Population Genetics and Germplasm Resources in Crop Improvement
AN INTERNATIONAL SYMPOSIUM
August 11 – 13, 1988 ■ University of California, Davis

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INTRODUCTION

The discipline of plant population genetics lies at the core of modern approaches to genetic resource conservation, plant breeding, plant population biology, and evolution. This is because population genetic theory defines the genetic composition of populations, and allows development of a formal, predictive account of how genetic compositions may change through time in response to the various evolutionary forces. In experimental practice, population geneticists study the patterns of genetic diversity and reproductive systems in both natural and agricultural populations of plants, and seek a methodological framework for evaluating the relative importance of the various adaptive and nonadaptive processes of evolutionary change.

This Symposium took plant population genetics as its central focus and presented the latest perspectives on the major topics and issues emerging from new developments in molecular biology, ecology, and genetic resource management. A key objective was to stimulate greater research interactions among population geneticists, ecologists, and plant breeders. The Symposium also highlighted deficits in research and imbalances between theory and experiment, thereby calling attention to areas wherein additional research is needed. Progress in both molecular and organismal studies of variation and evolution in plant populations was reviewed in the context of population genetic theory. The newly emerging applications of plant population genetics in genetic conservation, disease control, and varietal development received particular emphasis. The presentations of most of the invited speakers will be published in a proceedings volume that will be provided to all general registrants of the Symposium. These presentations are noted by an asterisk in the Symposium program included in Appendix I. It is anticipated that the resultant volume will be influential in guiding future research in plant population genetics and in its allied fields of application. Information for ordering this volume is on the next page.

The purpose of this report is to make available portions of the Symposium that will not appear in the proceedings volume. The Symposium opened with an address by Dean Charles E. Hess of the UC Davis College of Agricultural and Environmental Sciences, one of the sponsors. His address begins on page 3.

A major objective of the Symposium was to commemorate Robert W. Allard for his outstanding accomplishments and influence on numerous plant researchers. Classical population studies in plant species had been largely confined to quantitative measures of ecotypic variation or to investigations of the response of agricultural species to breeding practices. Following G. L. Stebbins' classic 1950 work, *Variation and Evolution in Plants*, the experimental science of plant population genetics emerged and was investigated intensely at UC Davis, most notably by Professor Allard and his students. Experimental plant population genetics represents attempts to understand the evolutionary potential of inbreeding and outbreeding species and to provide guidance to plant breeding so that the evolutionary consequences of breeding systems and of population homeo-
stasis can be exploited. Allard's initial program expanded into a range of problems dealing with the evolution of breeding systems, host-pathogen interaction, genetic resource conservation, and the use of molecular markers to study evolutionary processes. These developments have become widely recognized both nationally and internationally. A special evening session was set aside for commemorating these accomplishments. A presentation to Dr. Allard was made on behalf of the California Dry Bean Advisory Board by Mr. Chuck Cox, recognizing Allard's contributions to genetic improvement of lima beans. G. Ledyard Stebbins then introduced Dr. Allard who then presented an address. The proceedings of this session begin on page 6.

Another aspect of the Symposium was one session devoted to a panel discussion on facilitating genetic resources research and conservation. The proceedings of this session begin on page 19. A panel of six representing academia, national funding agencies, the US Department of Agriculture, and a private breeding and research company addressed needs, problems, and funding potentials for plant genetic resources. A noteworthy point emphasized in the discussion is that a major problem for maintenance of genetic resource collections is the lack of sufficient funding specifically for maintenance. Only the US Department of Agriculture currently supports long-term funding for collections and its level of support is not sufficient. No other funding agency, nor the Competitive Grants Program of the USDA, has programs for funding collections that may not currently be associated with research projects. There are many such collections that are jeopardized by this situation at the state and national levels.

The Symposium closed with an address by Dr. Lyndon W. Kannenberg. His remarks appear on page 36. The Symposium was attended by nearly 300 researchers in the related areas of theoretical and experimental population genetics, evolutionary biology, and plant improvement. The Symposium was truly international; 30 different countries were represented. While the majority of registrants were from California, there were registrants from 34 other states. Many of those attending also participated by presenting posters describing research related to the themes of the Symposium. The abstracts of these 56 posters are included in this report as Appendix II. More than half of the posters dealt with assessments of genetic variability in various crops, wild species, and germplasm collections and with techniques and strategies for such assessments. The remaining posters were rather evenly distributed among the general topics of population genetics, breeding issues, quantitative genetics, and evolution.
Welcome

It is a pleasure to welcome you to the International Symposium on Population Genetics and Germplasm Resources in Crop Improvement. As stated in the program announcement, there are two major objectives of this conference. One is to provide a focus for stimulating greater research interactions among population geneticists, ecologists, and plant breeders. We hope to identify gaps in knowledge and imbalances between theory and application and through both, call attention to areas wherein additional research is needed. This has been the thrust of other conferences that we have held at UC Davis in recent years, such as Genetic Engineering in Plants, Genetic Engineering in Animals, Tailoring Genes for Crop Improvement, and, just last week, Risk Assessment in Agricultural Biotechnology.

Everyone here this afternoon has been concerned with and has promoted greater attention to the subject of germplasm resources and genetic diversity. Fortunately, your efforts have been successful. There have been a number of meetings, and several studies about biodiversity and genetic resources are underway. For example, the Beltsville Symposium on Biotic Diversity and Germplasm Preservation — Global Imperatives was held last May. The National Research Council’s Board on Agriculture has in progress a three-year study on Global Management of Genetic Resources. I have the pleasure of serving on a National Science Board Task Force on Biodiversity. The National Science Board is the policy board for the National Science Foundation and its studies provide a focus to issues in science and often lead to new or increased program activity within the National Science Foundation.

In addition to conferences and studies, there have been accomplishments. For example, a component of the National Plant Germplasm System has been established at UC Davis and serves as the repository for a number of fruit and nut crops including grapes, walnuts, figs, and strawberries. Also, through a State initiative, the Genetic Resources Conservation Program was established, headquartered at Davis, to preserve plant and animal germplasm which may be endangered and to develop techniques to preserve germplasm in situ and in collections. Cal Qualset serves as Director of the Program. At the national level, the Joint Council on Food and Agricultural Sciences has as one of its top priorities for the 1990 USDA budget the following: “Genetically Improve Economically Important Plants. This priority concentrates on relating plant characteristics to end-uses and to improving the hardiness of plants relative to environmental stresses. A key component is to ensure the availability of adequate germplasm.” This priority also appears in the report of the Fiscal 1990 Budget Committee of the Division of Agriculture of the National Association of State Universities and Land Grant Colleges. This report is being presented not only to the
OPENING

USDA, but to the Office of Management and Budget and key Congressional committees. Although it is difficult to predict the outcome of next year's budget presentation because of the election, at least everyone in the agricultural research and education community is working together to convince the Administration and Congress that it would be wise to increase the research investment made in the area of germplasm resources in crop improvement.

Accomplishments in germplasm manipulation in the past and present have been impressive. The work of Charley Rick in tomatoes, Royce Bringhurst in strawberries, whose yields have increased from 5 tons per acre to 27 and even 70 tons per acre, and whose patents generate the largest amount of royalties in the University of California (over $1 million last year), Harold Olmo's grape varieties, Charlie Schaller's barley, Bob Allard's lima beans, Cal Quislet's wheats, which represent the predominant varieties grown in California today, and Julian Crane's work with pistachios are only a few examples.

But the challenges that face us today are even greater. We must develop an agriculture that is less dependent upon agricultural chemicals for the control of pests. Examples of the externalities that are forcing this are Proposition 65, California's Clean Water Act, the Endangered Species Act, and the concern of the public for the possible presence of chemical residues in the food that they eat. The new tools to transfer a gene from one organism to another has raised the anticipation level that new solutions to the challenges I have described are here or are on the horizon. However, most people agree that a lot of fundamental knowledge is required about gene expression and function and the basic biochemistry and physiology of plants and animals is needed before the full potential of the new technology will be reached. It will also take teamwork among the molecular biologists, the plant breeders, the ecologists, and the population geneticists if we are really going to make progress in agriculture and maintain our competitive edge. The availability of the new tools which facilitate genetic manipulation makes it ever more critical that we preserve germplasm resources.

One concern I have is that the area of traditional genetics and plant and animal breeding may not be as fashionable as it should be. I have been conducting a survey of biotechnology research in the Land Grant Universities for the years 1982, 1984, and 1986. There has been a substantial redirection of resources and an influx of new resources in research related to biotechnology. But the data also indicate a substantial reduction in the number of plant and animal breeders. For example, a comparable group of Land Grant Universities reported the following numbers of plant breeders:

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<tr>
<td>1982</td>
<td>391</td>
</tr>
<tr>
<td>1984</td>
<td>336</td>
</tr>
<tr>
<td>1986</td>
<td>271</td>
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This represents a 30% decrease which I feel is a serious loss because the application of biotechnology to agriculture depends upon teamwork including plant breeders as key members of that team.

At the opening, I said we have two major objectives. The second major objective of this symposium is to recognize the
tremendous contributions of Robert W. Allard as a scientist and teacher. Following the pioneering work of G.L. Stebbins, Bob Allard and his students have developed the experimental science of plant population genetics. We are very proud of Bob for his outstanding accomplishments and the influence he has had and continues to have on numerous plant researchers. As you know, this evening's session is dedicated to Bob and many of the participants throughout the program are his students.

We thank you all for joining us in this important symposium and hope that you leave with new ideas for research and collaboration. I want to recognize the sponsors of the symposium. In addition to the College of Agricultural and Environmental Sciences, they include Division of Biological Sciences, College of Letters and Science, Office of Graduate Studies and Research, Office of the Chancellor, Genetic Resources Conservation Program, National Science Foundation, California Crop Improvement Association, Calgene, Inc., Cornnuts, Inc., Monsanto Company, Pioneer Hi-Bred International, Inc., Rockefeller Foundation, California Dry Bean Advisory Board, Campbell Soup Company, Escagen Corporation, Northrup King Company, Sigco Research, and Biogenetic Services, Inc. I also want to recognize the tremendous work done by Cal Qualset and Patrick McGuire, Michael Clegg and Subodh Jain, co-chairs of the Organizing Committee, Neil Rutger, chair of the Local Arrangements Committee, and the members of these committees who have made the symposium possible. They all deserve our thanks and special gratitude for also arranging such great weather in August.

Thank you very much. Have a good conference!

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SESSION HONORING ROBERT W. ALLARD

Presiding:

Charles O. Gardner
Agronomy Department
University of Nebraska
Lincoln, Nebraska

Presentation to Dr. Allard

I am a lima bean grower from the west side of Stanislaus County. I brought with me our current chairman of the Advisory Board, Mr. John Thoming. The California Dry Bean Advisory Board is made up of varietal councils representing dry bean varieties grown for commercial use in California. It is funded by assessments levied for the purpose of promotion, education, and research. The research budget augments research projects carried out by the University of California and the Cooperative Extension. Our function as a committee is periodically to interface, as a group of industry people, with research people working on bean projects, focusing on specific problems we are experiencing in our fields, warehouses, and in the marketplace, as they relate to quality for the consumer.

Ever since I can remember, there have been lima bean trials on our ranch. My family takes great pride in the fact that we have had the opportunity to provide a field laboratory throughout the years.

Tonight we are honoring a man who has devoted a lifetime of work to plant breeding and plant genetics. And to whom we, as lima producers, are indebted for advancing the production capabilities of lima beans in our fields. The varieties Mackie, Westley, White Ventura, and White Ventura N resulted from his efforts. The baby lima Mezcla was developed for economic use also. Of course, I am speaking of Dr. Robert W. Allard. His contributions through research trials, publications, textbooks, and classroom instruction in his field of expertise is quite remarkable. I cannot begin to describe them adequately to you.

I have to share with you a couple of family reactions I encountered upon explaining what I would be doing tonight. My uncle, Stuart Cox, who worked closely with Dr. Allard in the early years on our ranch, remarked that he was pleased that Dr. Allard was still receiving recognition for his work with lima beans. My cousin, Bill Cox, who had Dr. Allard as a professor, could only remark that Dr. Allard's plant genetics class was the toughest class he ever had. Perhaps Bill's class was no joy for Dr. Allard either. So you see, when John Thoming asked if I would make this presentation, I felt honored and privileged, especially considering our mutual ties. At this time, I would ask that Dr. Robert W. Allard please come forward to receive this token of appreciation from the large and baby lima bean producers throughout the State of California.
The inscription reads:

The large and baby lima councils express their appreciation to Professor Robert W. Allard for his substantial and lasting contributions to the California dry bean industry, through the collection and introduction of genetic resources, the advancement of genetic knowledge, and the development of nematode-resistant germplasm and cultivars of lima beans. August 11, 1988.

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Introduction of Dr. Allard

Good Evening, Ladies and Gentlemen. I would first like to thank the organizing committee for this opportunity to say some words about my eminent colleague, who has shared with me the exciting research on genetic evolution during the thirty-eight years that we have been colleagues together here in Davis. Bob Allard came up into research by a way which is not usual, but perhaps should have been more usual, particularly for those of us who are interested in application of the research as well as discovering the basic facts. If you will look at his biography, it starts with actually working with his hands on his father’s farm. He knew agriculture from the bottom up, before he did any theorizing about it.

He then began a research career after he had received his training, first as an undergraduate here at the University of California at Davis, followed by the Ph.D. degree received from the University of Wisconsin just before World War II. After a brief service in the Navy, he came right back here to Davis in 1946, where he has remained since then.

I moved up from Berkeley in 1950, and was his colleague, first in neighboring departments, Genetics and Agronomy, and then in the same department. I can say that I, perhaps, was the wet nurse of a baby Genetics Department, which I founded in 1950. Later on as Chairman, Bob Allard became the tutor who was responsible for the maturity that department has now. Finally, he has come full circle, finished his career, and like me, is in that glorious position of being Emeritus, retired, or as the Spaniards say, jubilado — jubilee. Of which the single nicest characteristic is that when you come to your office and see those little bits of paper typewritten in multiple types, directed to Chairmen, Deans, Directors, etc., you can very simply take them and put them immediately in the circular file!

When he started his work, the first research that he did was practical breeding, for which he has received the very well-deserved honor that you have just heard. But during this time, he certainly did not neglect theory, and was always anxious to get to the bottom — the why and the how — of improving crop plants as well as the actual improvement itself. In 1960, he began, with several collaborators — Subodh Jain, Lyn Kannenberg, and others — a series of papers and research studies on the genetics of self-fertilizing crop species. The upshot of that, the theme of Bob Allard’s research life, has been that self-fertilizers do become homozygous, but not completely so. They...
do not sink into a long-continued monotony of homozygosity. You should cherish the exceptions, the heterozygosity out of which much of the excitement and improvement can come.

This theme was explored for nine years, which was followed by the consequence of the maturation of molecular evolution and molecular biology. I think we can honor our colleague as being the first plant scientist to recognize that, once enzyme differences were brought to our attention — first by a human geneticist, Harris, and then by *Drosophila* geneticists, Lewontin and Hubby — that we plant geneticists and evolutionists had better do something about this and learn something about the biochemistry of our organisms and their genes, as well as the morphological effects of those genes. All of you who know the present situation in plant genetics and evolution know that this was a little spark of tinder that has become a fire of enthusiasm which has sent people off exploring the basic genetics of populations of plants worldwide of many very different varieties.

It is not, therefore, surprising that Dr. Allard became a member of the National Academy of Science in 1973. I preceded him slightly, and was very happy to welcome him there. But he did more than that. He has continued in that Academy, working actively to promote the interests of research workers like you and me; he was not always heartily welcomed by some of the people on the other side, because all scientists are good friends, but some are better friends than others. It is a fact that he is now Chairman of the Section of Evolution and Population Genetics of that society, and is using his influence as he can so well do.

So, without going into details, that brings us to the modern era. But, we should remember, as many of you know, what he has done not only for himself, for this university, and for his colleagues, but also for plant population geneticists throughout the world. Just a few statistics: 88 people have studied under Bob Allard during his career and have gone out into the world profiting from his knowledge; these are now eminent professors, directors, and research workers in 16 different states of our union and in 23 different foreign countries. I wish I could even approach that record. But I cannot. So I will simply say that we have with us one of the great leaders of plant genetics and its application to give us more food. Because of Bob Allard, we are wiser as scientists and better fed. In other words, full of beans, as he is too! Bob, the floor is yours.
Future Directions in Plant Population Genetics, Evolution, and Breeding

Thank you very much, Ledyard, for your more than kind introduction. I will start by quoting a sentence from the very first brochure that was sent out to announce this symposium. This sentence reads:

The overall aim of this symposium is to increase understanding of the role of plant population genetics in guiding evolutionary theory and plant improvement.

The first inkling I had that a symposium with this goal might be in the works came three or four years ago, when I began to hear comments from various of my colleagues that plant population genetics had changed a great deal since I joined the staff at Davis in 1946, and that the time might be approaching to assess the present state of plant population biology and to attempt to look into the future. I thought it was a very good idea to have such a symposium, and I want to take this opportunity to express my appreciation to those colleagues who came up with the idea, especially to Cal Qualset for persevering and bringing this symposium about. I am most pleased with the program that the organizing committee has arranged, and I am also pleased with their decision to dedicate this symposium to me. It gave me a warm feeling to find that my efforts have been noticed.

One thing I insisted on when I learned that the symposium was indeed going to happen was that I would not be one of the speakers, especially at a session such as the present one. However, over the past couple of years, one thing led to another, primarily due to Cal Qualset, until here I am, confronted with the title “Future directions in plant population genetics, evolution, and breeding.” Now I find this title really quite intimidating. Consequently, I am not going to talk to it. But I will talk to a safer title that might go something like this: “Some directions I hope plant population genetics will take in the future.” Also, I plan to stick fairly closely to my notes tonight, in an attempt to avoid shooting myself in the foot with prophecies that are made on an impromptu basis.

I believe it is fair to say, at least as far as the textbooks were concerned, that plant population genetics had not been invented when I arrived at Davis in 1946. There was no population genetics textbook at the time. In fact, the term ‘population genetics’ did not occur even in the general genetics textbooks of the day, nor in the plant breeding, nor in the animal, textbooks. There was usually an opening statement in the genetics text to the effect that “a knowledge of the chromosome basis of heredity is essential to the evolutionist.”

In the breeding text, there was usually a statement that “such knowledge is essential to the breeder.” But what followed were then descriptions of one- and two-locus transmission genetics in segregating families, mind you, not in populations, but in segregating families. There were descriptions of genetic analysis of pedigrees, "multiple
factor inheritance,' tables of chromosome numbers, and discussions of techniques, such as polyploid breeding, interspecific hybridization, mutation breeding, and the like. So far as I am aware, the first volume in which the importance of population genetics is thoroughly stated is the second edition, the 1941 edition, of Dobzhansky's *Genetics and the Origin of Species*. In that volume, Dobzhansky recognized three levels at which genetics impacts evolutionary processes. The first level was that of mechanisms of transmission of hereditary characteristics from parents to offspring. Dobzhansky's comment was: "The signal successes of genetics to date have been at this first level ... types possessing a desired set of characteristics may, within limits, be synthesized at will, and the schemes of such 'syntheses,' as worked out in theory, are almost always realized in detail in actual experiments." Now the second level was that of gene action, which Dobzhansky considered to be "far from being solved." That was in 1941. The third subdivision, "... has as its province, the processes taking place in groups of individuals — in populations — and is therefore called the genetics of populations. The rules governing the genetic structure of populations are distinct from those governing the genetics of individuals ... although, in fact, they are only integrated forms of the latter." In his book, Dobzhansky gave Hardy's formula, and mentioned that Haldane, Fisher, and others had treated effects of nonrandom mating and selection on one-locus allelic and genotypic frequencies mathematically. He concluded, however, "that it is necessary to proceed by inference, because the theory has not been adequately tested in nature." He went on to say, "Nonetheless, a growing body of observational and experimental evidence gives at least a promise that an adequate analysis of evolutionary dynamics will be possible in the not-too-distant future." Dobzhansky was aware of Sewell Wright's 1931 paper entitled "Evolution in Mendelian Populations." He commented: "The importance of this work can hardly be overestimated. The experimental work itself, however, is still a task for the future."

What Dobzhansky seemed to be saying in 1941 was that, even though our ignorance at the time greatly exceeded our knowledge, we did have at least some notion of the future of evolutionary genetics. This leads me to the question, could plant-oriented persons of the 1940s have predicted the breadth and the depth of the remarkable series of advances in plant population biology indicated by the program of this symposium? Some of the research that was going on in the 1940s — for example, that of Harry Harlan and Coit Suneson with inbreeding species and that of Merle Jenkins and George Sprague with corn — leads me to believe that there were persons then who might have identified, at least in broad outline, the general course that plant population biology was to take. These workers were keen observers of genetic diversity in their experimental populations. They were aware that numerous biological factors, such as mating systems, variable selective values, genetically variable populations of pathogens, and complex interactions among such factors, all played a role in determining the course of genetic change. Their vision, which flew in the face of the single-gene approaches that many favor to this day, was that successive cycles of intermating, segregation and recombination with its numerous novel genotypes, and selection, both natural and artificial, reduced the frequency of the 'weaker sort,' as Harry Harlan put it, and increased the frequency of the more
favorable genotypes in their populations. This perspective led them to adopt population-type breeding programs, which foreshadowed the recurrent selection procedures that have been so successfully applied in recent years.

I will now attempt to assess the situation as it is at present to set the stage for a few concluding remarks on the directions I hope plant population genetics, evolution, and breeding will take in the near future. Fortunately, the titles of the papers of this symposium have already done most of the stage-setting for me, because the titles in themselves give a good idea of the broad scope and the broad range of issues that have been addressed and the richness of advances that have been made since the 1940s. However, I think it will be useful to introduce some information that comes from some long-term population studies that have been the central focus of my project for the past forty years. Although I have not yet fully analyzed the data from these experiments — these are project data of subsidiary populations, the things that most of the graduate students, post-docs, and so on worked on — the results that I have to date have pretty badly shaken some of the concepts that I have held over the years as established doctrine.

The studies I refer to grew out of two sets of observations that I made during the 1930s. The first observations were made in the period 1931 to 1937, when I planted, cared for, and harvested experimental populations of corn and ryegrass (both of which are outbreeders) and common beans, lima beans, garbanzos, and fava beans (all moderate-to-heavy inbreeders) that W.W. Mackie of the Berkeley campus grew on my father’s farm. The second set of observations were made here at Davis, when, as an undergraduate student, I worked for Coit Suneson on his composite crosses of barley and his natural populations of Avena fatua. I had an executive position with him; I was chief planter, a weed hoer, and that sort of thing. After my undergraduate work at Davis, I went to the University of Wisconsin as a graduate student. There, working under forced draft, because I was trying to complete a Ph.D. before the Navy called me to World War II duty, I really did not have much time to think about my experiences with plant populations. However, during World War II, the Navy provided me with fairly frequent slack periods, the famous military ‘hurry up and wait’ periods, during which I pondered the discussions I had had with Bill Mackie, Coit Suneson, Harry Harlan, Gus Wiebe, and some of the corn breeders, especially George Sprague. By the time I returned to Davis in the spring of 1946, I had in mind some experiments I wanted to do.

Mackie and Suneson were very encouraging, and they generously provided me with reserve seed of a succession of generations of their populations, many of which at that time had been going on for twenty years and had been synthesized from a known set of parents. We knew the initial composition of the populations. The main question asked in these experiments was, “What do alternative alleles of variable loci do in populations, and, in particular, how do specific alleles effect adaptedness at the population level?” Now this, it seemed to me, was the ‘bottom-line’ question of population genetics. What do loci do? What do they do about adaptedness defined as ability to live and reproduce in the population? Almost all organisms
live in populations; their natural state is not within pedigreed families and that sort of thing. They live in populations.

The structure of these experiments was really very simple. Basically, it involved determining the frequency of specific alleles of a large number of discretely inherited single-locus characters, while simultaneously determining the expression of a number of quantitative traits over many successive generations in experimental and natural populations of several different species. The populations were monitored over generations in two ways: first, they were monitored for those discretely inherited characters and for those quantitative traits that can be classified or measured conveniently on an entire population basis in populations grown in dense stands, that is, in their normal state; second, they were also monitored for those traits which are more conveniently classified or measured on a single-plant basis in spaced plantings. Quantitative characters that were monitored on an entire-population basis included such things as flowering time, height, and seed size. Also, seed yield was monitored on an entire-population basis, especially in the cultivated cereal and cultivated cereal legume species; however, yield testing, as many of you recognize, particularly when it is repeated in replicated yield trials over several seasons, is very labor intensive, and it is consequently done not every generation, but only at five- to ten-generation intervals. The original set of discretely inherited characters, the single-locus characters, which were monitored on an entire-population basis included several easily classified linkage map variants such as two-row versus six-row spikes and rough versus smooth in barley and the equivalent types of characters in the other species. However, in the 1950s, a second category was added, namely resistance versus susceptibility to specific pathotypes of fungal disease organisms. This resistance was determined by inoculating seedlings with single pathotypes in the greenhouse, and counting the numbers of individual seedlings which were resistant or susceptible, in order to determine frequency changes over generations. A third category of discretely inherited characters, a number of moderately-to-highly polymorphic isozyme variants detectable by starch-gel electrophoresis was added in the 1960s. A fourth category, a number of DNA-restriction-fragment loci was added in the 1970s. The restriction-fragment loci turned out to be by far the most informative, once we had worked out the relatively rapid assay methods. The reasons they were informative were discussed this afternoon by more than one of the speakers, and I will not go into them now.

The second way in which the populations were monitored was by isolating random individuals from a succession of generations of the populations, selfing these individuals, and classifying space-planted individuals within the resulting families for the discretely inherited characters and also measuring the same individuals for a dozen or so quantitative characters. Progeny test data were taken in such a way that a founder plant, which had been isolated from a population, would be categorized as heterozygous or homozygous for single-locus marker loci and also as to phenotype for quantitative characters. These family progeny tests were repeated in two or three seasons. This practice was adopted because it became apparent very early in these studies that estimates of quantitative trait expression made on individual plants varied so much as to be of very little use in
estimating parameters of quantitative variability. We also found that progeny test data taken in a single year were also pretty variable. Consequently, we went to multiple-season tests.

I want to emphasize that large populations were grown each generation with the goal of reducing the effects of genetic drift, that is, random events, to triviality. The actual results indicated that the effects of directed processes, such as selection and departures from random mating, were overwhelmingly larger than random processes for all the loci that we looked at. Their effects were usually two or more orders of magnitude larger than the random effects. Similarly, samples taken from the various generations were large enough so that standard errors of estimates for the quantitative characters were small. This was also the case for the enumeration data.

I will not attempt to give details of the various kinds of evidence provided by the massive data sets that accumulated over a forty-year period. Instead, I will proceed directly to an abbreviated summary of the main conclusions which emerged from studies of the several species which were investigated. In this necessarily terse overview, I want to make ten points total, proceeding from three points which emerged from studies of quantitative characters, to two points which emerged from the studies of discretely inherited characters, to five points from multilocus analyses of the discretely inherited characters.

First, three points concerning quantitative characters:

Number one: Reproductive capacity manifested as higher seed yields, larger numbers of seeds per plant, greater spike weight, and other traits that are directly related to reproductive capacity, increased over generations in all the populations. The reproductive capacity of all the populations increased. In highly variable populations of cereal grains and cereal legumes which had been synthesized from worldwide samples of germplasm, reproductive capacity increased during the first fifteen to twenty generations of natural selection from about sixty percent to about ninety-five percent of that of standard check cultivars. That is, when you start out with a very diverse population, including a lot of unadapted material, what we found was that reproductive capacity was about sixty percent higher than that of the standard cultivars of the time. Reproductive capacity continued to increase into the late generations. For example, it continued to increase for more than fifty generations in Barley Composite Cross II, which was one of the populations that I got from Sune- son. But the rate of increase slowed in the late generations. The decrease in seed yield in the early generations of populations which had been synthesized from locally adapted parents were very much smaller. There was very little decrease in seed yield in the early generations, so long as the parents were all adapted. Also, the rates of increase in seed yield were relatively small in all such populations.

Number two: Changes in traits directly related to reproductive capacity, such as seed yield and numbers of seeds per plant, positively and significantly correlated with each other in most generations. However, the increases in reproductive capacity were usually not significantly correlated, or they were only weakly correlated with any of the other quantitative traits measured, such as maturity data, height,
vegetative biomass, and the standard sorts of things that are measured in population genetic and population ecological studies.

**Number three:** Data from the quantitative characters indicated that the underlying genetic systems were complex and much affected by environment. In fact, that was the only thing they established very firmly: that genetic systems are complicated. However, the data from quantitative characters provided very little information about what was actually going on genetically within the populations.

Now to two points from analyses of data from discretely inherited characters:

**Number four:** Every discretely inherited marker locus, including the morphological variants that we started with originally, disease-resistant loci, the isozyme loci, and the restriction-fragment loci, have large effects on reproductive capacity and often on several or all of the other quantitative characters that were measured. We made persistent attempts to disassociate the quantitative trait effects from the specific alleles of the marker loci, but they were consistently unsuccessful. What this indicates is that the marker loci studied were major genes, not only for the discrete alternative characters for which they were named, but also for many quantitative characters. They affect enzyme systems that leave almost no aspect of the morphology or physiology of the plant untouched. Quantitative trait differences between marker-locus homozygotes were usually very large, which is to say that single-locus additive effects were large. However, single-locus dominance effects were nearly always small.

**Number five:** Allelic frequency changes of all marker loci studied were strongly correlated with changes in reproductive capacity. High grain yield and high seed number per plant, for example, were nearly always positively correlated with the predominant allele of the marker locus. In other words, the predominant allele was a good locus, what went with it was high grain yield and other characters that gave direct measures of reproductive capacity. No consistent patterns were detected for other quantitative characters. For example, early versus late flowering, short versus tall stature, and high versus low vegetative biomass were associated about equally frequently with those of low reproductive capacity and low survival ability as with marker-locus alleles with high reproductive capacity and high survival ability. One of the most interesting things to come out of this was that the great majority of alleles which were disease resistant, at least to the foliar diseases that we selected because they were easy to work with, had negative effects on yield and reproductive capacity. There is an old dictum in plant breeding that disease resistance is good. Well, it is not always good. In fact, in the majority of cases, when you get effects out by themselves, disease resistance alleles have detrimental effects on the physiology of the plant.

Now to five points from multilocus analyses of the marker loci:

**Number six:** Twenty-five or so marker loci were scored over many generations for most populations and most species, so that very large numbers of pairwise as well as three-locus, four-locus, and higher-order multilocus comparisons were ultimately available for analysis.
In fact, when you take this number of marker loci over a large number of generations, the data sets, or rather the paper they are written upon, occupy great amounts of space. Rapid build up of highly significant associations between pairs of loci was the norm. It was the usual situation in all the inbreeding populations. However, the extent of association between pairs of loci frequently changed significantly in amount and even in direction in ways that indicated that associations between pairs of loci were affected not only by year-to-year fluctuations in the environment, but also by evolutionary changes in the background multilocus genotype of the population. Studying one generation in one season does not tell you very much. You have to study a number of generations over a number of seasons to get much idea of the ultimate sort of associations that build up. These changes occurred in such bewildering patterns that I, anyway, was not able to deduce higher-order multilocus genetic structures from the two-locus structures. Another finding was that additive-by-additive types of interactions were large at the two-locus level, and more particularly, were large at higher-order multilocus levels, whereas additive-by-dominance and dominance-by-dominance interactions were small. What this says, then, is that the sort of heterosis that we observed in these populations was due to additive-by-additive interactions and that dominance has very little to do with heterosis. This was true for inbreeders and outbreeders.

Number seven: Log-linear, canonical correlation, and cluster analyses uncovered features of microevolutionary change that were not apparent from the two-locus analyses. That is, the two-locus analyses were bewildering. You look at them generation after generation, and the shifting patterns were such that you just could not, at least I was not able to, figure out how the higher-order interactions worked. But with log-linear, canonical correlation, and cluster analyses, we did start making some sense of this. The polymorphic loci monitored in various inbreeding populations became clustered in early generations into groups of three, four, or five loci each. A series of breakdowns of associations in complex repatterning and amalgamations then started, which led to clusters of six to eight or more loci in the later generations. The picture of adaptive change which emerged was that increases in adaptiveness in a given environment are correlated with the development of clusters of associate alleles and gradual amalgamation of clusters into large synergistically interacting complexes. Far less genetic structure developed within outbreeding than within inbreeding populations. Adaptiveness manifested as higher reproductive capacity also appeared to develop more slowly within outbreeding populations than within inbreeding populations. Evidently the clustering structure, that strong structure which developed in the inbreeders, led to very rapid changes or improvements in adaptiveness, manifested as increased reproductive capacity.

Number eight: None of the populations of either inbreeders or outbreeders had become genetically uniform, even after as many as fifty generations of propagation in closed, isolated populations in one single ecogeographical area. They became less variable, but they did not become fixed. Barley Composite Cross II, for example, still responded dramatically to artificial selection in both the plus and minus directions for quantitative traits, including traits that were rel-
evant to agricultural suitability such as earlier maturity, superior standing ability, and disease resistance, after more than fifty generations of propagation without conscious selection. Composite Cross II also remained highly variable for quantitative characters, and remained polymorphic for marker loci and complexes of marker loci, whether it was grown in a Mediterranean climate, a continental climate, or some other type of climate.

Number nine: All of the composite crosses of barley, and we had the most information on these by far, developed essentially the same multilocus structure when they were grown in ecologically similar environments, for example, in a Mediterranean climate. However, very different multilocus structures built up in each major climatic region in which they were grown. For example, the structure which developed in Mediterranean climates was very different from that which developed in continental climates. In cultivated barley, there appear to be only about a half dozen major genetic structures worldwide. That is in cultivated barley. There are more in wild barley. Cultivated barley has less variability and has a far smaller number of multilocus structures. The multilocus structures it has that are similar to those of wild barley tend to be structures that wild barley has in the most lush habitats where it occurs in the wild, which is perhaps not surprising. So, there are about a half dozen major genetic structures worldwide within barley, but there also appear to be a number of subtypes, relatively minor variations on the major themes, within each of the major structural types.

This leads me to my final point, the evolution of differing genetic organizations among populations of a species, which I will illustrate with *Avena barbata*, the slender wild oat:

Number ten: *Avena barbata*, which was inadvertently introduced to California from Spain (this was as a contaminant in cereal seeds and shipboard litter) during the explorer mission period, has become a major component of grassland and grass-oak savannah habitats in California. In such habitats in the lower elevations in California, it now appears in populations of millions and millions and millions of individuals. It is a prominent component of our lower elevation grasslands and grass-oak savannas. Surveys of about twenty loci, mostly isozyme and restriction-fragment loci, indicate that virtually all of the alleles present in the Spanish gene pool, other than a few rare alleles, are also present and at similar frequencies in California. We know that *Avena barbata* was introduced from Spain because Spain maintained California in a monopolistic fashion as a colony and the trade was with Spain. The Spanish gene pool was transplanted to California. Genetic identity measures showed that the Spanish and California gene pools are very similar to each other. They have the same basic ingredients in them. There is a big difference, though. The Spanish and California gene pools are both highly structured on a multilocus basis, and this structuring was highly correlated with various factors in the environment, particularly with moisture and temperature differences. Although some of the three- or four-locus associations found in Spain occur in California, not a single one of a half dozen or so large multilocus complexes, that is, ones with up to twenty loci in them, found in California, has been found in Spain. It is, therefore, apparent that within a period of 150 years or so, the
allelic ingredients of the Spanish gene pool have become structured under California conditions into a limited number of novel multilocus genotypes, each of which is very closely associated with a distinct specific habitat. Natural selection has done a very good job of breeding, if you please, strains or ecotypes, if you please, of this desirable range forage species that are uniquely adapted to all of the main ecological niches in California. There are seven or eight such major types within California.

Each of the ten points above has implications, and I believe they are important ones, concerning one or more aspects of plant population genetics, evolution, and breeding, for example, implications concerning the generality of the multiple factor hypothesis, host pathogen interactions at the population level, the evolutionary consequences of mating systems, genetic changes which occur during domestication, genetic resource conservation, and so on and so on. However, each of these is a story in itself, a presently incomplete story, that calls for further study. While I could say some things about them, I am sure you will be just as happy if I state that they are interesting problems on which more work should be done.

So much for attempts to assess the state of our knowledge of plant population genetics and evolution as it is at present. This assessment gives me a distinct feeling that I came onto the scene 40 years or so too soon. How I wish the issues had been as well defined 40 years ago as they are now. I would not have stumbled around in the way I did if that had been the case. How I wish the tools we have now, biochemical, and especially the DNA markers, the ways of measuring selection, mating system parameters, genetic organization, and other things statistical, and procedures for evaluating usefulness of specific genes under natural and agricultural conditions, how I wish they had been available then. I see the stage is now being set to improve the knowledge-to-ignorance ratio at rates that could hardly have been imagined 40 years ago, in fact, not even 10 years ago. But the rate of improvement that is now possible is unlikely to be realized unless we maintain the sort of balance among disciplines that we have had in our programs in recent years. My concern is that we are in the process of losing that balance by emphasizing ‘high-tech’ methodologies to the exclusion or near exclusion of the underlying genetic, ecological, and evolutionary components which have been essential to the progress that we report in this symposium. There is a great deal yet to learn about what really goes on genetically within and among different populations of a species. My hope for the future is that we continue a comprehensive and a balanced attack on the things that are really important to know.

Finally, with some trepidation, I state that several persons have asked me to comment on the impact of genetic engineering on future progress in practical plant breeding. With respect to ‘down-in-the-trenches’ plant breeding, my guess is that at least for the dozen or so main crops that feed and clothe the world, major progress is going to come in much the same way as it has in the past. That is, through efforts of ‘honest-to-goodness’ plant breeders, as one of my midwestern colleagues put it recently. Honest-to-goodness plant breeders patiently, or perhaps they are not so patient as some people think,
impatiently, putting together favorable complexes of genes, much in the same way that they are doing it now. Unless, of course, the production of honest-to-goodness plant breeders continues on its presently drastic downward course in our universities, including the University of California at Davis, and this leads that particular species of scientist to go extinct, as many fear is going to happen.

Concluding Remarks

Dr. Gardner

Thank you, Bob, for a most interesting talk. The book that Dr. Allard published many years ago, *Principles of Plant Breeding*, is a classic. I would like to see you revise that book, Bob. You told me ten years ago that book had been published in several languages. If you take the number of all the people who have benefitted from the book and add to it the number of students that Dr. Stebbins noted, you will perceive Bob Allard's tremendous influence and impact throughout the world. I am sure that all of you join me in congratulating Bob on his many, many accomplishments. We can all look forward to future contributions from you in the years ahead.
Facilitating Genetic Resources
Research and Conservation

There seems to be more than sufficient room for discussion on genetic resources with the current North-South controversies over the possession of germplasm, the Government Accounting Office report, the Jeremy Rifkin lawsuit dealing with the National Plant Germplasm System, the roles of the various international centers, some of whom take responsibility for their crops and their germplasm while other centers do not, the issue of the national programs that have been set up by the International Board for Plant Genetic Resources (IBPGR) from Rome, which has advocated very strongly the establishment of national germplasm systems, and the question of whether those systems are self-perpetuating, self-maintaining, or not.

While we have several very successful genetic resources programs — including one in tomatoes here at Davis that Dr. Rick has headed for many years and which one of our panel members, Allen Stevens, represents in a way, the rice collection at the International Rice Research Institute, which T.T. Chang has directed for many years, and the potato program which is divided between the International Potato Center in Peru and the efforts at Wisconsin, I suppose this panel might address in some way why, for most crops, our genetic resources are used as a last resort, and then they are used in backcrossing programs to introduce single genes. For the most part it sounds as though the modern biological techniques that are being introduced are going to promise more of the same thing, only with newer and fancier technologies.

What else the panel will discuss, I really do not know, but let us start with Beverly J. Berger, who represents the Office of Science and Technology Policy. Her Ph.D. degree, appropriately, was received under the direction of Bob Allard and she has done additional postdoctoral work at Berkeley. She is going to talk to us about the role of her office in the support of research.

The Office of Science and Technology Policy — A Friend for Plant Genetic Resources Development and Research

I am very pleased to talk to you about what the Office of Science and Technology Policy (OSTP) does and what its role is in research. The OSTP is not the Office of Technology Assessment (OTA). The OTA is a branch of Congress which, indeed, does assessment not policy issues, whereas OSTP, in fact, usually does not do assessment, but is very much involved in policy formulation, drawing on assessments usually done elsewhere.
The office is structured with a director and a number of assistant directors with well-defined responsibilities. The director of the OSTP also serves as Science Advisor to the President. We work out of the Executive Office of the President and are involved in all issues which pertain to science or technology in policy development. That means issues like acid rain, ozone, agent orange, AIDS, biotechnology - a plethora of issues. Those are the ones I work on. We are also involved in budget formulation, working very closely with the Office of Management and Budget (OMB) throughout the budget formulation process, and sit with the Director of OMB as the final decisions on the budget request are made before it goes to the President and then to Congress. We also work directly with agencies on budget issues and try to stimulate on occasion or enhance research efforts in appropriate areas.

Another function of OSTP is interagency coordination on scientific issues. The same statute that established the office in 1976 established the Federal Coordinating Council for Science, Engineering, and Technology (FCCSET) and associated committees. The FCCSET is chaired by the Director of OSTP and has as members a lead person from each agency for research. For example, from the National Science Foundation, the member of this council is the director, Eric Bloch. For agriculture, it is Assistant Secretary Orville Bentley who is responsible for research. In particular, a number of the committees that report to that council serve as coordinating committees across agencies. For example, there is a Committee on Earth Sciences, which looks at issues such as ground water and global climate. We have a Committee on Life Sciences, which spans that area. We have a Biotechnology Science Coordinating Committee which looks specifically at the science related to biotechnology. There are FCCSET committees for supercomputers and for materials. Altogether, there are a dozen active FCCSET committees, which serve to coordinate across agencies. A subcommittee of the Committee on Life Sciences, which I chair, is a Human Genome Subcommittee to help the coordination between the National Science Foundation, the Department of Energy, the National Institutes of Health, and the Department of Agriculture as well as the Howard Hughes Medical Institute on the project to map and sequence the human genome.

I tell you this to give you a bit of a sense of what OSTP does and is. I have come to appreciate that OSTP is right in the middle of policy making, on budget decisions, and on all the really important science and technology issues. My simple message is that it is useful to know about this very small agency. There are about 20 or 30 people who work there. We draw a lot on agencies and the private sector to provide information and resources because clearly so few people cannot quickly know everything there is to know about an important topic. We need a lot of resources. It is an agency right in the heart of government where decisions are made. It is a very good unit to keep informed about an important issue like biological diversity. I would encourage those of you who consider maintenance of biological diversity a fundamental concern and an important cross-cutting research issue to think in the future of ensuring that the staff who works with the life science part of OSTP is sensitized to the impor-
tance of the issue. If there are problems or concerns, make sure that OSTP staff is aware of them, because a well-informed person at OSTP can be an asset.

We will go through our roster of panel participants before opening up for questions. Next on our apparently alphabetical list is Joel I. Cohen, who works in the Office of Agriculture and Bureau for Science and Technology within the Agency for International Development (AID), where he serves as Project Officer for programs involving biotechnology, genetic resources, and commercialization of research. I am familiar with him because he got his degree under Walt Galinat, a colleague of mine who works in the area of corn evolution and breeding, and he has worked as a station manager for Dekalb Pfizer Genetics. He was in the trenches before he moved to the bureaucracy of AID.

U.S. Agency for International Development — Activities with Plant Genetic Resources

Each member of this panel has been asked to address mechanisms which strengthen the commitment toward research and conservation of genetic resources. I am pleased to be able to accept this opportunity, and in so doing, provide an international as well as an AID perspective on such initiatives.

To begin, though, I would like to speak first from the perspective I have gained in my previous professional experience, that of a commercial plant breeder in the US seed industry. When I joined the seed company, it became rapidly apparent that each of us responsible for breeding programs was very eager to obtain and use new genetic material of a demonstrated potential value. As the commercially based efforts in biotechnology increased, it became just as obvious that molecular biologists were eager to obtain, clone, and sequence genes and just as eager then to use them in transformation procedures. However, while the demand and competition for elite genes and germplasm has grown, the support available to rescue, maintain, and evaluate source material has increasingly become in jeopardy. In many cases, these factors have only accelerated a trend which had already begun.

My current perspective on these issues, now based upon international development, collaboration, and assistance in agricultural research, has produced even greater concern about this inadequate base of support. It has been difficult to provide a stable commitment to genetic resources while paying greater attention to traditional approaches of cultivar development and release, extension, and other high-payoff activities. However, new and innovative opportunities are emerging in the international arena which link traditional development programs with support for plant genetic resources (PGR). These programs are based upon a mutuality of interest between the US and many of the developing or graduate countries with which we work. I stress the term mutuality here, because AID, whenever possi-
ble, seeks to support projects based upon a true mutuality of interest in achieving a given set of objectives. This is especially important with regard to germplasm, which is an issue that transcends national boundaries, yet often becomes subject to national prerogatives.

**AID Activities.** The “Plant Genetic Resources” bilateral project between USAID and the Government of India is a prime example of mutuality at work. This project seeks to support germplasm activity through the Indian National Bureau of Plant Genetic Resources and hence strengthen India’s national germplasm system. It will collaboratively assist India to attain a more functional and operational role in the international exchange and conservation of germplasm. This project alone will offer both countries and their respective universities, agencies, and seed companies innovative opportunities for furthering research, acquisition, and evaluation of genetic resources. During the process of project development, much work was done to determine India’s policy regarding the free and open exchange of germplasm. A policy advocating free and open exchange is, of course, consistent with our own National Plant Germplasm System, and hence, US national policy.

Other AID mechanisms which enhance PGR research include support to the international agriculture research centers (IARCs), particularly the Consultative Group on International Agricultural Research (CGIAR) centers, including the International Board for Plant Genetic Resources (IBPGR). Ongoing support has been provided to the IBPGR since its founding. The IBPGR has not only helped to ensure that genetic diversity is collected, catalogued, and conserved, but also maintains a policy of free international exchange for these collections. It has, in many cases, provided direct assistance to national programs in genetic resources, through training and provision of equipment or critically needed funding associated with collecting or conserving important materials. In recent years, the IBPGR has more actively sought to encourage the use of scientific techniques to minimize the loss or destabilization of genetic diversity represented in collections. To this end, IBPGR is sponsoring research programs in collaboration with a variety of institutions regarding strategic areas relevant to plant genetic resource programs. Current research thrusts include: seed physiology, *in vitro* conservation, pathology and germplasm exchange, analysis of genetic variation patterns on an ecogeographical basis, and preservation of genetic integrity during accession regeneration.

Through its contribution to other IARCs, AID has supported varying degrees of germplasm activities on an array of important food crops. At some centers, the genetic resources units primarily constitute active collections directly supporting breeding programs. Others have developed a comprehensive world collection for their mandated crops, including wild relatives.

The above activities have been very effective. Each has been evaluated for relevance and contribution to overall agricultural development objectives. We anticipate that they, or something like them, would be needed for a considerable period in the future. However, they should not, and, perhaps in the long term, cannot, suffice if PGR opportunities and needs are to be fully addressed.
This is especially true as the scope of PGR work expands from collection and conservation to include more prominently characterization and utilization.

**Recent Developments**  
A number of developments — scientific advances, policy and priority shifts, and accomplishment to date — are prompting AID to reconsider the role of PGR activities within the context of international development projects. First, it must be noted that for some of the major food crops, a significant portion of the genetic diversity in primitive cultivars and landraces has been collected. As a result, increased emphasis is now being placed on characterization and utilization efforts which are often time consuming, labor intensive, and costly. The ability to divide efficiently and effectively these responsibilities among national and international genetic resource systems is desired and this will require the support of new projects linked to host-country development strategies.

A second factor increasing utilization and exchange of plant genetic resources is biotechnology. Presently, these technologies consist primarily of *in vitro* tissue culture procedures designed for germplasm conservation and exchange. The future potential for transferring genes and chromosomes through recombinant DNA technologies is just being realized. Potentially, they will make more possible the selective use of wild relatives or even completely alien genes. The increasing support provided through AID to biotechnology-based research needs to become more directly related to germplasm research.

In some developing countries, especially those in Asia, progress in rice and other staple food production has made remarkable gains. This progress has engendered interest in and demand for diversification in agricultural production. High-value horticultural crops are taking on new importance. Some of these may have had little improvement, especially at the local level. Scientists in developing countries may become increasingly interested in considering a broader variety of crops, some of which may have needs that require support from, or interaction with, an accessible germplasm collection.

**New Directions for Genetic Resources**  
The Latin American Maize Project (LAMP) provides a new model for international, public, and private collaboration supporting germplasm-based research. This project ties together the collection of evaluation data with the goal of applicability to a broad range of breeding programs. As Quentin Jones, the coordinator of the project, has noted, “It is available and useful data that provides the greatest support for the costly, but necessary, tasks of rescuing, maintaining, and evaluating our crop genetic resources.” Such a multidonor, collaborative project promises to be a significant bridging device between those anxious for new sources of evaluated germplasm and those who have invested their careers in conservation and collection.

At the recent AID-sponsored biotechnology conference, one recommendation which came from the Workshop on Wide Crosses and Genetic Resources was that the IARCs establish research networks to foster trait-specific work in wild relatives of mandate crops.
Let us move on to Mark Courtney, who has his Ph.D. in ecology and evolutionary biology from the University of Arizona, has been at the National Science Foundation for some time, and is now associate program director of the Population Biology Program. This is a program in which I think much of our audience would have an intense interest.

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**Funding for Biological Research Resources at the National Science Foundation**

Most of the funding from NSF is directed to individual research grants, where an individual or group of individual investigators may get together and pursue some conceptual advance in their particular field. I am not going to talk so much about that particular activity, but rather will focus my remarks on funding for the kinds of resources and the sorts of facilities that make the research possible. A minor disclaimer: these are not the programs that I work in, so I am going to make some fairly general comments about them.

The primary funding that relates to genetic resources and conservation is the support for Living Organism Stock Centers. The budget for this program is about $1.5 million per year. The majority of it goes for animal taxa, but there is support for bacteria, such as at the American Type Culture Collection (ATCC) and the *Escherichia coli* collection at Yale; a protozoan collection, again at ATCC; fungi, including the *Neurospora* collection at Kansas; and the endomycorrhizal collection at the University of Florida. The animal taxa represented are *Drosophila*, axolotl, rodents, and Madagascar primates.

The taxonomic diversity supported by the funding will change from year to year, depending on the research that is being funded in those areas. The support for Living Organism Stock Centers from NSF is primarily for uniquely valuable collections which have a long-term and strong commitment from an institution, but especially where the value of the collection lies in the utility of that collection for basic research that is funded by NSF.

Another program for biological facility funding at NSF is Biological Research Resources (BRR), which supports nationally important systematic collections of preserved organisms (plants, animals, and fossils).

The level of funding for systematic collections last year was about $5.5 million. The BRR program also provides funding for databases which have a utility for genetic resources. Some recent examples are the index to plant chromosome numbers at the Missouri Botanical Garden, the Natural Products Database at the University of Illinois in Chicago, and the hybridoma data bank at the ATCC. Also, the BRR program has funded floral and faunal surveys, although support for that activity has currently been transferred to the Systematic Biology Program.

The majority of the funding at NSF, of course, goes to individual research, and this research by individual scientists can lead to
those conceptual insights which are valuable for applications to conserving genetic resources. Most direct support for biological facilities themselves comes from the Biological Research Resources program or from the Division of Instrumentation and Resources, where the Living Organism Stock Centers Program is located.

Certainly not everyone in the audience has funding as their interest of highest priority, but probably almost everyone in the audience has funding at a fairly high level of interest. If there are those in the audience who currently have funding for genetic resources, at least of crop plants, it is most likely to come through the National Plant Germplasm System and it is most likely to come one way or another out of the office of Henry Shands, who has done his best in a relatively short time to modernize and seek aggressively to turn it into a really good program. I have been most impressed with his success in a very few years, and am very pleased to have him here with us today to talk about the role of the National Plant Germplasm System.

The U.S. Department of Agriculture — Support for Plant Genetic Resources from Multiple Sources

I represent the Department of Agriculture broadly with respect to plant genetic resources and will comment about the Agricultural Research Service (ARS) and the Cooperative State Research Service (CSRS) programs. I recognize that many of you are with the state university systems, and probably know a great deal more about some of the CSRS activities than I do, and you are perfectly welcome to comment, correct me, or discuss those activities in the discussion period.

Within the USDA, the Office of the Assistant Secretary for Science and Education provides oversight and management for the ARS, the CSRS, Extension Service, and the National Agricultural Library. The ARS is responsible for conducting basic, applied, and developmental research for the department as its in-house agricultural research unit. The CSRS is the department's principal entrée into the university system of the United States for the purpose of conducting agricultural research as authorized by the Hatch Act of 1887, the Cooperative Forestry Research Act of 1962, and the National Agricultural Research, Extension, and Teaching Policy Act of 1977, and their various amendments. The CSRS participates in a nationwide system of agricultural research program planning and coordination among the State Agricultural Experiment Stations (SAES), USDA, and agricultural industry.

The US National Plant Germplasm System (NPGS) is a coordinated Federal, State, and private sector effort to collect, maintain, and preserve plant germplasm for potential use in the improvement of crops used in agriculture and industry. The NPGS accomplishes its functions by use of specialized units organized to provide operational, advisory, and administrative support. Operations are mainly funded
and staffed by the ARS of the USDA with strong support, both financial and personnel, from state agricultural experiment stations.

Obtaining new federal funding for base programs is a multiyear process by ARS and CSRS. Currently, the FY 1990 program proposals, initiated in April of 1988, have made their way through the Agencies and are in review by USDA budget officers. After clearing the Department, they will be sent to the Office of Management and Budget for scrutiny and they will be formulated into the President’s Budget for presentation to the Nation in January, 1989. Meanwhile, the FY 1989 budget for agriculture has had House and Senate hearings with the respective committees on appropriations and the full chambers have approved their forms of the bill. A date for the conference committee to reconcile the differences has not been set. As noted in Science, there are many Congressional budget alterations to the Administration’s recommendations this year. Neither ARS nor CSRS maintain a general fund to have complete flexibility in their response to specific, nonbudgeted requests. Each headquarters has funds which are taken off the top for administration and for certain agency needs. In ARS, funds are available during the year from salary lapses which are applied to high priority needs of the various management units. These may be used for special equipment purchases which normal budgets do not permit. Although it is desirable for units to operate with 75% or less of their budgets used for salaries, often the percentages are much higher as a result of Gramm-Rudman-Hollings reductions or salary increases which all must come from operating funds. Usually, Congressionally authorized salary increases are followed with a comparable percentage increase the subsequent year.

National program priorities at CSRS are based on the priorities of the Experiment Station Committee on Organization and Policy (ESCOP). Program orientation and funding, as in ARS, come from requests to the Congress as well as from redirection of funds to new initiatives from low-priority or terminating projects. Major research areas are included in the competitive grants program while ongoing programs are supported by Hatch Act funds dedicated to regional research projects. Hatch Act funding above the base allowance for each state requires dollar-for-dollar matching by each state. Special grants coming from Congressionally directed funds make up the third major type of funding.

ARS, the USDA’s in-house research arm, is obviously unable to staff for all research needs, nor should it. Likewise, it should not attempt to conduct new research outside of its capabilities. For those appropriate activities within the ARS national mission, and for which it does not have the expertise available, ARS provides specific cooperative agreements, grants, and contracts. ARS is a problem-solving agency and not a granting agency. It will not normally fund long-range, nonproblem-oriented research activities. ARS and CSRS will likely be teaming up to support new initiatives in the area of plant genetic resources in the near future.

In the area of plant genetic resources, ARS supports a national program funded at $26.1 million. This is down 1% from FY 1988. Funding for the various aspects of the genetic resources continuum
(those being acquisition, conservation, evaluation, and enhancement) will be affected. ARS feels that its primary germplasm responsibility is to conservation. After that, acquisition, evaluation, and enhancement are given priority in that order. ARS supports a national program for plant exploration. Funds are provided from ARS for proposals which are submitted through a peer review process involving the Regional Plant Introduction Station advisory committees, the related Crop Advisory Committees (CACs), the Plant Germplasm Operations Committee, and the Germplasm Matrix Team. Some explorations are solicited from scientists to fill gaps in the working collections. Others are generated by scientists interested in special materials needed in their programs. In all cases, justification must be made on reasons such as: national need, habitat vulnerability, and political opportunity. The collected materials must be shared with the donor country and incorporated into the NPGS to be freely available for research.

Small amounts of funds within ARS are available for a limited number of evaluation efforts on plant germplasm. Prioritized recommendations are provided by the CACs to the Germplasm Matrix Team (National Program Staff at Beltsville) which determines the projects to be funded. Unfortunately, this area is grossly underfunded with respect to the needs. No funds are currently available for genetic enhancement (prebreeding) efforts which CACs recommend to the NPGS.

Special ARS funds are available to fund 200 postdoctoral associates each year. Plant genetic resources have received a fair number of these; we have had difficulty getting candidates for some. Also, special attention is given to cooperative associates of minority background and to cooperative programs with the 1890 colleges and universities.

ARS does fund a limited number of overseas genetic resources activities. Some are funded through Specific Cooperative Agreements, usually involving university scientists. Other overseas projects involve ARS scientists and even postdoctorals. There is an active program of this type with Israel. A proposed exchange program with the People's Republic of China (PRC) is in development. ARS will also become more involved with the international biodiversity conservation effort through cooperative interactions, including nongovernmental organizations such as the World Wildlife Fund.

Other overseas genetic resource projects have been available through the use of local foreign currencies from the PL-480 Commodity sales. Currently, we have cooperative projects in Poland, Yugoslavia, India, and Pakistan. They are administered by ARS and the Office of International Cooperation and Development (OICD) of USDA. The OICD also administers several Bilateral Exchange Agreements, such as with the USSR and the PRC, where Federal, State, and private scientists participate in germplasm exploration and exchange.

In summary, the federal budget process is a multiyear activity in which priority program considerations are developed for budget thrusts to the various agencies of ARS, to the Department, and finally
to the Administration which proposes them to the Congress. The Congressional appropriations committees hold hearings on the proposals and reconcile their respective actions in conference committee. The whole Congress then must approve the budget bill which the President executes. The days of Administration flexibility and nonprogrammed funds for research initiatives no longer exist. Creative financing through program shifts, terminated projects, and end-of-year funds open the avenues to funding special research needs.

Dr. Goodman

Let us move on to our representative from private industry, Allen Stevens, who is Director of Agricultural Research for the Campbell Soup Company. His background, appropriately enough, has included a fairly long-term stint with the tomato genetics program that Dr. Rick has been involved with here for many years.

The Value of Public Plant Genetic Resources to Private Plant Breeding

Industry provides very limited funding for germplasm conservation. However, we are very much interested in it, and there are a few active programs in the private sector. As has already been pointed out, most of my interest has been with tomato, so I would like to use tomato as a model to indicate to you some of the concerns regarding germplasm conservation and utilization. Tomatoes are a representative of that group of cultivated plants with limited genetic variation, perhaps a result of severe depletion during domestication. It has been demonstrated with biochemical markers that there is very limited genetic variability in the older tomato cultivars of Europe and North America. There is much more variability in the primitive cultivars and vastly more in the wild species.

As the world population grows and exploitation of land resources accelerates, it seems clear that germplasm collection must remain the number one priority. Germplasm collections should represent as much of the existing variation as is humanly and economically possible to assemble. If this diversity is lost, an important resource will be gone. For the tomato, it is fortunate that we already have a very good collection of exotic germplasm, since much of the germplasm is already seriously eroded in the native habitats. Many of the important populations which occur in sites in the heavily populated coastal strips in South America have already been annihilated by human activity. The process is proceeding up into the valleys of the Andes and may soon extend into more remote areas. The primitive cultivars in Peru and Ecuador are virtually extinct as a result of the replacement of older, more diverse cultivars with more productive introduced cultivars. Even though world germplasm collections of tomato are fairly large and complete, the book must not be closed on continued collection activity. Some of the more remote areas have not been explored and undoubtedly some surprising extensions of the species' distribution and completely unexpected areas of high genetic variability still will be encountered. Charles Rick has shown that there are yearly variations in genotypes due to extreme differences in the amount of rainfall and flooding that can result in
different genetic composition of the populations. Temporal collections may be an important activity.

Germplasm evaluation and prebreeding do not receive sufficient attention. Before I go any further, I would like to paraphrase a story that was told by Jack Harlan. He said, “My father, H.V. Harlan, was an excellent plant breeder who worked with barley. On occasion, people would ask him about the use of wild relatives in a breeding program. He was likely to answer to the effect that you are working with the wrong end of the equation. If you must go back to the wild, try crossing the plant breeder with a monkey, perhaps you could get breeders with four hands who could handle the extra work.” This story well illustrates a problem faced by many commercial breeders, who generally do not use exotic germplasm. Most do not have the time, resources, or motivation to go back to the wild species to find a needed character. Tomatoes are an example of a crop where there has been successful exploitation of the wild species. With few exceptions, the crosses with exotic sources and the germplasm enhancement or prebreeding were done by public breeders. It will require a fairly serious reordering of priorities if any level of prebreeding is going to continue in the future. Genetic engineering is the biggest game in town. There are many more jobs for the new breed of gene jockey who generally has very little interest in or patience for the rather long-term problem of transferring a character from a wild species. Funding and positions for traditional geneticists interested in germplasm enhancement are rare. Who will do this activity in the future? At least for horticultural crops, there is limited potential that this will be done by the seed or food processing companies.

There are many levels of germplasm evaluation. The tomato collection maintained here at Davis in the Tomato Genetics Stock Center by Charles Rick is extremely valuable because of the observations which he made on the autecology of the accessions. The habitat features can provide an important clue to the useful assets of the respective collections and this has been proven time and again with this collection. As examples, root rot disease resistance was obtained from collections from regions of high rainfall in eastern Ecuador; salt tolerance was obtained from collections from salt-spray zones on the Galapagos Islands; chilling tolerance was obtained from high altitude collections.

More than once, the statement has been made that if the trait desired from the wild species involves more than one dominant gene, then you had better forget it. However, there is an experience with tomatoes which shows that it is possible to move complex traits from the wild species. Dr. Rick noted that certain accessions of Lycopersicon chmielewskii have soluble solids in the fruit of 12 to 14 percent, which is more than double that of the cultivated tomato. Using backcrossing techniques, Rick transferred part of that genetic potential into enhanced germplasm. These high solids lines have been used in the development of several cultivars which are important in California. A rough calculation indicates that this rather modest effort is worth more than $7 million per year to the processing tomato industry in California because of the higher solids resulting from this single cross. More importantly, this effort has sparked other breeders to
look for additional sources of high solids in the wild species. I wish to make a plea for increased efforts to evaluate and enhance the important characters of wild taxa so that they are more useful as crop genetic resources.

General Discussion

Thank you, panel, for your interesting comments. Now could we now have some questions for our panel?

How can we increase the student interest in traditional plant breeding?

On this panel, I de facto represent the university level. Obviously, the decrease in interest in plant breeding on the part of graduate students is a perceived decrease in the opportunity for employment. It is up to the faculties of our institutions to change that perception. I receive calls at North Carolina State on practically a monthly and sometimes weekly basis from various private plant breeding companies, searching for quantitatively trained plant breeders. When I talk to my colleagues in plant breeding, they also find no shortage of employment for good, well-trained plant breeders. Everyone I have talked to in the business of training graduate students indicates that there is no shortage of employment possibilities. My last Ph.D. student went out at a salary of over $40 thousand per year to do germplasm incorporation in maize in a private company. There are private companies in addition to Campbell Soup who represent an interest in well-trained plant breeders, and I think it is up to us as faculty members to get the point across to promising undergraduate and beginning graduate students that there are a lot of opportunities.

Not only in plant breeding do we find a shortage of students, but across the board in science and technology and mathematics. This is not a concern right now, but it is a concern down the road that we do not have enough students in the pipeline. The problem seems to be a matter of motivation. Students — all young people, I believe — need to be stimulated and exposed to professionals who have gone through a lot of training and who have interesting and exciting jobs in science, engineering, and mathematics. You can reach out by going to your schools and your churches. You can reach young people, and talk about the kinds of things you do, and stimulate their interest in science. It is particularly true that women are underrepresented, and minorities even more so. It is something we at OSTP are concerned about. I think most of it comes down to individuals, not programs or government money. It is personal interaction that stimulates students into thinking that this is what they want to do when they grow up.
I do not have the problem of finding students. I have the problem of finding support for qualified students.

I can speak as a graduate student interested in plant breeding. Obtaining support is a problem.

There are qualified, interested students. There is a continuing need for trained breeders and germplasm managers. Can industry help mobilize support for students in these areas?

My experience at UC Davis indicates to me that industry and grower organizations, particularly commodity groups, are all excellent sources of support for certain programs. There is added pressure from this support if you are a professor at UC Davis and receive that kind of support; the pressure is on from the commodity groups for essentially finished varieties, because that is where the recognition comes. The University was ambivalent about the production of finished varieties, and there were feelings that this was not the role of the University. The University urged that germplasm enhancement was a more appropriate role. A good way to tap industry support is through their organizations. At Campbell Soup Company, we provide limited funds or grants, but generally in areas that are of specific interest to the company.

I would agree with that. The group I am most familiar with is the American Seed Trade Association, and they are involved in quite a number of policy determinations. Recently one concerned patenting as it relates to plant variety protection. I think it would be very important for a group like that to do a similar paper on the issue of genetic resources conservation, and to make a statement to the Seed Trade about the urgency of the situation. I think that is very effective. They are based in Washington; they know how to get information across.

The American Society of Agronomy has recently started funding a fellowship program for a fellow to work in Congress and to report in the Agronomy Newsletter. This is a mechanism similar to the one the American Association for the Advancement of Science provides; it works both in the Executive Branch and the Congressional Branch to bring the urgency of scientific questions to the attention of law and policy makers. This is another avenue where you can get a lot of attention if these people are used creatively.

As a third point, I want to go back again to the LAMP program. I know Quentin Jones is just now finishing some of the initial information on that. It has been a remarkable process involving tremendous
financial support from the Pioneer Hi-Bred International seed company, as well as a number of the developing countries, the international centers, and other donors. It seems to me that as a stepwise concept beyond the LAMP program, it would be possible to do something similar with and for breeding. It should be possible to activate that same type of interest and generate the same type of matching support from multiple donors so that this crisis can be averted. The LAMP program took a long time to develop. It seems like a similar momentum is needed in this situation.

Dr. Stevens

I wonder if industry in general is aware that there is a problem. If the resources are not available for training traditional geneticists anymore, it seems to me that is a fairly important message that ought to be gotten across. There will probably be a response.

Dr. Courtney

In response to the question about graduate students, I would say that from the basic side, the National Science Foundation also provides support at the doctoral level, for improvement in doctoral dissertations. Obviously it has to be addressed to some topic of basic importance, but that is a source of support for graduate students. There are also postdoctoral research fellowships in environmental biology, which includes plant population genetics and plant ecology. There are also plant biology postdoctoral fellowships which are available from the Cellular and Molecular Biosciences Division.

Dr. Goodman

I would like to add something to the urgency of Cal Qualset's question. Some of you in the audience may not be aware of it, but the USDA Competitive Research Grants Program has had a reasonably successful panel on plant genetics and molecular biology operating for the last ten years or so, and Cal has certainly played a major role in parts of that on an advisory basis, and as a panel manager. That program is currently in danger in Congress of being packed with pork barrel projects. For the first time, this year, the pork barrel is on both the House and the Senate side. If that does, in fact, go through, the competitive grants program in plant genetics, plant stress, plant physiology, and various other areas that affect many of the people in this audience is, I think, effectively doomed. It will take industrial lobbying and, perhaps professional lobbying by professors at major universities to salvage that program. I am not sure Cal agrees, but I think that is what it is going to take. It will be a serious loss, because it has been a very high quality program supporting some very good research, much of it at UC Davis, as a matter of fact.

Dr. Berger

Perhaps university professors cannot lobby Congress. Certainly members of the Executive Branch cannot lobby Congress either. But all of us have an obligation to keep Congress well informed. There is a fine line there. When you are in Washington, going to see your Congressman or going to see the key staff person to a Congressman who sits on a key committee, is a very important thing to do. Take a message that is simple, broad, conceptual, and has only a few points
to it rather than something highly complex. In such a situation, it is better to keep on a higher plane and focus on the bigger issues. You have a good opportunity to educate people who work on Capitol Hill. I do not think you should give up. There are lots of talented people there who are interested and very eager to learn.

I am concerned about the situation with plant breeding. I think Dr. Hess mentioned that a survey had showed there were three hundred and some plant breeders and it is down now to about two hundred and seventy-five. This is a significant reduction. I do not know the time frame on it, but there are several things that have come together to create this whole situation. We had, number one, the new biotechnologies coming in, and a great interest in that area developed. As many of the post-World War II breeders were retiring, the deans and directors seemed to hear a voice to get biotechnologists as replacements. We did not hear voices of the plant breeders saying, "We still need somebody there to do this." At the same time, the National Council of Commercial Plant Breeders in the American Seed Trade Association recognized that there were opportunities for the seed companies that they felt were being lost, because of the competition with public plant breeding. This would be in many of the self-pollinated crops, perhaps stemming in part from the Plant Variety Protection Act of 1970.

These two factors came at the same time, so you had two forces operating very nicely for the deans and directors to slip in those people able to use the new technologies and to phase out the plant breeding activity. The ARS at the same time was lobbied by the American Seed Trade Association and others not to continue breeding activities. The agreement reached was basically that we would discontinue breeding activities with those crops where industry was involved and could make it a privatization type of arrangement. We would continue breeding in those minor crops of lesser value to industry, where industry did not have the input and was dependent upon the public source of material to proceed with them.

With this background, I visited with several of the deans and directors that I am associated with in regard to the Plant Introduction Stations. They are hurting to get information when there is a need for replacement. They are dependent upon people, the staff of the university, outsiders, to recommend to them where their program should be going. I think we have a responsibility, whether it be as breeders, other scientists, or as members of the Crop Advisory Committees which are relied on very heavily in the National Plant Germplasm System, to go to the deans and tell them, "This is an important activity. Perhaps you have the last program involving this or that crop in the country. Do not discontinue it." Dropped programs create a problem for me, because what do we do with the material? We suddenly have to absorb it in some way and curate and maintain it, in case somebody might want to use it again at some later point in time. But more than that, we have lost that resource.

The other thing we have not done well along this line is to make an opportunity for retired plant breeders to come back and work with the collections that they have assembled during their careers. The
collections could be sorted, the most important materials designated, and inventories circulated to commercial companies and to other breeders. Thus, material in which we have a large public investment could be more easily saved and utilized.

We have an area director here in this western region of ARS, Norman James in Albany, who is retiring from his area director job, but who I will fortunately have available to work on some germplasm activities. In trying to develop a program and directions for the germplasm system, I am trying to identify what the user-breeder community is. Where do we need to channel our efforts in the way of collection, evaluation, and prebreeding that can support the critical areas? To do that, we are going to have to take some kind of a survey of what is the present state of the user-breeder industry. I am working out a plan with Dr. James for when he steps down from his area director job. He has been a sugarcane breeder and he has been in ARS administration and area jobs for many years. He is an excellent person, who I think can put together a reasonably good survey for us that we can focus on. If in any way you become interactive with him, I hope you will give him all the support you can, because he is going to try to ferret out who is left and what are their needs. Then we will try to tailor a germplasm program that hopefully will address those needs for the future of this country.

James C. Brewbaker
Horticulture Department
University of Hawaii
Honolulu, Hawaii

Dr. Shands

What are the panel’s thoughts on the use of royalties on licensed varieties?

Dr. Shands
Assistant Secretary of Agriculture Bentley is providing a grant to the American Society of Agronomy to cooperate with the Horticulture Society and other groups to address this exact issue. I think it is a very important one. We are all getting caught up in some aspect of this issue in some way at this time. Some of the things are not very pleasant. I think a problem has been created because of, basically, a lack of knowledge of the prior art in the Patent Office. This is my personal feeling. However, the pendulum is now over on one side and as it swings back the situation will improve. The Patent Office has put on more people and they are now realizing that they have to go into scientific literature to get their information. They are trying to staff up to deal with it. We can only hope that comes swiftly. Next January, Cal Qualset, as incoming president of the Crop Science Society of America (CSSA) and Don Duvick, as current past president of CSSA, will be co-hosts of a meeting to address this issue.

Dr. Goodman

My own position is that public funds should not be spent on private goods. Nonetheless, I would like to tell a story that sort of shocked me. In speaking with a plant breeder from Eastern Europe, specifically from the Soviet Bloc, he expressed total surprise that, for example, a line like B73 could be developed at Iowa State University and used so widely in the corn breeding industry that it could pay probably, not only for the corn breeding program at Iowa State University, but also for the entire operation of Iowa State University from now into the indefinite future. His surprise was not that such a line could be developed at a university in the United States, but that
those people and the program responsible for that line would receive essentially no benefits. In the Soviet Bloc of Eastern Europe, capitalism is not quite so fashionable as it is here. Apparently, it is quite customary for the plant breeder and the program to receive benefits from the development of cultivars. So here we have quite a striking contrast in the economic system and philosophies.

I realize my view is very tainted by my background, but I think it is very reasonable and acceptable for royalties from licensed cultivars to go to the breeders and programs that develop them. I think having an economic incentive will provide an initiative to do important things.

One of the most urgent needs is for commitments to long-term maintenance of genetic resource collections. What agencies can do this? What mechanisms exist? What changes in granting-agency policies need to be made?

As with all things discussed here, it tends to come down to a question of funds. The fact that the National Science Foundation does not provide long-term support because a particular collection exists now does not mean that it might not find that justified if the community comes to us and says that that is an important enough resource to preserve, or to continue supporting. We largely reflect the intensity of the community's response. But as far as I know, the existence of what may be a very large number of collections of that sort does not, at least in the near future, justify support just because they exist. It is going to have to be tied to a particular research problem.

For the present, it is only the Department of Agriculture through the National Plant Germplasm System that provides long-term support for genetic resources.

I am interested in why this symposium has had this session. The sessions have otherwise been technical. What is the strategy of this? I would hope that one purpose is to get some of the issues discussed here out into the public arena.

I assume that the Genetic Resources Conservation Program which Cal Qualset heads was involved in the structuring of this symposium. I am convinced that to get effective action, we need the support of private industry and private lobbying groups, because these are the people who are heard, at least on Capitol Hill. I do not think the group that Cal heads is quite yet in the category of lobbying groups. Perhaps it should be. I have already testified on Capitol Hill that Dr. Shand's NPGS budget should be at least doubled and I see no retreat from my comments there.
Role of Basic Knowledge in Utilization and Conservation of Plant Genetic Resources

This Symposium has provided a forum from which to review and update our present knowledge on the genetic structure of plant populations according to their mating system — predominantly self-fertilized, cross-fertilized, mixed mating, apomictic, or intragametophytic (as in ferns). The genetic structure within populations, among neighboring populations, and among populations for the species overall has been characterized for the various mating systems, and their subdivisions, using such tools as (1) molecular markers (isozymes and more recently RFLPs), (2) sophisticated models based on advanced population genetic theory, but rooted in empirical investigation, and (3) computer simulation employing these models to allow projection of the long-term consequences under various likely scenarios.

How can we use this basic knowledge in the utilization and conservation of plant genetic resources? The remarks to follow are coming from someone who has made considerable use of corn genetic resources, but has never been involved in the collection of germplasm. Hence those of you with such experience may detect my considerable naïveté in these comments. Nevertheless, it seems to me that the most obvious way in which knowledge of the genetic structure of plant populations can be put to use is in the intelligent design of procedures to be employed in germplasm collection. By knowing the mating system of the species being collected, procedures can be designed to allow adequate sampling of the germplasm but with a minimum number of collections. For our major crops species, which are generally considered to be adequately sampled, collecting strategy is probably no longer of great significance, but where enough information is known about the sampling procedures that were employed, it may be possible to determine whether the collection is indeed adequate. It may also be possible to determine whether certain accessions might be composited to reduce the overall numbers.

Knowledge of the genetic structure of populations might also be employed in the design of core collections, as proposed by Sir Otto Frankel; i.e., in place of maintaining a large number of individual accessions, ‘core collections’ are constructed which consist of accessions of similar kind as identified, for example, by cluster analysis techniques. An understanding of population structure would certainly be essential to the intelligent design and construction of ‘gene parks,’ for those species in which this tactic might be useful. In some species, an understanding of genetic structure would be critical to the design and construction of populations to be used for breeders’ ‘back-up’ germplasm, or, for that matter, in the design and construction of the germplasm used directly by the breeder in developing cultivars. Such might be the case, for example, in tree breeding.
I want to consider now how MAGIC can be used to deploy and utilize genetic resources, i.e., Molecular Assisted Genetic Improvement of Crops. As Paul Gepts suggested, molecular analysis can be employed to determine which wild germplasm has contributed to our present domestic types. Knowing this, the breeder may find it desirable to resample systematically the original donors and/or explore other wild sources for their potential contribution to the breeding of modern cultivars. Molecular analysis might also be used to determine whether cultivars from different areas of the world have been derived from different wild germplasm sources. In such cases, the breeder might elect to enrich the working gene pool by using the foreign cultivars themselves rather than the unimproved wild germplasm. The hypervariable minisatellite sequencing technique that Michael Clegg spoke of would seem to be of potential value in this sort of analysis.

**MAGIC in breeding of qualitative traits.** Some of the possible approaches that have been noted are:

1. The selection of environmentally obscured traits through selection of tightly linked molecular markers.

2. The use of molecular markers to bracket a desired gene (or gene block) that is difficult to select for directly so that by selecting for the segregant carrying both molecular markers, there will be a high probability that the desired gene has also been selected.

3. Selection directly for the gene product itself rather than on the final phenotypic manifestation of the gene.

4. MAGIC is also used to incorporate genes from other life forms via transformation techniques, as, for example, *Agrobacterium*-mediated transformation as related to us by Mark Vaeck. Microinjection and DNA ‘shot from guns’ (high velocity microparticles) are other transformation techniques. The incredible feature is that any life form is a potential donor of desired genes and the genes actually function in their new home! A word of caution though, for if I understand correctly, Michael Clegg indicated there is some evidence that such genes may be excised eventually from the genome.

5. MAGIC can also be used for *in vitro* gene construction based on DNA sequencing information. I understand from our department biotech people at Guelph that Allelix, an Ontario-based biotech company, used published information on the DNA sequencing of the gene for atrazine resistance in corn to construct this gene, via their gene machine, and have incorporated it into rapeseed.

Such examples of gene construction and transformation give us latitude to stretch our imaginations a bit. It should be possible eventually as species barriers to MAGIC techniques are broken down, and as our basic knowledge increases on the molecular and biochemical basis of resistance to disease organisms, insect pests, physiological stresses, etc., to tailor-make genes that will impart resistance not only to ongoing, but also to expected, races of a pathogen or insect. Perhaps, Jeremy Burdon’s low-cost resistance genes are next out of the gene machine!
Now another thought to ponder. As was mentioned yesterday by Major Goodman, the predominant role of germplasm banks for most crop species is as a source of material to screen for resistance to new diseases and insects. Will MAGIC eventually make this function obsolete? Will gene banks become gene libraries to be used as repositories of constructed genes ready to be fired off to the breeder to quell a predicted disease or insect outbreak?

**MAGIC in breeding of Quantitative Traits** Selection of QTLs (quantitative trait loci) is being effectively accomplished through linked marker genes. Currently RFLP-mediated selection is the most powerful marker-facilitated selection technique, but isozymes and morphological markers have also been employed effectively. The strategy of accumulation of favorable QTLs in a desired background by adding new QTLs from other sources as they became known, should be a viable breeding technique, provided the QTL response is not affected adversely by the genetic background of the host.

I would like to see answers to the following questions at Allard Symposium II:

- What is the nature and source of genetic variability for QTLS?
- Do QTLs consist of tightly linked blocks of genes scattered throughout the nuclear genome?
- Are such blocks the basis for long-term selection response, as per the Illinois selection study for high and low oil and protein content which was initiated in 1895 or are transposable elements (TPEs) and/or unequal crossing-over in repeated DNA segments, or some other mechanism) creating de novo variability?
- A recent review by Walbot and Cullis (Ann. Rev. Plant Phys., 1985) reports that TPEs are more active under stress. (This is not physiological stress, but rather stress resulting from some form of disequilibrium.) Walbot and Cullis suggest that if a plant gets into a state of chronic sub-optimal growth, there may be a metabolic feedback that induces mechanisms for rapid genomic change, (via TPEs). Is this the reason that when corn is inbred, i.e., it reaches a condition of chronic sub-optimal growth relative to its normal outcrossed state, it apparently has a high mutation rate? For example, studies at Iowa State University published in the early 1960s showed exceptionally high mutation rates for quantitative traits both in long-term inbreds and doubled-monoploid lines of corn. Breeders also frequently find changes in inbred lines when they are maintained at different locations.
- Another potential source of QTL variability is through unequal crossing-over in repeated DNA segments. Ron Phillips at the University of Minnesota considers this to be an important mechanism for creating variability in the Illinois long-term study on selection for oil and protein in corn. Do outcrossers have a built-in mechanism so that their mutation rate increases when they undergo inbreeding?
- Another critical question regarding QTL variability is: What is the effect of regulatory genes on quantitative traits? We know very little about regulatory genes and how they work. Yet these are the major determinants of the plant phenotype.
These questions give rise to an important consideration regarding conservation of plant genetic resources, namely: Do we need germplasm banks for quantitative variability or is its supply virtually unlimited due to its continual creation (via TPEs, unequal crossing-over, gene conversion, etc.)?

As we accumulate more and more basic knowledge about the creation of genetic variability, to include construction of desirable genes as well as the de novo origin and regulation of these genes, we may very well find it necessary to re-evaluate the role of germplasm banks and very probably will deploy genetic resources in ways quite different from today.
Appendix I  Symposium Program

Thursday, August 11

REGISTRATION
1:00-4:45pm

Session One

WELCOME
Calvin O. Quaile
Director, University of California Genetic Resources Conservation Program
Charles E. Hess
Dean, College of Agricultural and Environmental Sciences, University of California, Davis

THEME I: KINDS OF GENETIC DIVERSITY
Chair: Daniel Zohary
Botany Department, Hebrew University Jerusalem, Israel

Plant Quantitative Genetics — The Impact of Recombinant DNA Technology*
Oliver Mayo
Biometry Section, The Waite Agricultural Research Institute, Adelaide, Australia

Allozyme Diversity in Plant Species*
James L. Hamrick
Botany Department, University of Georgia, Athens

Seed Storage Protein Diversity in Plants*
Paul Gepts
Agronomy & Range Science Department University of California, Davis

Molecular Genetic Diversity in Plant Populations*
Michael T. Clegg
Botany & Plant Sciences Department University of California, Riverside

DNA Polymorphism and Adaptive Evolution*
Mitsatoshi Nei
Center for Demographic & Population Genetics University of Texas, Houston

7:30-9:30pm

Session Two — Honoring Robert W. Allard
Chair: Charles O. Gardner
Agronomy Department, University of Nebraska, Lincoln

Utilization of Genetic Resources for Crop Improvement: The Common Bean*
Frederick A. Bliss
Horticulture Department University of Wisconsin, Madison

Introduction of Dr. Allard
G. Ledyard Stebbins
Emeritus Professor of Genetics University of California, Davis

Future Directions in Plant Population Genetics, Evolution, and Breeding
Robert W. Allard
Agronomy & Range Science Department University of California, Davis

Closing Remarks
C.O. Gardner

Friday, August 12

8:00am-noon

Session Three

THEME II: STRUCTURE AND GEOGRAPHIC ORGANIZATION
Chair: James A. Harding
Environmental Horticulture Department University of California, Davis

Statistical Measures of Genetic Organization*
Bruce S. Weir
Statistics Department North Carolina State University, Raleigh

Genetic Characterization of Plant Mating Systems*
Anthony B.D. Brown
Division of Plant Industry CSIRO, Canberra City, Australia

Spatial Patterns of Genetic Variation Within Populations*
Bryan K. Epperson
Botany & Plant Sciences Department University of California, Riverside

Patterns of Genetic Diversity Among Plant Populations
Subodh K. Jain & Francisco Molina
Agronomy & Range Science Department University of California, Davis

THEME III: MICROEVOLUTIONARY PROCESSES
Chair: Timothy Prout
Genetics Department University of California, Davis

Detection and Measurement of Selection*
Richard A. Emmons
Forestry & Natural Resources Department University of Edinburgh, Scotland

The Interaction of Linkage and Selection in Plant Populations*
Alan M. Hastings
Mathematics Department, University of California, Davis

1:15-3:00pm

Session Four

THEME III (cont.): MICROEVOLUTIONARY PROCESSES

Selection in Multilocus Genetic Systems and the Build-Up of Coadapted Gene Complexes*
Julian P. Adams & Paul Gresso
Biology Department, University of Michigan, Ann Arbor

Population Genetics of Host-Pathogen Systems*
Jeremy J. Burdon
Division of Plant Industry CSIRO, Canberra City, Australia

Genetics of Adaptation: Examples from Wheat
Calvin O. Quaile
Agronomy & Range Science Department University of California, Davis
3:30-5:00 pm PANEL DISCUSSION: FACILITATING GENETIC RESOURCES RESEARCH AND CONSERVATION

Chair: Major M. Goodman
Crop Science Department
North Carolina State University, Raleigh

Panel:
Beverly J. Berger
Office of Science and Technology Policy
Executive Office of the President

Joel L. Cohen
Bureau for Science and Technology
US Agency for International Development

Mark W. Courney
Population Biology Program
National Science Foundation

Henry L. Shands
National Program Leader for Germplasm, USDA-ARS

M. Allen Stevens
Campbell Soup Co., Camden, NJ

7:30-9:30 pm POSTER SESSION

Saturday, August 13

8:00 am-noon Session Five

THEME III (cont.): MICROEVOLUTIONARY PROCESSES

Genetic Demography*
Kermitbuilt
Botany Department, University of Toronto, Canada

Genetics of Plant Colonization*
Spencer C.H. Barrett & B. Husband
Botany Department, University of Toronto, Canada

THEME IV: GENETIC DIVERSITY AND ITS UTILIZATION IN PLANT IMPROVEMENT

Chair:
Kenneth J.R. Edwards
Knighten Hall, University of Leicester, England

Sakti Jana
Crop Science & Plant Ecology Department
University of Saskatchewan, Saskatoon, Canada

Crop Genetic Resources — Current and Emerging Issues*
Donald R. Marshall
Agronomy Department, The Waite Agricultural Research Institute, Adelaide, Australia

Selection Strategies for the Improvement of Autogamous Species*
W. Eberhard Weber & Günter Wricke
Institut für Angewandte Genetek, Universität Hannover
Federal Republic of Germany

Calvin G. Qualse
Agronomy & Range Science Department
University of California, Davis

Plant Population Genetics in Forest Tree Improvement*
Oul Anitra Muona
Genetics Department, University of Oulu, Finland

Quantitative Changes Induced in Gene Loci by Transposable Element Insertion and Excision*
Oliver F. Nelson
Genetics Department, University of Wisconsin, Madison

1:30-5:00 pm

THEME IV (cont.): GENETIC DIVERSITY AND ITS UTILIZATION IN PLANT IMPROVEMENT

Organization of Plant Multigene Families*
Jan Drofell
Agronomy & Range Science Department
University of California, Davis

Molecular Markers in the Manipulation of Quantitative Characters*
Charles W. Stuber
USDA & Department of Genetics
North Carolina State University, Raleigh

Crop Improvement Through Genetic Engineering
Mark Vaech
Plant Genetic Systems, Inc., Ghent, Belgium

SYMPOSIUM SUMMARY, INTEGRATION, AND OVERVIEW

Chair: Subodh K. Jain
Agronomy & Range Science Department
University of California, Davis

Role of Basic Knowledge in Utilization and Conservation of Plant Genetic Resources
Lynden W. Kassenberg
Crop Science Department
University of Guelph, Guelph, Canada

Discussion
Closing Remarks

* This presentation will comprise a chapter in the Symposium Proceedings Volume. See Introduction for ordering information.
Appendix II  Abstracts of Posters Presented

AUTHOR INDEX

In the case of posters with multiple authors, the author who presented the poster is designated by an asterisk in the abstracts themselves. The numbers in the index refer to the following pages.

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Electrophoretic Analysis of the Origin of Radiate Groundsel

R.J. Abbot* and J.A. Irwin, Dept. of Biology & Preclinical Medicine, Univ. of St. Andrews, Fife KY16 9TH, SCOTLAND.

Senecio vulgaris L. (Common Groundsel) forms populations which are polymorphic for capitulum type in Britain. The rarer radiate morph is of recent origin and was first reported in 1866. Starch gel electrophoresis has been used to examine the theory that this morph evolved following introgression of S. squalidus genes into non-radiate S. vulgaris. Staining for esterase isozymes using β-naphthyl acetate as substrate showed that the radiate and non-radiate morphs of S. vulgaris usually possess two β-esterase loci. In contrast S. squalidus possesses three such loci, two of which correspond to those in S. vulgaris. In one S. vulgaris population from York, England, the radiate morph contained all three β-esterase loci present in S. squalidus. It is concluded that the York radiate variant represents an early stage in the origin of radiate S. vulgaris via introgression of S. squalidus into S. vulgaris.

Geographical Diversity in an Iranian Wheat Collection of Khorasan Province

C. Abd-Mishani, Dept. of Agronomy, Univ. of Tehran, Karaj, IRAN.

A sample of 764 entries of Iranian wheat from Khorasan province representing 16 geographical origins were evaluated for eight characters. The germplasm collection showed a large amount of variation for the characters studied. Five clusters were delineated among the 16 geographical origins: (i) Torbat Jam, Bojnord, Kashmar, Sabzevar, Torbat Heydarieh, Fariman, and Gonabad; (ii) Ghouchan, Neyshabour, Daregaz, and Mashad; (iii) Tabas and Shirvan; (vi) Sarakhs; (v) Birjand. The clustering pattern of the geographical origins followed their agroecological conditions except for one case.

Evaluation of Regrowth Characteristics of Non-Winterdormant Middle Eastern Alfalfas

Al-Doss Abdullah and S.E. Smith*, Dept. of Plant Sciences, Univ. of Arizona, Tucson, AZ 85721.

Inherent yields of alfalfa (Medicago sativa L.) have improved relatively little with 40 years of active plant breeding. This is especially true in the Southwestern U.S. where emphasis has been primarily on improved pest resistance. Alfalfa germplasm from low elevations in the Middle East may be useful in improving seasonal yields due to its reduced winter dormancy and rapid regrowth following harvest. Regrowth and forage yield of accessions from Saudi Arabia, Egypt, Sudan, and Morocco and a U.S. cultivar ('Lew'—derived from African and Indian germplasm) were evaluated for eight harvests (February to July) at Tucson, AZ. Few significant differences were observed in forage yield among Middle Eastern accessions and Lew. However, ecotypes from Saudi Arabia and Egypt produced forage having a higher leaf:stem ratio suggesting higher yields of protein. Stem elongation rates (SER) in the first and second weeks of post-harvest in spring and early summer were positively correlated with dry matter yield. Arabian and Egyptian ecotypes exhibited higher SER than Lew only in the first week post-harvest. These ecotypes also produced stems from both the crown and stubble while other entries produced regrowth primarily from the stubble.

Effective Pollen Dispersal in a Eucalyptus Regnans Seed Orchard

W.T. Adams, Dept. of Forest Science, Oregon State Univ., Peavy Hall 154, Corvallis, OR 97331-5705.

Eucalyptus regnans, an important forest tree species in southeastern Australia, produces large numbers of hermaphroditic, insect-pollinated, self-fertile flowers. All 285 trees within a portion of a 10-year-old seed orchard were mapped according to location and genotyped at 10 allozyme loci. Trees averaged 20 M tall and were fairly uniformly spaced at 7 × 7 M. The pollen parents of 150 outcross offspring were inferred using a paternity analysis procedure, whereby the likelihood of paternity for each potential male was based on its relative fecundity, distance to the mother tree, and degree of genetic identity with the offspring. Paternity was assigned to the potential pollen parent with the highest likelihood value. Mean distance between mother trees and inferred male parents was 41.2 M (SE = 4.7), indicating effective pollen dispersal is quite high. Further evidence for considerable cross-fertilization among trees is the large number of different male parents inferred (58) and the high estimated effective male population size (N_e = 57).

Genetic Diversity and Breeding Potential of Natural Populations of Bromus Catharticus Vahl

M.J. Arturi*, F. Laos, and M.F. López Armengol, F. Agronomía, CIC-PBA and F. Ciencias Naturales, C. Correo 31, 1900 La Plata, ARGENTINA.

Entries of Bromus catharticus, a native forage plant, collected at 14 locations of provinces of Buenos Aires and Santa Fe, Argentina, were tested to estimate components of the phenotypic variance and to search for patterns of regional diversity. Data gathered from several field experiments revealed a fairly high degree of genetic variability for leaf and tiller traits related to forage yield. Among them leaf width exhibited genetic variation explained in a major proportion for additive effects. Significant positive correlations among yield components were detected, indicating that progress through multiple trait selection could be achieved. Numerical taxonomy techniques were used for germplasm grouping as a base for ecological genetic studies and for breeding purposes.
EVALUATION OF SEED STORAGE PROTEINS IN AN ENTIRE COMMON WHEAT COLLECTION FROM NEPAL

S. Benedettelli, Agroforestry Inst., C.N.R., Porano (TR), ITALY; B. Margiotta, Germplasm Inst., C.N.R., Bari, ITALY; and C. Tomassini, E. Porceddu, and D. Lafrandi, Agrobiology & Agrochemistry Dept., Univ. of Tuscia, Viterbo, ITALY.

An entire common wheat collection from Nepal has been electrophoretically evaluated for its variation in storage proteins, gliadins, and glutenins. Gliadin analyses showed the existence of a high degree of variation. The consistent presence of seeds lacking the entire cluster of gliadin components controlled by the 1D chromosome has been observed in some samples. These seeds were found to be present, in most cases, in mixtures with seeds having normal gliadin patterns, but some samples were made only by seeds without 1D-controlled components. Higher incidence of these seeds was found in samples collected at higher altitudes. Variation in glutenin components was also quite large, especially at the 1B and 1D complex loci (Glut-1 loci). Also in this case seeds without some glutenin subunits have been detected, but they did not show any apparent relationship with the altitude. New allelic variants at both Glut-B1 and Glut-D1 loci have also been detected.

THE POPULATION GENETICS OF A POLYPLOID COMPLEX: NEUTRAL AND SIMPLE SELECTION MODELS


Without selection, a population of randomly mating monoecious diploid, tripod, and tetraploid individuals (a polyploid complex) will maintain its frequency of haploid and diploid gametes as well as the total allele frequency. In gamete frequency equilibrium, \[ f(a) = rp, \quad f(A) = r(1-p), \quad f(aa) = (1-r)p^2, \quad f(1A) = (1-r)p^2p, \quad \text{and} \quad f(1A1A) = (1-r)p^3, \] where \( r \) equals the frequency of haploid gametes and \( p \) equals the total frequency of the a allele. A computer simulation of the genetics of this polyploid complex indicates that up to thirteen generations are required to approach this equilibrium. All types and strengths of allelic selection explored, including a selection regime which is ploidy-neutral at gamete frequency equilibrium, cause changes in the frequency of haploid and diploid gametes. This "ploidy-neutral" selection regime is frequency dependent with respect to gamete ploidy. The unexpected selection on ploidy levels results from selection preventing gamete frequency equilibrium, causing differential average fitness of diploid and tetraploid adults.

INTERSPECIFIC HYBRIDIZATION IN THE GENUS LEUCAENA

James L. Brewbaker* and Charles T. Sorensen, Dept. of Horticulture and Dept. of Agronomy & Soil Science, Univ. of Hawaii, 3190 Maile Way, Honolulu, HI 96822.

The mimosoid genus Leucaena Bth. is a widely used and versatile tropical fuel and fodder tree. It comprises 13 species ranging from Texas to Peru that differ widely in chromosome number (52, 56, 104, 112), morphology, and ecology. Over 900 accessions representing all species have been grown in Hawaii. Essentially all of the 13-entry diallel crosses among these species have been made. Of these, 60 produced offspring, including all crosses with the commercial L. leucocephala. The entire genus thus serves as a base of generic diversity for Leucaena improvement. We suspect that this model will prove rather widely applicable to tropical woody legumes, and possibly to most tropical arboreal genera. Interspecific hybridization breeding is underway in Leucaena to incorporate desired cold and frost tolerance, acid tolerance, psyllid insect resistance, and seedlessness into commercial cultivars through species hybridization. Examples of commercial interest in Leucaena species hybrids will be portrayed.

ALLOZYME VARIATION AND CONSERVATION OF GENETIC VARIABILITY IN VACCINUM § CYANOCOCUS


Starch gel electrophoresis and allozyme analyses were conducted on two species representing Vaccinium L. § Cyanococcus A. Gray. The purpose of this study was to examine the patterns of genetic variability in blueberry and to propose improved sampling procedures for germplasm conservation of this fruit crop. Population samples of Vaccinium tenellum Ait. and diploid V. corymbosum L. were collected from Virginia to Mississippi. Samples comprising whole plants or hardwood cuttings were propagated and are being maintained at the Rutgers Blueberry and Cranberry Research Center. Consistent with expectations for self-incompatible, outcrossing species, these two taxa exhibited high levels of variability within populations. For germplasm conservation purposes, these data suggest that large population samples should be collected in order to conserve a larger portion of the gene pool. It appears some taxa are genetically more variable than others and should receive greater attention in plant exploration programs; populations of V. tenellum exhibit notably high levels of allozyme variability.

VARIATIONS IN HIGH-MOLECULAR WEIGHT GLUTENIN SUBUNITS IN LANDRACES OF HEXAPLOID AND TETRAPLOID WHEAT FROM SPAIN

J.M. Carrillo*, M. Rodriguez de Quijano, and A. Galliano, Dept. de Genética, E.T.S.I. Agrónomos, Universidad Politécnica, Ciudad Universitaria, 28040 Madrid, SPAIN.

Variation for high molecular weight (HMW) glutenin subunits in more than 300 Spanish wheat landraces was investigated using SDS-PAGE. Some novel HMW subunits of glutenin were detected in durum as well as in hexaploid wheat. They are presumed to be coded by genes on chromosome 1B at the Glut-B1 locus. The results are related to the bread-making quality potential of Spanish wheat landraces.
EVALUATING THE PROTEIN RESOURCES OF WILD BARLEY
Harold Corke* and Dan Atsmon, Dept. of Plant Genetics, The Weizmann Institute of Science, Rehovot 76100, ISRAEL.

In order to make use of known variation in wild relatives of crop plants, for improving quantitative traits in cultivars, more research is required to evaluate possible selection criteria for breeding. We report on traits related to nitrogen economy and nitrogen source-sink relationships in wild (Hordeum spontaneum) and cultivated (H. vulgare) barley. H. spontaneum accessions were generally higher in nitrogen content of leaves and stems, but lower in dry weight at anthesis, than H. vulgare. Higher nitrogen content in H. spontaneum was combined with high nitrogen harvest index, but low harvest index for yield, resulting in extremely low nitrogen levels in the culture medium. The low levels of nitrogen in the culture medium. The low levels of nitrogen in the culture medium.

GEOGRAPHICAL VARIATION AMONG 212 ACCESSIONS OF EGILOPS SQUAROSA FOR GLIADIN PAGE PATTERNS

*Egilops squarosa*, the donor of the D genome to hexaploid wheat, grows wild through Asia from Turkey to China. We evaluated polyacrylamide gel electrophoregrams of gliadin proteins from kernels of 212 accessions of *Eg. squarosa* collected by Kyoto University scientists. There were 133 distinct patterns for gliadins coded by the *Gl-D1* block of loci, and 178 coded by *Gl-D2*. Polymorphic indices for *Gl-D1* and *Gl-D2* were 0.85 or greater within five regions: northeastern and western Afghanistan, the vicinity of the Caspian Sea in Iran, northwestern Iran, and the Caucasus of the USSR. Polymorphic indices were 0.73 and 0.00 for *Gl-D1* in Pakistan and Turkey, respectively; they were 0.87 and 0.00 for *Gl-D2*. Of 52 sites where multiple samples were taken (mean of only 2.5 samples per site), 37 and 44 were polymorphic for *Gl-D1* and *Gl-D2*, respectively. Of 35 sets of accessions with identical *Gl-D1*-coded patterns, 11 were collected within a locality, 11 ranged over less than 50 km, and 5 ranged over more than 200 km. Representative figures for *Gl-D2* were 12, 9, and 0. Highly variable loci such as *Gl-D1* and *Gl-D2* are more useful for eliminating regions (e.g., Turkey) from further collection or screening than for locating centers of diversity.

DNA FINGERPRINTING IN RICE
J.F. Dallas, Dept. of Agronomy, Curtis Hall, Univ. of Missouri, Columbia, MO 65211.

The human minisatellite probe 33.6 detects several restriction fragment length polymorphisms in varieties of Asian and African cultivated rice. Certain fragments appear to be inherited in a Mendelian fashion and may represent unlinked loci. The hybridization patterns appear to be variety-specific and largely unchanged after the regeneration of plants from tissue culture. The probability of a chance match in 33.6 hybridization pattern between two rice varieties suggests that these regions of the rice genome can generate variety-specific DNA fingerprints. If such regions are detectable in the genomes of the many plant species, possible applications include varietal classification, parentage studies, and assessing relatedness in germplasm collections.

RIBOSOMAL DNA SPACER LENGTH POLYMORPHISM IN DASYPYRUM VILLOSUM POPULATIONS
V. Delre, C. De Pace*, F. Maggiini, and G.T. Scarascia Mugnotta, Agrobiology & Agrochemistry Dept., Univ. of Tuscia, Viterbo, ITALY and C.O. Quaset, Dept. of Agronomy & Range Science, Univ. of California, Davis, CA 95616.

Progenies from different populations of Dasypyrum villosum were assayed for the Bam HI, Eco RI and Taq I restriction patterns of the ribosomal RNA genes (rDNA repeats). The survey revealed that there was heterogeneity in rDNA repeats attributable to variability in the length of the intergenic spacer (IGS) and in the number of Taq I restriction sites within the IGS. The within-progeny variability observed for the rDNA restriction fragment phenotypes suggested that rDNA repeats were clustered in one locus that showed at least three allelic variants. However, a within-locus rDNA repeat heterogeneity, or the occurrence of rDNA repeats at more than one locus, was not excluded. Different populations showed different frequencies of rDNA restriction fragment phenotypes. Population 84-16a showed one rDNA allele that was absent in the other populations.

ISOZYME AND SEED STORAGE PROTEIN POLYMORPHISMS IN DASYPYRUM VILLOSUM POPULATIONS
C. De Pace*, Agrobiology & Agrochemistry Dept., Univ. of Tuscia, Viterbo, ITALY, C.O. Quaset, Dept. of Agronomy & Range Science, Univ. of California, Davis, CA 95616, G.T. Scarascia Mugnotta, V. Delre, and D. Vittori, Agrobiology & Agrochemistry Dept., Univ. of Tuscia, Viterbo, ITALY.

The isozyme and seed storage protein polymorphisms were analyzed using polyacylamide gel electrophoresis. Progenies from five geographically separated populations of *Dasypyrum villosum* collected in Italy were analyzed. There was extensive allelic variability within populations for GOT-2, GOT-3, and EST isozyme systems, and a broad polymorphism for the electrophoretic mobility of gliadin-like polypeptides and glutenin-like subunits. The within-population pattern of variability of the electrophoretic variants for seed storage proteins was larger than for the isozyme systems, and the pattern of variation was similar to that expected for outcrossers. The variability within populations accounted for 90% of the total variation. The interpopulation diversity was greatest only between the most distantly collected populations (600 km apart).
POPULATION GENETICS OF TWO TROPICAL TREES: IMPLICATIONS FOR CONSERVATION

Luis E. Eguiarte*, Nidia Pérez, and Daniel Piñero, Centro de Ecología, Universidad Nacional Autonoma de México, Apartado Postal 70-275, México D.F. 04510, MEXICO.

We studied the population genetic structure, the reproductive biology, and the population ecology of two tropical trees at the rain forest of Los Tuxtlas, México. We present data on genetic variation, outcrossing rates, and F coefficients based on electrophoresis and estimations of the strength of genetic drift, natural selection, and gene flow. The studied species are the palm Astrocaryum mexicanum, and the distylous tree Psychotria faxuscura. Both species present high levels of genetic variation and also high outcrossing rates. These data are used to propose general ideas to approach problems in genetic conservation of tropical species.

GENETIC STRUCTURE AND MATING SYSTEM PARAMETERS IN WILD AND CULTIVATED PHASEOLUS COCCINEUS L.


The parameters of the genetic structure and mating system are presented for two wild and two cultivated populations of Phaseolus coccineus L. near Mexico City. The estimations were made by starch gel electrophoresis. Estimates of population substructure (using F coefficients) and multilocus outcrossing rates were obtained with data from at least five polymorphic loci. The results are compared both within and between populations; the observed differences are discussed under the light of their possible causes. Finally evidence of gene flow between wild and cultivated populations is presented with a discussion about its economic and genetic importance.

GERMPLASM RESOURCES FOR DEVELOPMENT OF GUAYULE AS A DOMESTIC SOURCE OF NATURAL RUBBER

Ali Estilaki*, J. Giles Waines, and Ahmad Hashemi, Dept. of Botany & Plant Sciences, Univ. of California, Riverside, CA 92521.

To reduce the absolute dependency of the United States on foreign sources of natural rubber – an industrial commodity of strategic importance, guayule (Parthenium argentatum Gray), a desert plant native to Mexico and southwest Texas, is being developed as a domestic source of rubber. A significant increase in the rubber yield is needed to make guayule a viable commercial crop. Germplasm resources being used for improving guayule include facultatively apomorphic polyploids with 2n = 54 and 72 chromosomes, sexually reproducing diploids with 2n = 36 chromosomes, and 16 other Parthenium species which are valuable sources for introducing desirable traits into guayule. Diploid guayule, which is confined to a small locality near Mapi in Durango, Mexico, was collected in 1986. The progenies are currently being evaluated for their rubber productivity. The highest rubber producers will be added to the ongoing recurrent selection program to improve guayule at the diploid level. A total of seven new germplasms, Cal-1 through Cal-7, were developed and released by the University of California. Two of these germplasms, Cal-6 and Cal-7, are now being tested for their rubber and resin yield in Arizona, New Mexico, Texas, and California.

MATHEMATICAL EXPRESSION OF EFFICIENCY IN PLANT BREEDING

A.C. Fasoulas, Dept. of Genetics & Plant Breeding, Aristotelian Univ. of Thessaloniki, GREECE.

Efficiency is mainly determined by the rate of genetic gain per generation of selection. Systematic studies on the factors affecting response to selection helped to express efficiency mathematically by the following general response equation for simultaneous selection among and within progenies or entries: R = XFPIE, where X is the overall mean yield per plant, F is the coefficient of inbreeding, PIE is the evaluation index across environments, and I is the intensity of selection. According to the formula, response to combined individual and progeny selection is maximized 1) by maximizing the overall mean yield per plant through optimal plant spacing, high soil fertility, and increased soil homogeneity; 2) by taking measures that enhance inbreeding and increase homozygosity (large F); 3) by advancing generations from grid-selected plants belonging to progenies that rank first on the basis of EIE (number of grid-selected plants per progeny across environments in replicated honeycomb designs that use moving replicates); and 4) by applying high selection pressures, i.e., by using hexagonal grids of large size. As to the inclusion of EIE in the equation, the idea is that if progenies with a high EIE occur, this suggests a high efficiency of selection among and within progenies, because only parental crosses with exceptional combining ability and heritability can yield such progenies. In other words, occurrence of progenies with a high EIE indicates high genetic variation for superiority among and within progenies and hence high response to selection.

SURVIVAL AND POLYEMBRYOGENESIS OF NORWAY SPRUCE AND LOBLOLLY PINE CELL CULTURES FROZEN IN LIQUID NITROGEN

B.J. Finkle*, Dept. of Pomology and P.K. Gupta and D.J. Duran, Dept. of Environmental Horticulture, Univ. of California, Davis, CA 95616.

Picea abies and Pinus taeda polyembryogenic cell cultures were treated with a cryoprotective mixture (polyethylene glycol 8000-glucose-DMSO, 10%-90%-10% w/w), cooled at 1°C/min to -30°C, immersed in liquid nitrogen at -196°C for 10 m, thawed rapidly and transferred to a modified Murashige-Skoog culture medium. After a growth lag of up to 5 wks, normal appearing somatic embryos appeared (6-7 per gram f.w.), ca. 50% of the number in cultures of unfrozen controls. At the third 10-day subculturing of cell masses the rate of embryogenesis was equal for frozen and unfrozen embryonic cultures. It is suggested that lines of
polyembryogenic cell cultures may be safely and economically stored in liquid nitrogen in a living, stable condition for many years, to fulfill clone maintenance, breeding program, and progeny testing needs.

Genetic Structure of Avena barbata Spanish Populations
P. García and M. Pérez de la Vega*, Dept. Genética, Universidad de León, E-24071 León, SPAIN.

The frequencies of multilocus complexes of alleles for 14 duplicated allozyme loci have been determined in 42 populations of A. barbata (2n=4x=28) spanning the eco-geographical range of the species in Spain. Twelve of the 14 allozyme loci showed variability in our samples. The genetic structure, and the alleles present, in the Spanish and Californian populations are similar, supporting the hypothesis of the exclusive Spanish origin of the Californian populations. In contrast, the multilocus genotypes which are most common in California are either not present or are not common in Spain. The populations from Andalucia have shown higher genotypic variability within populations, and are more similar to the Californian populations than the ones from other parts of Spain.

Genetic Diversity in Phytophthora infestans

An understanding of fungal population genetics is a prerequisite to elucidating host-pathogen interactions at the population level. An initial characterization of genetic diversity in the diploid, heterothallic fungus Phytophthora infestans (the causal agent of late blight of potato and tomato) has been undertaken using our culture collection of over 300 isolates collected worldwide. Isolates from areas in which only one mating type has been found are characterized by extremely low levels of allozyme diversity. Diversity is highest in isolates from Mexico, the presumed center of origin of the fungus where sexual reproduction is an integral part of the life cycle. An interesting situation exists in the Netherlands where the A2 mating type has been introduced recently. Isolates from this country are characterized by intermediate levels of allozyme variability, and by a unique allozyme genotype that has not been found elsewhere. In addition, a mitochondrial DNA variant found in Israel and the Netherlands, consisting of a 1.5 kb addition to the 36 kb mitochondrial genome, has not been found among a limited sample of isolates from Mexico, the United Kingdom, and the United States. The number of di-locus allozyme genotypes varies from 2 or 3 in areas with no sexual recombination, to 5 in the Netherlands, and 14 in Mexico.

Chloroplast DNA Polymorphism Occurs Within Individual Trees
Diddahally R. Govindarajan* and David B. Wagner, Dept. of Forestry, Univ. of Kentucky, Lexington, KY 40546-0073 and Graydon P. Smith and Bruce P. Dankic, Dept. of Forest Science, Univ. of Alberta, Edmonton, AB T6G 2H1, CANADA.

A large number of chloroplast DNA variants, identified by restriction fragment analysis and Southern hybridization with a 9.0-kilobase-pair Fst I fragment of the Petunia hybrida chloroplast genome, are known from previous studies of Pinus banksiana and P. contorta. Many of these variants are unusual in their distributions and have not been observed in surveys of the allopatric species ranges; instead, they appear to be restricted to the geographic region of natural hybridization between these two closely-related pines. We have now tested the hypothesis that the unusual, "sympatric" chloroplast DNA variants are due, at least in part, to heteroplasmy (the presence, within single individuals, of two or more chloroplast variants). DNA was purified from needles of five or more sectors of the crown, for each of six individual trees with unusual, "sympatric" chloroplast variants. Polymorphism was detected among samples within four of these six trees, suggesting that chloroplast DNA chimerism may not be uncommon in hybrid zones of conifers.

Progressive Heterosis for Quantitative Traits in Autotetraploid Alfalfa (Medicago sativa L.)

Progressive heterosis is unique to autopolyploids (polysomic polyploids) where heterozygosity and heterosis are not maximal in a single cross hybrid of inbred parents. In an autopolyploid, heterozygosity and heterosis are progressively increased with additional generations of hybridization. This study was designed to evaluate progressive heterosis for important quantitative traits of autotetraploid (2n=4x=32) alfalfa using two types of partial inbreds. In one experiment, inbreds were derived by chromosome doubling of diploid genotypes. In another experiment, inbreds were derived by selfing tetraploids to the S1 generation. In each experiment, populations of increasing heterozygosity were constructed by successively hybridizing the inbreds and their progenies. Populations were evaluated for yield of forage and seed. In both experiments, performance improved with increasing heterozygosity and progressive heterosis was demonstrated.
A PROGRAM TO CONSERVE AND UTILIZE PEPPER (PIPERACEAE) GERMPLASM IN SRI LANKA
P. de A. Gurusinghe, Dept. of Minor Export Crops, Matale, SRI LANKA.

A program was launched to collect both cultivated and wild species of Piper to upgrade the Black Pepper (Piper nigrum) germplasm base. Four wild species (P. argyrophyllum, P. sylvestre, P. attenuatum, and P. thwaitesii) and three cultivated species (P. leucostele, P. longum, and P. betel) have been identified. Over 500 accessions of P. nigrum were collected. 206 were selected on mother vine parameters and their yield was evaluated using nine seasons’ data. Based on the criterion total wet weight of berries, 30 accessions qualified from the cut-off point one standard deviation above the mean. The 10 best regular bearing lines have been identified for release as early improved material. The smallest numbers of years of natural selection. When yield-tested for 14 stations years in Montana all CCI generations were lower than the best check cultivar and later generations were not better than early generations. Regional yield trials of the F2 generation and F3 generations of CCI for 42 station years showed 10% less yield for CCI compared to Unitan. Moccasin-developed CCI material was about 82% two-rowed. Yields component data indicated a deficiency of the CCI material in tiller number. Apparently the germ base is not diverse enough or the selection pressure severe enough to develop a high yielding population at Moccasin or Bozeman.

NONLINEAR RELATIONSHIP BETWEEN SINGLE-CROSS HYBRIDS AND THEIR PARENTAL LINES

The objectives of this paper are to develop equations to express the relationships between hybrids and inbred lines, and to give a theoretical explanation of the low linear correlations observed in practical inbreeding hybrid breeding programs. Under the assumptions of no linkage and no epistasis, a non-linear relationship between inbred lines and hybrids was found. According to this non-linear relationship, the expected genotypic value of the hybrids depends on the means of favorable loci in the parental lines and the differences between the two lines. Correlations between observed genotypic value and predicted genotypic value based on the non-linear model were examined by computer simulation. If all possible crosses of a set of randomly sampled lines from a population were tested, the correlation between observed and predicted genotypic value was high. However, if only a few lines were tested, the correlations were lower than that of all lines tested. The smallest correlation was observed from High × High group crosses. Low correlations between inbred lines and hybrids are expected in practical inbreeding and hybridization breeding programs. These poor correlations could arise from the random combination between the dominant favorable loci in the two parental lines. For a particular cross, we may not predict the hybrid performance based on the parents. In a long term breeding program, however, selection for lines per se would increase both the performance of lines per se and the probability of getting high performance hybrids.

EFFECTS OF NATURAL SELECTION IN ADVANCED GENERATIONS OF CCI

Composite cross 1 (CCI) originated from crosses between 11 barley varieties by H.V. Harlan in 1921. CCI material tested in these replicated yield trials was grown at Moccasin, Montana for 20, 22, 24, 28, and 32 years and at Bozeman, Montana for 6 and 10 additional years after 22 years at Moccasin. The composite cross material is compared to a parental mix and four barley cultivars. The objectives of this study are to determine if increased agronomic worth is obtained in CCI through a greater number of years of natural selection. When yield-tested for 14 station years in Montana all CCI generations were lower than the best check cultivar and later generations were not better than early generations. Regional yield trials of the F2 through F4 generations of CCI for 42 station years showed 10% less yield for CCI compared to Unitan. Moccasin-developed CCI material was about 82% two-rowed. Yield component data indicated a deficiency of the CCI material in tiller number. Apparently the germ base is not diverse enough or the selection pressure severe enough to develop a high yielding population at Moccasin or Bozeman.

HOPE, THE HIERARCHICAL, OPEN-ENDED BREEDING SYSTEM FOR MAIZE: AN UPDATE
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Genetically broad-based populations generally are poor sources of elite breeding lines. The HOPE breeding system is designed to maximize genetic diversity while still allowing for development of useful inbred lines for maize hybrid production. The following describes the HOPE system as recently revised, based on field evaluation and computer simulation studies. The system employs a hierarchy of four performance levels—Low, Intermediate, High, and Elite—in each of two complementary sets of populations. Favorable genes are moved progressively upward in the hierarchy via introgression of selections from the immediately lower performing population. Increasingly stringent selection procedures are practiced at each higher level of the hierarchy to include mass selection in the Low level populations, half-sib family recurrent selection in the Intermediate populations, selfed (S) progeny recurrent selection in the High populations, and reciprocal recurrent selection in the Elite populations. The Elite populations are the sources for inbred lines. Introductions—over 750 since 1977—are incorporated on a continuing basis into one of the Low level populations according to the heterotic pattern as identified in topcross performance with the Elite populations. About 10% of the introductions have high enough performance to be also incorporated into the Intermediate or High level populations.
A Detailed Genetic Map of Lactuca Species with Restriction Fragment Length Polymorphism Markers and Its Use for Assessing Levels of Variation and Rates of Evolution

Rick Kesseli* and Richard Michelmore, Dept. of Vegetable Crops, Univ. of California, Davis, CA 95616.

The genetic map of Lactuca species now possesses more than 120 RFLP, 5 downy mildew resistance, 5 isozyme, and 4 morphological markers. This detailed map is a major component of our strategy to clone resistance genes. Additionally, using these markers taken at intervals throughout the genome, we have assessed levels of variation among 70 cultivars and wild species of Lactuca, detected differences in rates of evolution within different regions of the genome, and analyzed the effects of backcross and pedigree breeding programs. Parallel studies in the pathogen causing lettuce downy mildew, Bremia lactucae, are also being undertaken in our laboratory.

Genetics and Evolution of the x=9 Brassica Species
Shahryar F. Kianian* and Carlos F. Quiros, Dept. of Vegetable Crops, Univ. of California, Davis, CA 95616.

Forty-two accessions including ten different Brassica species classified under the Brassica oleracea cytodeme (x=9), are being used in this study. Morphological characters, isoenzymes—GOT, LAP, MDH, PGM, 6-PGDH, and TPI—and RFLP markers—r DNA, cruciferin, napin, and random cDNA probes—served to determine the extent of variability within this cytodeme. Variation in some previously believed invariant isoenzymes was observed (i.e., 6-PGDH). In order to understand the evolutionary relationship of these species, intra- and inter-specific hybrids are being analyzed. Cytological examination of some F1 hybrids (i.e., B. oleracea x B. insularis; B. incana x B. oleracea) show evidence of translocations which agrees with their reduced pollen fertility (56.5% and 50.8%, respectively). To gain genetic information on the evolution of the B. oleracea cytodeme, hybrid progenies will be analyzed as to their fertility, chromosomal aberrations, and any distortion of expected segregation ratios for the marker loci.

Enzyme Variability of Natural and Cultivated Populations of Melilotus Alba
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Natural populations of sweet clover (Melilotus alba) examined electrophoretically according to four enzyme systems (acid phosphatase, leucine-aminopeptidase, peroxidase, and malic enzyme) show a high degree of polymorphism. Two different strains: annual and low-coumarin content 'Selgo' strain as well as one dwarf line were compared to natural populations using the same enzyme systems and showed enzyme variability unknown so far for the species. A minimum spanning tree constructed on the basis of Euclidean distances as well as diagrams of principal component analysis illustrate interpopulational differences of the species in question.

Seed Storage Proteins: Usefulness of Their Evaluation in Gene Bank Collections
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The intensive collecting activities of the past decades has resulted in the accumulation of valuable genetic stocks (landraces, wild relatives) stored in different gene banks throughout the world. It has been stressed on several occasions that the value of this material depends on its utilization. Sources of variation for useful traits have been evidenced and in many instances incorporated in breeding programs. Recently seed storage proteins, both in cereals and legumes, have been the object of very intensive biochemical, genetical, and molecular studies because of their impact on qualitative aspects and also for the possibility of using them as a tool to trace evolutionary pathways. As for many other traits, useful variation for seed storage proteins can be observed in gene bank collections. Examples for Triticum, Phaseolus, Vicia, and Vigna are described. The variation present within each genus allows us to identify geographical areas of diversity and the possibility of using the information in sampling strategies.

Estimation of Genetic Effects from Variety Diallel Cross and Related Populations of Maize
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A model presented by Gardner and Eberhart (Analysis I) was used to estimate genetic effects for yield and other agronomic traits of maize. The yield trial entries included six parental composites, F1's selfed and F1's random-mated. Heterosis effects were also estimated in addition to the main genetic effects. Results from the two trials showed that the model had a good fit for yield, ear diameter, plant and ear heights where it accounted for more than 90% of the total variation among means. Dominance gene effects were the most important contributor to the inheritance of the studied traits, except for the number of days to silking and weight of 1000 kernels where additive gene effects were more important. The genetic estimates were used to predict the performance of possible composites that can be derived from the six parents. Breeding schemes were suggested for intra- and interpopulation improvements.
DETECTION OF GENETIC INTERACTIONS FOR MILLING AND BAKING QUALITY USING INTERCROSSES OF SUBSTITUTION LINES


Cheyene (Cnn) wheat chromosomes were substituted individually into Chinese Spring (CS) wheat by R. Morris. Nine of these lines (1A, 1B, 1D, 6A, 6B, 6D, 4B, 5D, and 7B) were crossed to CS and in diallel. F1 and F2 generations were examined for milling and baking parameters. Cnn chromosome effects were mainly additive, no epistatic interactions between homoeologous chromosomes were detected, dominance effects were often observed, especially for Cnn 1A and 5D for flour protein. Epistatic effects were observed between nonhomoeologous chromosomes of groups 1 and 6, especially for dough-mixing time, loaf volume, and SDS sedimentation (SDS-sed). Cnn 1D and 7B, when homozygous, gave positive effects for SDS-sed and loaf volume, but these chromosomes appeared antagonistic.

INVESTIGATIONS ON ISOZYME AND MORPHOLOGICAL DIVERSITY IN BRASSICA CAMPESTRIS

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Morphological variation in Brassica campestris (2n=20) is extensive with no fewer than eight subspecies ascribed. Subspecies generally follow geographical distribution in three broad centers of diversity. The Mediterranean group includes turnip-rape (B. oleracea – oilseed), turnip (B. rapifera), and vegetable crops (broccoli raab), as well as wild or feral types. The Chinese center is most diverse and includes leafy vegetables (B. chinensis – pak choi; B. pekinensis – pe-Isal Chinese cabbage), mustard, and turnip forms. The Northeastern Indian subcontinent contributes saxson (B. trilobulais) and toria (B. dichotoma) oil-seed crops. Seventeen accessions representing the various subspecies were sampled for isozyme variation. Zymograms for 4PGD, LAP, GOT, PGI, MDH, PGM, SDH, and IDH were obtained via starch gel electrophoresis and scored for allele frequency. In the systems employed, seven loci appear fixed, seven loci polymorphic, and others not well resolved. Inheritance studies of morphological traits and isozyme loci are in preliminary stages. Hybrids have been obtained from turnip pak choi, or toria as female crossed with each of the eight subspecies. Hybrids are generally intermediate in morphology, although some exceptional and reciprocal differences are noted. F2 populations have been scored for isozyme segregation.

PLANT GENETIC RESOURCES IN THE MEDITERRANEAN GENE CENTER

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The Mediterranean is an important center of diversity for several families of cultivated plants: Leguminosae (48), Gramineae (33), Labiatae (17), Compositae (14), Umbelliferae (13), Cruciferae (12), Chenopodiaceae (6), etc. From 1971 to 1988 the Germplasm Institute, in collaboration with other national and international organizations, like FAO, IBPGR, ICARDA, IITA, etc., has organized and conducted 62 collecting missions covering nearly all countries of the Mediterranean center, plus Ethiopia, Iran, and Southern Africa. In all, more than 11,000 samples have been collected, multiplied, stored, and distributed about four times (44,000), to more than 400 institutions, including departments of plant breeding, botany, crop science, plant pathology, and horticulture, seed companies, farmers, other gene banks, etc., throughout the world. The Germplasm Institute is one of the four centers with the responsibility of preserving the wheat world collection. More recently new projects have been started for collecting and domesticking new crops from species originated or diversified in the Mediterranean area. Characterization, evaluation, and other basic research for a better conservation and exploitation of the collected and stored germplasm carried out at the Institute are also illustrated.

A COMPARISON BETWEEN CALIFORNIA AND OLD WORLD GERMPLASM OF AVENA BARBATA

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The Mediterranean wild oat species Avena barbata was introduced into California during the Spanish colonization. This species, a successful invader, is presently an important floristic element in the Western USA. Our paper compares Old World and California A. barbata germplasm. The strong divergence between the ancestral and the California invader gene pools is illustrated by several methods of categorical multivariate analysis. Regional patterns within the Old World data are shown. East-West and North-South differences can be recognized among the allozyme multilocus associations detected in this survey. Two families of rDNA spacer-length variants were identified comprising, together, twenty-three elements. An East-Westcline in the frequency of these elements appears to distinguish geographically the two rDNA families.

ESTIMATES OF GENETIC IDENTITY AMONG SAMPLES OF AVENA STERILIS L. AND A. SATIVA L. FROM THE NATIONAL SMALL GRAINS COLLECTION


Estimates of genetic identity (I) between 100 accessions of the wild/weedy Avena sterilis L. from Ethiopia, Iran, Lebanon, and Morocco and 25 U.S. oat (A. sativa L.) cultivars were calculated for genotypic frequencies over 13 polymorphic enzyme systems. Overall mean I between the cultivated and wild species was 0.77. Little variation was found between the mean I of the cultivars and A. sterilis from the different countries: Ethiopia (0.75), Iran (0.77), Lebanon (0.79), and Morocco (0.76). The number of genotypes per enzyme varied from two for six-phosphogluconate dehydrogenase and superoxide dismutase to seven for alcohol dehydrogenase with a mean of four. The group of culti-
vars contained only one unique genotype which was not found in any of the A. steriliis accessions, while A. steriliis had 18 genotypes which were not present in the group of cultivars. The probability of a unique genotype in A. steriliis from Ethiopia, Iran, and Lebanon was twice that of the cultivars, while the Moroccan accessions were less likely to have unique genotypes. Accessions of A. steriliis contain unique polymorphs and can be used as an additional source of genetic variability. These data suggest that variation in A. steriliis is spread over the geographic range of the species, with a somewhat less polymorphic diversity in the Moroccan wild oat accessions.

GENETIC RESOURCES SAMPLING STRATEGY BASED ON VARIANCE COMPONENTS ESTIMATED
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Forty populations (P) of oil palm were sampled at random in Nigeria. At each site (population) five palms (families—F) were sampled and the seeds from each palm were kept separate and 12 seedlings (S) per family were field planted in a completely randomized design. ANOVA showed significant differences between populations (P) and families (F) for most of the traits. The estimates of intra-clas correlation of population (r_p) ranged from 0.28%, families (r_f) 3-25%, and seedlings (1 - r_f) 74-94%. Using the estimates of x, r_p, r_f, and r_s, a minimum sample size for N_P, N_F, and N_S were computed. The results show that various combinations of N_P, N_F, and N_S could be chosen to attain the expected x at 95% probability.

GENOTYPE VARIABILITY IN VIGNA ACONITIFOLIA
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Analysis of genotypic variability (mean, range, standard range, and phenotypic, genotypic, environmental coefficients of variance, expected genetic advance, genetic advance, and broad sense heritability) for eleven characters, including nine yield-related characters, in forty genotypes, collected from various parts of Western India, of Vigna aconitifolia (moth bean) revealed the existence of variability for all the eleven metric traits. The seed protein production, seed yield, and clusters per plant showed high heritability and genetic advance implying thereby that the three characters of this protein rich (22%) food and forage legume have greater significance in selection and breeding high yielding genotypes.

INFORMATION SYSTEM TOOLS FOR CONSERVATION OF GENETIC RESOURCES
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Value is added to genetic raw materials by maintenance of both diversity and structure on site (in situ conservation) and by acquisition of knowledge about materials, sites, and their interrelationships (research and experience). If we are to effectively realize such values, prospective users of genetic resources must have ready access to information on these elements and to tools for the review and use of such information. Over the past five years, GENREC has initiated the development of several information system tools designed to improve recognition, conservation, and use of genetic resources. Two software programs, now available, are being demonstrated at this symposium. The California Forest Genetic Sources Catalog, developed with support from the Wildland Resources Center of the University of California, contains information on designated preserved areas in California where genetic conservation or preservation of forest tree species is a mandated or acknowledged long term objective. Data on location, size, land use, ownership, and other characteristics, and on occurrence of tree species and vegetation types are cross indexed to a bibliographic database. This application was developed using dBase III Plus (Ashton Tate) for use on an IBM PC/XT/AT or compatible computer with hard disk. It is available in both dBase III Plus program and Clipper compiled versions. Software modifications and refinements are planned for both DOS and Macintosh environments.

USE OF DNA RESTRICTION FRAGMENT LENGTH POLYMORPHISMS (RFLPS) TO ASSESS GENETIC DIVERSITY IN A CITRUS GERMLASM COLLECTION
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Accessions in germplasm collections of citrus and other species with both sexual and asexual reproduction can be grouped into three classes reflecting their degree of genetic divergence: 1) accessions differing only by mutations, 2) accessions resulting from hybridization between other accessions, and 3) accessions derived from different ancestral genotypes and having distinct alleles. Preservation of genetic diversity will be greatest if maintenance of accessions with the greatest allelic diversity (class 3) is emphasized. Codominant molecular markers such as isozymes and RFLPs can be used to assess these types of divergence. A survey of RFLPs in 68 accessions from the Citrus Variety Collection at Riverside using random cDNA probes distinguished several accessions as having unique alleles at one or more loci. Other genotypes are highly heterozygous and apparently are hybrids. Some accessions differ in morphological or physiological traits, but are identical at all markers. Such genotypes evidently differentiated only by accumulation of mutations.

MATERNAL AND GENETIC INHERITANCE IN COCONA: EVOLUTIONARY EFFECTS OF HUMAN SELECTION?

Solanum sessiliflorum, cocona or the Amazonian peach-tomato, shows maternal inheritance for human-selected traits (fruit size and shape), and simple one-gene Mendelian inheritance for others (spines). Reciprocal
CROP IMPROVEMENT THROUGH MUTATION BREEDING IN PEANUT AND SORGHUM

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Dormant seeds from one of the highest-yielding varieties of peanut and sorghum were treated with gamma radiation at doses of 10-40 kR. Untreated seeds from the same sources were used as control. The M₄ generation of both species were field grown dose-to-row and bagged upon flowering to insure self-pollination. The M₅ plants of peanut were screened for reaction to the leaf-spot disease through artificial inoculation with spores of the causal fungus previously cultured in agar-salt medium. The M₅ progenies of three uninfected plants were multiplied and the M₆ and M₇ generations were similarly screened for resistance to the fungal infection. The absence of disease symptoms indicate the production of leaf-spot resistant mutations. Other useful mutations such as large pods and white testa were also obtained in the M₇ generation. In sorghum, the M₂ seedlings were inoculated with suspensions of the mosaic virus from sweet corn seedlings and sugarcane leaves. One M₃ line without disease symptoms was obtained. The mutation proved to be true to type up to the M₇ generation. Other useful mutations in the M₇ lines were big seed and white testa in contrast to the brown to brick-red seed coat colors of all sorghum varieties.

USE OF DIPLOPERENNIS TEOSINTE IN A TROPICAL MAIZE BREEDING PROGRAM

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Zea diploperennis (2n=20), a newly discovered perennial species of teosinte from Mexico offers immense potential as a very valuable gene source for tropical maize improvement. Being the only related diploid perennial species to Zea mays, it crosses very freely with it and serves as a very useful gene source for many disease and insect resistances. A concerted breeding program was started at the University of Hawaii using Zea diploperennis in crosses with a series of tropical maize inbreds developed at Hawaii (Hi 25, Hi 26, ..., Hi 35). Different generations, viz. F₁, F₂, BC₁, S were generated and studied in the winter and the summer. The F₇s were very vigorous, intermediate in many characters like filling, ear traits, etc. The F₃ plants were not true perennials as evidenced by the lack of rhizomes. F₃ progenies showed wide variability for the different traits, although a corn-like perennial recombinant was not to be seen. Genetics of rhizomes appears to be very complicated with a possible nuclear/cytoplasmic interaction. A composite named HIC 9 was developed with 75% Z. mays : 25% Z. diploperennis genotype and is being maintained in isolated interbreeding.

CHARACTERIZATION OF REPETITIVE DNA IN TRIPSACUM AND ZEA

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A species-specific repeat was isolated for Tripsacum dactyloides. Although the probe is composed of mainly knob heterochromatin (180 bp tandem repeat), it hybridizes to two other apparent sequence classes in Eco RI Southern blots of T. dactyloides total DNA (a dispersed repeat and a tandem repeat). A plasmid that contains the latter tandem repeat was isolated. This repeat is distinct from the 180 bp knob repeat. It hybridizes to high MW DNA on Hae III Southern blots, whereas the knob repeat hybridizes to a low MW monomer (180 bp) on these same blots. The repeat is present in Zea mays and throughout Tripsacum and shows polymorphism between these taxa. It is being further characterized by in situ hybridization, its hybridization to genomic DNA is restricted with a variety of endonucleases (Nsi I, Bam HI, Hind III, etc.) and its homology to known maize repetitive DNA classes. These results should be informative on the structure and evolution of the maize genome.

GENE FLOW AMONG SORGHUM SPECIES OF DIFFERENT PLOIDY LEVELS


The genus Sorghum includes species with 2n=10, 20, 30, and 40 chromosomes. Sections Parasorghum (S. versi-
color and *S. purpureo-sericeum*) and *Sitosorghum* (*S. stipeoides* and *S. intrans*) have a somatic chromosome number of 10. Section *Sorghum* includes domestic and wild species with somatic chromosome numbers of 20 (*S. bicolor* and *S. arundinaceum*) and 40 (*S. halepense*). Analyses of karyotypes of *S. versicolor* imply that it is distantly related to *S. bicolor*. Fertilization occurred in three hours when *S. bicolor* was crossed to *S. halepense*. In contrast, only a few pollen grains germinated, and fertilization never occurred, when *S. bicolor* was pollinated by *S. versicolor*. Thirty-chromosome hybrids of *S. bicolor* and *S. halepense* formed 10 trivalents, and the two species showed similar restriction endonuclease patterns of mitochondrial DNA. Gene flow between species of the section *Sorghum* and those of 10-chromosome sorghums is expected to be very limited, whereas there is no barrier for gene exchange among species within the section *Sorghum*. Genome organizations of *S. versicolor* and *S. bicolor* are remarkably different with respect to repetitive DNA probes so far analyzed.

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**DIFFERENTIAL ISOZYME EXPRESSIONS OF PG1 AND AAT IN CONIFERS**

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In population genetic studies of conifers, haploid megagametophytes and diploid embryos or young seedlings have been most frequently used in electrophoretic surveys of enzymes. However, caution should be exercised when there exist different developmental or tissue-specific isozyme activities. Among 17 enzyme systems surveyed for 10 coniferous species in this study, PG1, AAT, MDH, ME, IDH, PER, GDH, 6-PG, and ACO exhibit differences in isozyme activity at specific loci between each of the megagametophyte-embryo pairs. Differential isozyme activities of MDH, ME, IDH, PER, GDH, 6-PG, and ACO appear to be developmental, whereas isozyme expressions of PG1 and AAT are more tissue specific. The cytosol PG1 isozymes are coded by two, tightly linked structural genes in the megagametophyte, with each gamete showing a three-band phenotype, but only the cathodal gene is active in the embryo or young seedlings, showing a single-band phenotype when homozygous. Certain AAT isozymes are active (inactive) in the megagametophyte, but inactive (active) in the embryo. Tissue-specific PG1 and AAT isozyme activities were found in spruces, pines, and, to a lesser extent, Douglas-fir, which were selected on the basis of seed availability and viability. Lack of this information when conducting electrophoretic studies may lead to misinterpreting the number of isozyme loci or alleles, misidentifying maternal genotypes, or failing to understand the inheritance of isozymes and ultimately could lead to errors in the estimates of population genetic parameters.

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**THE GENETIC CONSEQUENCES OF COLONIZATION AND THE EFFECT OF RAY FLORETS ON OUTCROSSING RATE IN POPULATIONS OF BIDENS PILOSA L.**

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The theoretical consequences of the colonization process, the breeding system, and the effect of ray florets on the level of outcrossing in wild populations of *Bidens pilosa* on the Hawaiian islands were examined. Little or no variation was found at 34 enzyme loci in two non-radiate populations on the island of Kauai and a slightly higher level of genetic variation was found in the radiate population on the island of Hawaii. Auto-seedset in the greenhouse averaged 93%±7.5%, and no reduced fertility or viability was observed in the progeny of repeated selfing. Outcrossing rates were estimated for the radiate and non-radiate plants in a polymorphic population. The radiate plants outcross at greater frequencies (t=0.088±0.039) than the non-radiate plants (t=0.048±0.024). Genetic identity between populations of different islands was 95%. This study suggests that the depauperate amounts of genetic variation both within and between populations of *B. pilosa* could be due to the joint effect of population bottleneck and predominant inbreeding. However, fixed heterozygosity due to polyploidy may provide genetic versatility contributing to the success of this weedy species in colonization.

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**TRANSMISSION OF ALIEN CHROMOSOMES IN DIPLOTAXIS ERUCOIDES-BRASSICA NIGRA ADDITION LINES**

*P. This*, O. Ochoa, and C.F. Quiros, Dept. of Vegetable Crops, Univ. of California, Davis, CA 95616.

Chromosome addition lines were constructed by backcrossing an interspecific diploid hybrid of *D. erucoides* (x=7) × *B. nigra* (x=8) to *D. erucoides*. This cross yielded 6 monosomic and 2 double monosomic addition lines. The addition lines were characterized cytologically and by six species-specific isozyme markers. Three of these markers, *Ip*-1, 6-*pgd*-1, and 6-*pgd*2 were located in one of the *B. nigra* chromosomes, while the other three were located independently in other *B. nigra* chromosomes. The two other lines did not have any of the *B. nigra* markers studied but because of their different morphology they might carry different *B. nigra* chromosomes. The transmission of the extra-chromosome upon selfing of each line ranged from 8 to 30%. Alien chromosome transmission by crossing to the Diploptaxis parent ranged from 0 to 21%. The lines carrying the *Got*-1 marker had the highest transmission. No disomic addition lines were recovered in any of these progenies. Further analysis and characterization of these lines is being attempted by developing RFLP markers. Also additional progenies are being generated in order to complete the whole series of lines.
ISOLYME GENETIC VARIATION IN WILD CHESTNUT POPULATIONS FROM ITALY

F. Villani*, S. Benedetti, M. Cherubini, and M. Paciucci, Agroforestry Institute, C.N.R., Pontano (TR), ITALY and C. Tomassini, Agrobiology & Agrochemistry Dept., Univ. of Tuscia, Viterbo, ITALY.

The genetic variation of wild populations of Castanea sativa from three regions of Italy was investigated on the basis of electrophoretic analysis. Samples were examined by means of starch gel electrophoresis of the following 11 isozyme systems: ADH, DIA, PER, SKDH, IDH, G6P, PGM, LAP, EST, GPI, and 6PGDH. Allelic frequencies were compared within and between regions by Nei's genetic distance value (D), with high genetic variability between populations within regions as observed at Dia-I, Est-I, Gpi-2 loci. An alternate form of Gpi-2 locus, named 105, was not detected in the samples from the southern region of Calabria. A diagram of cluster analysis calculated by the genetic distance matrix shows a poor correlation in a number of cases between genetic differentiation of populations and their geographic locations, possibly due to anthropic effect.

GENETIC VALUES OBTAINED FROM DOUBLED HAPLOID BARLEY


Haploids have been considered for many years to represent a rapid method of cultivar development. Generally, for completely inherited traits, a savings of four to five generations can be expected as well as a greatly reduced population size. The experiment was conducted on 80 doubled haploid-derived progeny of nine crosses. Half sib and full sib analyses were conducted on six agronomic traits. Variance within plots from doubled haploid-derived lines was less than parental check lines for plant height, main spike length, and 25 seed weight. While not unexpected, the greater uniformity supported haploid theory. Heritability estimates using haploids allowed the authors to use full sib analyses to calculate heritability since no dominance was present in the doubled haploid lines. This also provided a rapid assay of parental breeding value to inbreeding plant materials.

MORPHOLOGICAL AND SEX FORM VARIATION AMONG BUFFALOGRASS [BUCHELOE DACTYLOIDES (NUTT.) ENGELM.] POPULATIONS

Lin Wu* and David R. Huff, Environmental Horticulture Dept., Univ. of California, Davis, CA 95616.

Buffalograss seed samples were collected from eight locations along two east-west transects crossing the shortgrass prairies of Oklahoma, New Mexico, and Texas. Plants were grown under common field environment. Eight morphological characters were measured. Seven characters are significantly different among the eight populations; only the sexual reproductive effort was not significantly different among the populations. The sex ratio of male to female individuals was consistent at 1:1 for all the eight populations. However, the frequency of monocious plants was found to vary, and the highest frequencies (30-35%) were found in the geographically marginal populations. In the central distribution where the density is high, the frequency of monoecious plants was less than 5%. The results of this study indicate that there is a wealth of genetic variation at both the morphological and monoecious plant frequency levels, and it may serve as a genetic resource for buffalograss breeding.

LONG BEAN BREEDING IN MALAYSIA

T.C. Yap, Dept. of Agronomy & Horticulture, Univ. of Agriculture Malaysia, 43400 Serdang, Selangor, MALAYSIA and C. Mak, Dept. of Genetics & Cellular Biology, Univ. of Malaya, 59100 Kuala Lumpur, MALAYSIA.

All possible crosses were made among the seven varieties of long bean to study the inheritance of some agronomic characters. The results showed that additive gene action played an important role for the genetic variation. With the exception of pod length, the heritability values for pod yield, number of pods per plant, and seed protein were low. Three selection methods were used to handle five high-yielding and five low-yielding F1 hybrids and the results revealed that selection based on the average index method was able to give more high-yielding progenies compared to the visual pedigree and the modified bulk methods irrespective of the performance of the F1 generation. Among the promising lines developed, Line 30 outyielded many other genotypes in the regional trials. This line with pod length of 42 cm is able to give pod yield of about 15 tons/ha. This line may be released for commercial production.

GENETIC STRUCTURE OF PEATLAND AND UPLAND BLACK SPRUCE

Francis C. Yeh, Mei Sun*, and V.J. Liefers, Dept. of Forest Science, Univ. of Alberta, Edmonton, Alberta, T6G 2H1, Canada.

Mating system and genetic variation in a geographically proximate (2 kilometers apart) peatland and an upland black spruce (Picea mariana (Mill.) B.S.P.) population from Alberta was analyzed for 16 enzymes encoded by 34 structural loci. Multilocus estimate of outcrossing rate suggested a mixed mode of mating, at 0.95 and 0.94 for peatland and upland population, respectively. Amount of genetic variation between populations was comparable. On average, populations were polymorphic and heterozygous at 27.8 and 90.0% of their loci, respectively, and had 1.2 alleles per loci. There was, however, significant allelic heterogeneity at four of ten polymorphic loci. Analysis of F-statistics indicated substantial differentiation between populations and an 11.0% deficiency of heterozygotes relative to Hardy-Weinberg expectations. These results suggest ecological differences between peatland and upland populations of black spruce have resulted in allozyme differentiation within the species.
## Appendix III

### Names and Addresses of Symposium Registrants

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