field with high standards of experimental and theoretical rigor. His investigations ranged from elegant experiments to dissect the genetic factors responsible for quantitative genetic variation, to the study of gene-environment interactions, to the analysis of selection in long-term experimental barley populations. But his most significant work was encompassed in a series of papers on the genetics of inbreeding populations, where he overturned conventional dogma by showing that inbreeding plant populations have substantial levels of genetic variation. In the course of his work on inbreeding species, he turned to the characterization of the genetics of wild and naturalized species and contributed to the origins of the field of plant ecological genetics. He was also a teacher *par excellence*, training more than 50 Ph.D. students and an even larger number of postdoctoral students over a career that spanned more than

50 years, and he led the University of California, Davis, Genetics Department to preeminence during the 1960s and 1970s.

EARLY INFLUENCES

Bob Allard was born in the San Fernando Valley of California on September 3, 1919. In the years between the two world wars the San Fernando Valley was largely pastoral and Bob's early years were spent on the family farm. Around 1930 his father relocated his farming operation to the San Joaquin Valley about 15 miles west of Modesto. Like many farmers of the era, Bob's father cooperated with University of California agricultural researchers by dedicating a portion of his land to experimental trials. A UC Berkeley plant breeder named W. W. Mackie maintained plots of lima and common beans on the Allard farm, and Bob was assigned the task of assisting Mackie with the maintenance of the experimental plots. This turned out to be the formative experience of Bob's young life, because Mackie instilled in Bob a lifelong fascination with the causes of phenotypic variation. In an oral history interview, Bob much later recalled that Mackie introduced him to the new science of Mendelian genetics during this period, thereby contributing to his later choice of scientific career.

In recounting these early experiences, Bob would passionately describe the pleasure he took in listening to Mackie and in hearing his theories about genetic variation and its practical exploitation. Bob was not a man to dwell on the past; he strongly preferred to look toward the future. His occasional recollections of Mackie were exceptional and reflected the enduring impact of this period on his later scientific development. According to Bob's much later memories, Mackie was also interested in the ecological bases of adaptation and he introduced Bob to other plant species common in their Central Valley environment, including the slender wild oat (*Avena barbata*) that would later feature importantly in some of Bob's research.

It seems likely that Mackie influenced Bob's decision to enter UC Davis as a student of agriculture in the fall of 1937. During his undergraduate years Bob worked as a student assistant for Coit Suneson of the U.S. Department of Agriculture, and this also had an enduring impact on Bob. Suneson, along with Harry Harlan and Gus Wiebe, was engaged in developing bulk populations of wheat and barley, known as composite cross populations. The theory at the time was that bulk populations would both act as a reservoir for useful genetic variation while at the same time evolving toward greater adaptation under standard agricultural conditions. Years later Bob would use these composite cross populations as a powerful resource for studies in experimental population genetics. These early experiences did much to define Bob's approaches to plant genetics and they serve to illustrate the powerful impact that scientific mentors can have on young minds.

After finishing his undergraduate training, Bob entered the graduate program at the University of Wisconsin, Madison. Certainly the biggest thing that happened to him at Madison was meeting and marrying Ann, his wife of 59 years. On the rare occasions when Bob would talk about his graduate school days, his chief recollection was being called into World War II service just prior to the scheduled date for his final dissertation defense. It seems that the university would not reschedule the defense, and Bob had to return to Madison after the war to defend his thesis. Bob's Ph.D. research was on wheat cytogenetics, and aside from publishing his dissertation work following the war, he never returned to this topic. There were strong influences at Madison, including Rubush G. Shands (his major professor), Charles E. Allen, and R. A. Brink, but I always had the feeling that Bob had a clear idea of his future research directions by the time he left Davis.

After entering World War II service, Bob was sent to the Naval Supply School at Harvard. Later he was assigned to a research unit at Fort Detrick, Maryland, where he was engaged in work on biowarfare, a subject he never discussed, except to say that he had been in a research unit for part of the war. Still, this provided Bob's only postdoctoral training and broadened his research experience.

In 1946 Bob returned to UC Davis as assistant professor of agronomy and assistant geneticist in the Agricultural Experiment Station, and he remained at Davis affiliated with the Agronomy Department throughout his career. He was hired as a bean breeder and his particular focus was on the improvement of the lima bean. At that time Davis was a branch of the Berkeley College of Agriculture and had little autonomy. It was also a very small school with fewer than 800 students, most of whom were there for two-year terminal degrees in agriculture. Bob was an important player in a faculty generation that turned Davis from a small satellite agriculture campus into a thriving and world-renowned university.

From the beginning Bob's work blended both basic genetics and practical plant improvement. In the initial years he focused on both the identification of disease-resistance genes and applications of the backcross method of breeding for the incorporation of disease resistance into elite lines of lima beans. The search for disease resistance genes led to an extended field trip to Central and South America to collect wild relatives and primitive land race materials as genetic resources for future breeding efforts. He later published an article for the California Dry Bean Research Conference on plant exploring in Latin America. The conservation of genetic resources remained an abiding interest, one that was communicated to a number of Bob's students.

At heart Bob was a geneticist, and along with his practical work on lima bean improvement, he began to develop genetic markers in lima beans. These were largely seed coat markers based on an amazing range of seed coat color patterns. Bob and his early students patiently dissected the inheritance of these discrete color polymorphisms and then employed them as markers to study adaptive change in the lima bean. A particularly fascinating aspect of the color patterns was the interactions between different genetic factors that lead to the mosaic patterns evident on the seed coats. We learn and generalize from our empirical experiences, and these are based on the materials that we choose to study. In Bob's case the theme of gene interaction, based in part on his observations of seed coat color patterns in the lima bean, continued to dominate his thinking throughout his career.

The practical side of Bob's program prospered in these early years. He released a number of new varieties of lima beans; one variety, "Mackie," was named for his childhood mentor. He also began work on a novel plant-breeding text. The book, *Principles of Plant Breeding*, published in 1960 had an enormous impact and was ultimately translated into 17 languages. It remained the premier plant-breeding text for a generation. The book was novel because it emphasized genetic principles rather than methods and this contributed to its great success. Bob was also a very fine writer and this, too, contributed to the wide acceptance of *Principles of Plant Breeding*. He took great pains with everything he wrote, and the result was always a model of clarity and precision. Bob would not put his name on a paper until he had worked through it carefully, reanalyzed the data, and improved the exposition. He did not believe in honorary authorships and he was very economical with citations. His practice was to cite only essential supporting papers.

For many years Bob's plant-breeding colleagues urged him to write a second edition of *Principles of Plant Breeding*, and he promised to do so, but it was not until 1999, almost 15 years after Bob's retirement and just four years before his death that a second edition was published. Bob admitted that the second edition was really an entirely new book that contained little carried over from the parent book published 39 years earlier. The second book is really a plant population genetics book that synthesizes a life's study of plant evolution. It is uniquely Bob, both in the lucidity of the writing and in the presentation and articulation of his vision of evolutionary genetics.

QUANTITATIVE GENETICS

The field of quantitative genetics had a large impact on agricultural research in the 1940s and 1950s. The origins of quantitative genetics derive from R. A. Fisher's 1918 paper reconciling Mendelian genetics and Darwinian evolution by natural selection. Quantitative, or biometrical, genetics aims to partition phenotypic variation into genetic and environmental components and it provides a scientific basis for designing efficient schemes for selection. In later years Bob recalled that while a student at Wisconsin, he had been influenced by Sewall Wright, who along with R. A. Fisher was the other great architect of the field of quantitative genetics. It is clear from Bob's later recollections that he was anxious to move beyond lima bean breeding by mastering the skills of quantitative genetics. During the academic year 1954-1955, Bob found the opportunity to hone his skills in statistics and quantitative genetics by taking a year's sabbatical leave in Birmingham, England, to work with Kenneth Mather, one of the era's leaders in quantitative genetics. A few years later, in 1960, he returned to England to work at Oxford with Norman J. T. Bailey, a leading statistician in the field of mathematical genetics. These sabbaticals had an enduring impact on Bob's research directions.

In the middle 1950s Bob began to publish papers that attacked various biometrical issues of the day. One paper was devoted to maximum likelihood estimators for recombination, others focused on the analysis of various diallele crosses, and still others concerned the problem of estimating gene-environment interactions. He began publishing more frequently in broadly based genetics journals rather than in agricultural journals so that his papers would reach a broader audience of geneticists. He also continued to publish on applied topics throughout his career. One paper of this period that deserves special mention is an elegant dissection of the genetics of heading time in wheat (1965). In this paper Bob showed that a major gene controlled heading date, but he went beyond this to show how the remaining phenotypic variation in heading date could be resolved into additional genetic components, revealing the influence of multiple genetic factors of unequal effect. The paper pushed the approaches of quantitative genetics to their experimental limits. By this time Bob's research had evolved beyond the lima bean to exploit other plant species more appropriate for investigating basic questions of quantitative genetics. By the early 1960s Bob's lab was regarded as a leading lab for the study of plant quantitative genetics. Even as he achieved this goal, Bob was moving in new directions.

THE GENETICS OF INBREEDING POPULATIONS

Stimulated in part by his colleague G. Ledyard Stebbins, Bob began to investigate the genetics of inbreeding species. In his classic 1950 book, *Variation and Evolution in Plants,* Stebbins had claimed that inbreeding plant populations should be largely devoid of genetic variation. The argument put forward by Stebbins was that inbreeding leads to homozygosity and the superior inbred type should outcompete all other lines leading to a homogeneous population. Bob knew from his plant-breeding experiences that inbreeding crops, such as lima beans, had large stores of genetic variation and showed rapid genetic responses to selection. Stebbins had repeated what was the conventional dogma of the time, but this provided the stimulus for Bob to begin what became a classic series of experiments to characterize genetic variation in inbreeding plant species. Stebbins, for his part, encouraged this effort to look more deeply at the genetics of inbreeding species. The quest led Bob into an entirely new field, ecological genetics, which sought to combine population genetics with ecology, where Bob played a foundational role. It also began a series of papers on population studies in predominantly self-pollinated species that spanned a period of more than 20 years.

The studies of inbreeding populations led Bob from quantitative genetics into population genetics. Bob quickly established the leading program on plant population genetics of the 1960s, and he and his students found novel ways of approaching the fundamental questions of this field. One important innovation harked back to the composite cross populations of his early undergraduate days. At the time, population genetics was dominated by *Drosophila,* partly because the short generation time of *Drosophila* permitted experiments over many generations, thereby allowing the direct observation of evolutionary changes in gene frequencies. Bob had become the custodian of the composite cross populations, and he quickly realized that the populations he had helped synthesize in his youth would allow a multiple generation approach in longer-lived annual plant species as well. The basic reason rested on the fact that seed could be stored over a number of years, allowing an investigator to analyze gene frequencies in past generations. To see how this worked it is necessary to describe the system for propagating the composite cross populations. The practice was to advance the populations each year by growing a new generation under standard agricultural conditions at Davis, while also storing a portion of seed from each year's harvest for several years. The saved seed would then be rejuvenated by growing out a new generation every five years or so. This provided a parallel series of populations that represented early, intermediate, and late generations. By the early 1960s the oldest populations had about a 30-year history and the youngest had a history of only five or six generations. Because of this scheme, the barley and wheat composite cross populations provided a unique resource to follow changes in phenotypic traits, gene frequencies, and disease resistance loci over 30 or more generations.

Bob used every tool available to study genetic change in the composite cross populations, beginning with simple morphological polymorphisms and quantitative characters and moving on to isozymes and finally to restriction fragment length polymorphisms (RFLPs) near the end of his career. Bob was among the first to adopt the isozyme method when it appeared in the middle 1960s. Isozymes had an enormous impact, because for the first time they allowed the investigator to sample a large number of genes that coded for various enzymatic proteins. Prior to this, students of population genetics were limited to morphological variants, such as the seed coat color polymorphisms of lima bean or to quantitative traits where the underlying genes were impossible to resolve. Isozymes allowed one to sample many individual gene products and to ask questions about genome-wide levels of genetic variation. RFLPs offered the advantages of isozymes while also permitting the investigator to measure variation for portions of the genome that do not code for enzymatic proteins. Throughout his career Bob was always among the first to adopt new approaches to address scientific questions. He was undaunted by obstacles or by the investment of effort associated with acquiring new technologies.

Regardless of the experimental approach employed in studying the composite cross populations, substantial changes in trait or gene frequencies were always observed over time, and these were too large to be ascribed to genetic drift, leaving selection as the only plausible explanation. The next natural question was, could selection be quantified at individual loci? Theodosius Dobzhansky and Sewall Wright had developed approaches to the quantification of selection on inversion polymorphisms in *Drosophila pseudoobscura*, but these depended on the assumption of random mating. The basic estimation technique was to derive transition equations that predicted genotypic frequencies in one generation based on their frequencies in previous generations after accounting for the mating process. A set of weights that mapped the predicted frequencies onto the observed frequencies quantified the strength of selection.

Barley is a predominantly self-fertilizing plant, so the random mating assumption could not be employed. A quantitative theory of mating and a method to estimate the parameters of such a quantitative model was required. A quantitative theory, known as the mixed-mating model, which allowed for a mixture of self-fertilization and random outcrossing, had been published in 1951 by Fyfe and Bailey (the same Bailey that Bob had worked with on sabbatical in Oxford, England). Bob and his students employed this model to estimate the single outcrossing parameter that indexed the mixed-mating model and to derive transition equations to estimate selection in the composite cross and other populations. The technique for estimating the proportion of outcrossing relied on another important property of plants; the fact that one can easily collect numerous progeny of a single maternal plant as seed. With the use of marker genes it was possible to estimate the fraction of self-fertilization and its complement—the fraction of outcrossing—from family structured data.

Armed with a quantitative characterization of the mating process one could quantify selection at individual marker loci. But self-fertilization has another important consequence that rendered it impossible to attribute selection to the marker loci actually observed. Because self-fertilization leads to homozygosity, effective recombination is greatly reduced and any statistical associations among different loci decay slowly over time. Populations like the composite cross populations, with a relatively short history, would still retain statistical associations between loci from their initial composition. Bob and his students initiated the theoretical study of the behavior of linkage disequilibrium (the technical term for correlations between loci in allelic state) in mixed-mating systems in the middle 1960s. At a time when computer simulations were just beginning to be applied to genetic problems, they published an important simulation study describing the complex behavior of linkage disequilibrium in predominantly self-fertilizing populations. Later estimates of the magnitude of linkage disequilibrium in the composite cross and other populations showed that it was typically large. The conclusion was that chromosomal segments containing the marker loci were subject to strong selection in virtually all observed cases, but that one could not resolve selection to the level of individual loci.

Bob was not satisfied with the study of artificial populations. The question he sought to answer was the broader question concerning levels of genetic diversity in inbreeding populations of plants in nature. By the early 1960s he had launched a program to study natural populations of inbreeding plants, and this work included a broad variety of species, including *Avena* species (wild oats), other grasses native to California, such as fescue, and annual native California dicots, such as *Collinsia* species. These efforts began an intensive period of ecological genetics research that spanned nearly two decades. *Avena barbata*, the slender wild oat, was a particular target of investigation during this period. *A. barbata* is a naturalized component of the California oak savannah that was introduced into California during the Spanish Mission period from the Mediterranean basin (almost certainly from Spain). The time dimension is known, and this meant that genetic changes over a two-hundred- to three-hundred-year period could be documented.

Near the end of his life Bob recalled having been introduced to *Avena barbata* by W. W. Mackie; once again this powerful early influence determined a scientific direction, and it was a fortunate choice, because *A. barbata* showed markedly different patterns of evolution in different regions of California. As later shown by two of Bob's Spanish students (Marcelino Perez de la Vega and Pedro Garcia Garcia), these changes were not replicated in Spain, so they must have arisen since the introduction of *A. barbata* to California. Particularly dramatic were contrasting patterns of isozyme variation between the foothills of the arid Central Valley of California and the cooler and moister intermontane valleys of the costal strip. The arid regions were nearly monomorphic for a single multilocus genotype, while populations from the coastal regions exhibited substantial levels of variability. I was fortunate to play a role in these findings, and it was a wonderful way to start a research career.

INTERACTING GENETIC SYSTEMS

A pervasive theme of Bob's research and writing was the importance of interactions among genes, between genes and environments, and even among genotypes within populations. Bob believed that context was essential and that marginal effects were less important. I recall Bob attributing this belief in the importance of interactions to his early mentor W. W. Mackie. Regardless of the source, it clearly dominated Bob's thinking. This view went counter to conventional population genetics theory that is based on the notion that complex systems can be characterized by marginal gene frequency changes. It also went counter to quantitative genetics theory where additive effects were thought to account for most variation. To this day the importance of interaction remains an open question.

Beginning in the middle 1950s, Bob published experimental work on gene environmental interactions. In the 1960s he turned to the problem of interactions among genes at different loci. His approach of measuring linkage disequilibrium as a surrogate for gene interactions was stimulated by the theoretical calculations of R. C. Lewontin and K. Kojima giving the precise relationship between selection and recombination required for nonzero linkage disequilibria. These highly simplified models showed that only nonadditive selection over loci could retard recombination and maintain permanent linkage disequilibrium. Thus Bob focused on the estimation of linkage disequilibria in experimental plant populations as a means of detecting interactions. It later became clear that the existence of linkage disequilibrium is neither necessary nor sufficient for the existence of interlocus interactions, especially in inbreeding systems. Despite this, Bob did show that correlations among loci could be pervasive in inbreeding plant populations and that this would in turn affect their evolutionary potential.

Together with his students, Bob studied the impact of neighboring genotypes on the fitness of individual plants. This system of intergenotypic interactions creates a frequency dependent pattern of selection and widens the conditions for the maintenance of a genetic polymorphism. As with much of Bob's work, theoretical calculations were supplemented by direct measurements from experimental populations to provide a predictive framework. Bob was also a strong proponent of the idea that genetic mixtures would perform better than single pure lines in an agricultural context, although the evidence to support this view has been meager.

A LIFE'S ACCOMPLISHMENTS

As noted above, Bob worked in, and in some cases helped found, several distinct but related areas of plant genetics. He had an enduring impact on plant breeding, largely through his book but also through his early work in biometrical genetics. These contributions were later recognized through the DeKalb-Pfizer distinguished career award of the Crop Science Society and the Crop Science Award of the American Society of Agronomy. Bob was elected to the National Academy of Sciences in 1973, where he chose to affiliate with the genetics section and later with the section on population biology, evolution, and ecology after it was formed, rather than with the agricultural sections. This choice illustrates that his first love was genetics, despite a lifelong devotion to agriculture.

More than any other worker, Bob Allard is responsible for laying the rigorous experimental foundations for plant population genetics, and he played a major role in melding the union of ecology and genetics that emerged as ecological genetics. Perhaps his most enduring scientific legacy was the series on population studies in predominantly self-pollinated species. This series illustrated one of Bob's greatest strengths. He was first and foremost an empiricist who found innovative ways to test theory and to expand our empirical understanding of genetic systems. His belief in interaction ran counter to the dogma of his time and often led to intense arguments, but he never modified his views. He was passionate about his scientific views and at times the strength of his convictions seemed to overwhelm the available evidence. In retrospect, his intuition was excellent and his views have been largely vindicated.

Bob was a prolific teacher and mentor of graduate and postdoctoral students. Altogether he trained 56 Ph.D. students, and he hosted numerous visiting scientists and postdoctoral students; he also trained a host of M.S. students. He had a large number of international students, and many have become prominent figures in countries around the world. I recall students from all continents, and as a consequence he left a global intellectual legacy. He taught throughout his long tenure at UC Davis in both the Department of Agronomy and the Department of Genetics. He wrote a wonderful set of lecture notes on population genetics that were used in the introductory genetics course at Davis. During the late 1960s, I encountered his lecture notes as an undergraduate and immediately decided I wanted to study population genetics. He also taught in the introductory genetics course for many years as well as a graduate course in quantitative genetics and an undergraduate course in population genetics. He was not a classroom performer, but his lectures, like his writing, were clear and carefully organized to make a central point.

Around 1967 Bob became chair of the Department of Genetics at UC Davis, where he served with energy and skill. He played a major role in bringing Th. Dobzhansky and F. J. Ayala to Davis in the early 1970s and helped catapult the Department of Genetics to international preeminence. At its peak the department included among its faculty five members of the National Academy of Sciences. He also served on virtually every major committee of the university and for a period chaired the Davis division of the UC Academic Senate. Bob was an active member of the National Academy Sciences, where he chaired Section 27 for three years. He served on a number of National Research Council committees, including a committee that produced several volumes on managing global genetic resources. He was unstintingly generous with his time, and he served the university and the academy he loved with great devotion.

Bob retired in 1986 but remained very active. He published a remarkable number of research papers during his retirement, along with the new edition of his classic plant-breeding book. During this period, Bob and Ann Allard spent much of their time at their home at Bodega Bay on the northern California coast. He loved walking on the seaside cliffs examining plants, especially *Avena barbata,* and speculating about their unique adaptations to the California environment. He was always eager to entertain friends and colleagues; evenings with the Allards at Bodega Bay were very special events. Bob loved wine and was an accomplished student and collector of fine wines, so any dinner was resplendent with excellent wine. Bob finally had to leave his Bodega Bay home about two years before his death, owing to the onset of Alzheimer's disease and circulatory difficulties. He died on March 25, 2003, in Davis at the age of 83.

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