PLANT BREEDING REVIEWS

Volume 22

edited by

Jules Janick

Purdue University

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Contributors

William A. Berzonsky, Department of Plant Sciences, North Dakota State University, Fargo, ND 58105, Bill.Berzonsky@ndsu.nodak.edu

Ray A. Bressan, Department of Horticulture and Landscape Architecture, Center for Plant Environmental Stress Physiology, Purdue University, West Lafayette, IN 47907, bressan@hort.purdue.edu

Cuauhtemoc T. Cervantes-Martínez, Universidad Autónoma Chapingo, Carretera México-Texcoco, km 38.5, Chapingo, 56230, Mexico, c_cervant@tauras1.chapingo.mx

P. S. Chew, Applied Agricultural Research Sendirian Berhad, 47000 Sungei Buloh, Selangor, Malaysia, aarsb@po.jaring.my

Hongjian Ding, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83844, hjding@uidaho.edu

I. L. Goldman, Department of Horticulture, 1575 Linden Drive, Madison, WI 53706, ilgoldma@facstaff.wisc.edu

Scott D. Haley, Soil and Crop Sciences Department, Colorado State University, Fort Collins, CO 80523, shaley@lamar.colostate.edu

Marion O. Harris, Department of Entomology, North Dakota State University, Fargo, ND 58105, Marion.Harris@ndsu.nodak.edu

P. M. Hasegawa, Department of Horticulture and Landscape Architecture, Center for Plant Environmental Stress Physiology, Purdue University, West Lafayette, IN 47907, hasegawa@hort.purdue.edu

C. Corley Holbrook, U.S. Department of Agriculture–ARS, P.O. Box 748, Tifton, GA 31793, holbrook@tifton.cpes.peachnet.edu

James B. Holland, U.S. Department of Agriculture–Agriculture Research Service, Plant Science Research Unit, Department of Crop Science, Box 7620, North Carolina State University, Raleigh, NC 27695-7620, james_holland@ncsu.edu

T. Y. Hor, Applied Agricultural Research Sendirian Berhad, 47000 Sungei Buloh, Selangor, Malaysia, aarsb@po.jaring.my

Robert J. Lamb, Cereal Research Centre, Agriculture and Agri-Food Canada, Winnipeg, Manitoba R3T 2M9, Canada, rlamb@em.agr.ca

Robert J. Lambert, Department of Crop Sciences, University of Illinois Urbana–Champaign, Urbana, IL 61801, rjlamber@uiuc.edu

Tracie K. Matsumoto, Department of Horticulture and Landscape Architecture, Center for Plant Environmental Stress Physiology, Purdue University, West Lafayette, IN 47907, traciem@purdue.edu

R. I. H. McKenzie, Cereal Research Centre, Agriculture and Agri-Food Canada, Winnipeg, Manitoba R3T 2M9, Canada

J. P. Navazio, SEEDS, 608 West Benton Street, Iowa City, IA 52246, jpnavazio@earthlink.net

Wyman E. Nyquist, Department of Agronomy, Purdue University, West Lafayette, IN 47907-1150, wnyquist@purdue.edu

Herbert W. Ohm, Department of Agronomy, Purdue University, West Lafayette, IN 47907, hohm@dept.agry.purdue.edu

José M. Pardo, Instituto de Recursos Naturales y Agrobiologia, Consejo Superior de Investigaciones Cientificas, P.O. Box 1052, Sevilla 41080, Spain

Fred L. Patterson, Department of Agronomy, Purdue University, West Lafayette, IN 47907

Frank B. Peairs, Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, fbpeairs@lamar.colostate.edu

David R. Porter, U.S. Department of Agriculture–ARS, Plant Science and Water Conservation Research Laboratory, Stillwater, OK 74075, dporter@pswcrl.ars.usda.gov

Roger H. Ratcliffe, U.S. Department of Agriculture–ARS, Department of Entomology, Purdue University, West Lafayette, IN 47907, roger_ratcliffe@entm.purdue.edu

Thomas G. Shanower, U.S. Department of Agriculture–ARS, Northern Plains Agricultural Research Laboratory, Sidney, MT 59270, tshanowe@sidney.ars.usda.gov

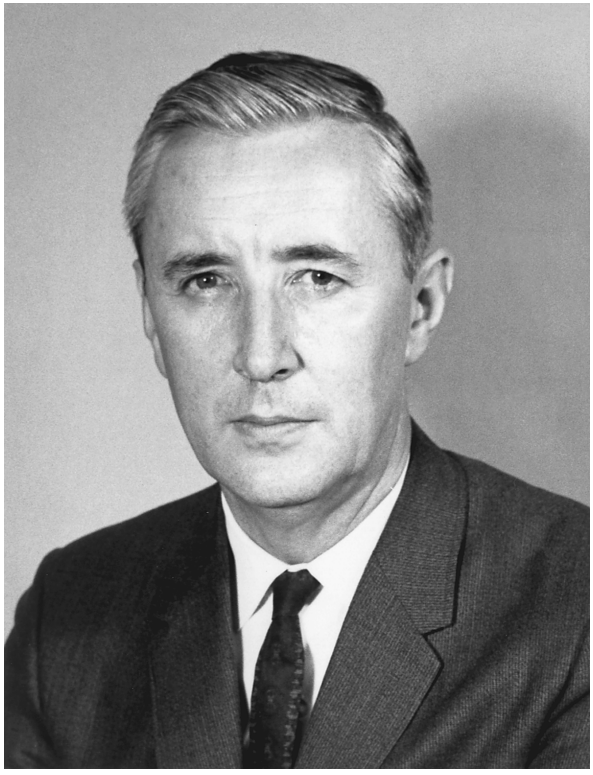
A. C. Soh, Applied Agricultural Research Sendirian Berhad, 47000 Sungei Buloh, Selangor, Malaysia, aarsb@po.jaring.my

H. Thomas Stalker, Department of Crop Sciences, North Carolina State University, P.O. Box 7620, Raleigh, NC 27695, HTS@unity.ncsu.edu

C. C. Tan, Applied Agricultural Research Sendirian Berhad, 47000 Sungei Buloh, Selangor, Malaysia, aarsb@po.jaring.my

G. Wong, Applied Agricultural Research Sendirian Berhad, 47000 Sungei Buloh, Selangor, Malaysia, aarsb@po.jaring.my

Shizhong Xu, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, xu@genetics.ucr.edu



Denton E. Alexander

1

Dedication: Denton E. Alexander Teacher, Maize Geneticist, and Breeder

Robert J. Lambert
Department of Crop Sciences
University of Illinois Urbana–Champaign
Urbana, Illinois 61801

Denton E. Alexander (Alex) was born on a farm near Potomac, Illinois, on December 18, 1917. He was farm-reared and educated in rural elementary and secondary schools in the area. From 1935 to 1937, Alex attended Illinois State Normal University in Normal, Illinois, receiving an elementary school teacher certificate. He taught in a rural school, near his home, for two years. He attended the University of Illinois Urbana–Champaign from 1939 to 1941 receiving the B.S. degree in Agriculture.

During the early months of World War II, Alex was an aircraft engine instructor in the U.S. Army Air Corps (1941–1943). From 1943 to 1947, he was involved with mass spectrographic separation of uranium isotopes at the Manhattan Project, Oak Ridge, Tennessee. He returned to Illinois in 1947 and entered graduate school at the University of Illinois, Urbana–Champaign and received the Ph.D. in 1950. In 1950 to 1951, he served as a postdoctoral Fellow with Marcus M. Rhoades in the Botany Department. He joined the Department of Agronomy faculty at the University of Illinois Urbana–Champaign, as an instructor in 1951 and attained the rank of Professor of Plant Genetics and Breeding in 1963.

Alex's early tenure in the Department of Agronomy was devoted to organizing and teaching the first undergraduate introductory course in genetics in the College of Agriculture. This course was cross-listed with Animal Science, Dairy Science, Horticulture and for a time, Veterinary

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Medicine. He taught more than 5000 undergraduate students from 1951 to 1985. He was particularly insistent that really superior students in his classes obtain advanced degrees in Genetics. Several dozen of these students have had successful commercial and academic careers. The best description of Alex's teaching abilities comes from one of his peers who said, "Alexander is one of those fortunate individuals who are articulate, have an infectious enthusiasm, and establishes an excellent rapport with students. He justly merits his reputation as an inspiring teacher." Alex received several awards for his excellence in teaching.

In 1964, Alex established the Illinois Corn Breeders School, an outreach program for commercial U.S. Corn Breeders. The objective of the school is to update corn breeders in the latest techniques in corn breeding, biotechnology, and related disciplines. From 1964 to 2001 attendance has varied from about 80 to 150. Alex continues to serve on the advisory committee of the school. The 37th annual session was held in 2001.

CYTOGENETIC RESEARCH

Alex's early research in the Department of Agronomy was strongly influenced by his postdoctoral research with Marcus M. Rhoades. That single year's work resulted in detailed studies of the frequency of spontaneous haploidy and of the meiotic behavior of chromosomes during microsporogenesis of maize. Barbara McClintock had earlier reported that bridgelike figures occur during haploid microsporogenesis. Alex found many of these "aberrants" in the hundreds of haploid plants he isolated. He and his students found that spontaneous exchanges occur between nonhomologous chromosomes and proposed these facts as evidence that modern maize is a derived alloploid. More recent studies by others support this theory.

Immersed in cytogenetic studies, Alex became interested in Rhoades' *elongate* (*el*) gene. Rhoades had found this recessive allele, when homozygous, affected the second meiotic division in such a way that microspores received the unreduced chromosome number (20). This immediately suggested a method to inexpensively "tetraplolidize" maize on a large scale. Alex crossed the *el* allele into a large array of diploid maize genotypes that included both diploid inbreds and synthetics. Crosses were pollinated by Randolph's 4*n* tester to obtain putative tetraploids. These tetraploid kernels were used to form 4*n* synthetics and 4*n* inbreds were developed by the backcross method. Six 4*n* synthetics were developed: R4*n*A [(2*n* WF9 × *el*) WF9]; R4*n*B (25, 2*n* inbreds × *el*); R4*n*C (11, 2*n* inbreds × *el*); R4*n*D (60, 2*n* line × *el* plus crosses of 4*n* ker-

nels from each lines × Syn B plus 360 kernels from Syn C); R4*n* O.P. (56, 2*n* open pollinated cultivars × *el*); R4*n*C-D (mixture of equal quantities of seed from R4*n* Syn C and R4*n* Syn D and random mated). Mass selection for increased seed-set was carried out in 4*n* Syn C, 4*n* Syn D, 4*n* Syn C-1, and 4*n* Syn O.P. and showed an increased seed set from about 50 percent to 60 percent range in five selection cycles. Additional selection for ten cycles resulted in seed-set in the 90 to 95 percent range for these synthetics. Alex's research on tetraploid maize expanded our knowledge of tetraploid qualitative genetics. The materials served as a basis for the quantitative genetic research by Dr. John Dudley, also of the University of Illinois.

HIGH OIL MAIZE

Alex's most consequential research contribution has been to the improvement of nutritional properties of maize. The Department of Agronomy at the University of Illinois has had a tradition of breeding for enhanced levels of protein and oil in corn, dating back into the nineteenth century. In the 1920s through the 1940s, substantial effort was devoted to breeding for higher levels of both protein and oil. These efforts largely failed, not because higher levels of oil and protein were not reached in commercial hybrid candidates, but because of their inferior performance. The "new" idea that corn grain could be improved nutritionally was intriguing. Failure to produce commercially useful high-oil inbreds, stemmed back to an inferior parent population (i.e., the Illinois High Oil strain). Alex concluded that a wide based population should be recurrently selected for oil content that would serve as source of commercial inbreds. So in 1956, he began selection for increased oil in a 56-cultivar open-pollinated population. The program consisted of cycles of selfing, analysis, and recombination of the highest oil selections. This process was carried out for six cycles with budgets of no more than $500 per year!

Extension activities can be a useful effort for researchers. Alex spoke to a group of farmers and businessmen about his high oil research, and complained bitterly about the cumbersome and expensive analytical scheme. Why not analyze single kernels nondestructively and get a single cycle of selection per year instead of the normal two years? A member of the audience, Dr. Stan Watson, came to Alex after the session and suggested that an instrument (wide-line nuclear magnetic resonance-NMR) that Corn Products Company was using at its Argo, Illinois, plant to analyze for water in starch might, just might, do the job. There was a concern that single kernel analysis was beyond the instrument's ability.

Alex provided samples and the exploratory run on large samples turned out to be practical. Two months later, Stan and Tom Conway reported single kernels could be accurately analyzed in a minute or two! That time was soon reduced to 30 seconds and ultimately to 2 seconds. Selection for oil immediately became an inexpensive, effective scheme with the development and application of NMR. It permitted inexpensive, precise, non-destructive analysis of oil levels in bulk samples and individual kernels. Evaluation of selection progress over 28 cycles of single kernel selection showed oil concentration increased from 4.5 percent to 22 percent. This same level of increase took about 90 generations in the classical Illinois selection experiment which uses bulk samples. Alex also developed several other high-oil maize synthetics that have received commercial interest. He used these materials to develop high-oil single-cross hybrids to promote commercialization of high-oil corn. In the early 1970s, Alex expanded into research on fatty acids and later on Vitamin E. He and Charles Poneleit demonstrated single gene control of oleic to linoleic transformation in 1965. He was able to isolate the recessive *ln1* gene that controls conversion of oleic to linoleic fatty acids in maize. He and several of his students evaluated the genetic variation for alpha and gamma tocopherol in a maize synthetic and isolated two strains contrasting in high alpha and high in gamma tocopherol.

Although the University of Illinois has a long history of research on high oil maize, most of the research never was used in the marketplace until about 1990. Alex's enthusiasm, perseverance, and intellect convinced administrators of the value of high-oil corn in the marketplace. As a result of several discussions with administrators and several commercial companies the university signed the first joint research and market development agreement on high-oil maize in 1990 with Pfister-DuPont. This agreement had two components, one involved research on high-oil corn, and the other for Pfister-DuPont to develop a marketing system for the product. Approximately 1.25 million acres of high-oil maize was produced in 2000. The success of this program is due in large part to Alex's application of "sound science," enthusiasm, and a conviction that high-oil corn had commercial value. This is a unique trait for a plant breeder.

HONORS

Alex has received several honors during his career of teaching and research. Among them are: Phi Kappa Phi, Crop Science Research Award, Fellow American Society of Agronomy and Crops Science Society of America (1970), the first Paul A. Funk award in research from the

College of Agriculture, University of Illinois (1971), Foreign member, Soviet Academy of Agriculture Sciences (1970), Distinguished Service Award for contributions to maize program, La Molina, Peru (1978), and Honorary member Association of Genetic Societies of Yugoslavia (1981).

Alex officially retired from the university in 1989 and has remained a Visiting Professor in corn breeding. He comes to the office every day and still has the same zeal for high-oil corn that he had in 1956. Alex's long career in corn breeding, genetics, and teaching stimulated his enthusiasm to develop new and challenging ideas that had the potential to help mankind, but also to add to our knowledge of the science of plant breeding. His intellect stimulated new ideas to his colleagues, especially the undergraduate and graduate students he influenced to obtain advanced degrees. Some people are born to lead, and Alex has definitely been a leader in many agricultural endeavors. During one's lifetime, most scientists do not have an opportunity to be associated with a person of intellect, enthusiasm, compassion, excellent work ethic, and an all-around good fellow. People who have had the opportunity to be associated with Alex are grateful for his effect on their lives. Some maize breeders are "out-front" in terms of their research programs; Alex's program over the years has been in this category. Alex is an all-around good and delightful fellow. Alex and Betty, after 60 years of marriage, continue to live in Urbana and, as always, enjoy visits from his former graduate students.

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2

Estimating and Interpreting Heritability for Plant Breeding: An Update

James B. Holland
U.S. Department of Agriculture-Agriculture Research Service
Plant Science Research Unit, Department of Crop Science, Box 7620
North Carolina State University
Raleigh, North Carolina 27695-7620

Wyman E. Nyquist
Department of Agronomy
Purdue University
West Lafayette, Indiana 47907-1150

Cuauhtemoc T. Cervantes-Martínez
Universidad Autónoma Chapingo
Carretera México-Texcoco km 38.5
Chapingo, 56230 Mexico

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I. THE MEANING OF HERITABILITY

Heritability was originally defined by Lush as the proportion of phenotypic variance among individuals in a population that is due to heritable genetic effects (Nyquist 1991, p. 248). This definition is now termed "heritability in the narrow sense" and is designated h^2 (Nyquist 1991, pp. 248 and 250). Variations on this idea are often also referred to as heritability of one kind or another, such as heritability of family means (h_f^2), the proportion of the phenotypic variance of family means that is due to family genetic effects, and "heritability in the broad sense" (H), the proportion of phenotypic variance that is due to all genetic effects (Nyquist 1991, pp. 239, 312–313; Falconer and Mackay 1996, pp. 123, 232). Whereas Lush's definition was based on his experience as an animal breeder, in which the basic unit of observation and selection is nearly always the individual animal, plant breeders deal with a great diversity of observational units and mating systems. This complicates both the procedures for estimating heritability and the meaning of heritability itself. As Nyquist (1991, p. 238) observed,

> The plant kingdom presents a great diversity of natural modes of reproduction, varying from reproduction without sexuality (asexual) to reproduction by sexual means, cross-fertilization (allogamous), or self-fertilization (autogamous). Mixtures of these main modes of reproduction also exist. With self-fertilization, inbred populations exist and many unique difficulties arise. . . . Considering the diverse array of plant populations which can arise, many different estimators have been labeled heritability, and sometimes it is not clear what the exact nature of the estimator is or what is being estimated.

Hanson (1963) urged plant breeders to unify their concept of heritability as "the fraction of the selection differential expected to be gained when selection is practiced on a defined reference unit." Therefore, throughout this review, various heritability estimators are evaluated in terms of response to selection. Heritability has meaning only in reference to defined selection units and response units, and these can vary among breeding schemes.

Nyquist (1991) critically reviewed the substantial literature on estimating heritability and predicting response to selection in plant populations, and he clarified many of the issues that affect heritability in plants. Little can be added to his review of the topic except to address some newer methods of heritability estimation that have developed and been used in the last ten years. These newer methods include mixed models analysis of unbalanced data, pedigree analysis, and use of DNA markers to estimate genetic components of variation. Mixed models analysis in general terms has been reviewed thoroughly by McLean et al. (1991), Searle et al. (1992), and Littell et al. (1996), but the use of mixed models analysis for plant breeding applications has not been reviewed. Use of pedigree information to estimate genetic variance components in plant breeding was reviewed by Xu (2003). Ritland (2000) reviewed the use of DNA markers for estimating heritability and other population genetic parameters. Marker-based methods will have the greatest impact on studies of natural populations with unknown pedigree relationships and perhaps on domesticated species whose breeding systems are not easily controlled. Recently, these methods have become practical in part because of advances in computing power that have made powerful but previously computationally unmanageable estimating procedures almost routine.

This chapter focuses on placing mixed models analysis procedures in the context of typical plant breeding experiments and provides examples of computing code that can be used to obtain heritability estimates and their standard errors with the commonly used SAS system (see

Appendices 1 to 4). To place the estimation procedures in context, the interpretation of heritability estimators obtained from different mating schemes and generations is discussed.

II. RESPONSE TO SELECTION

A. Applications of Heritability Estimates

The main purpose of estimating heritability and the genetic parameters that compose the heritability estimate is to compare the expected gains from selection based on alternative selection strategies. One can use heritability estimates to predict gain from selection, for example, based on single, unreplicated plot values, and compare this to gain from selection expected if materials are replicated within and across macroenvironments (Hoi et al. 1999). Heritability estimates are useful for comparing the gain from selection under different experimental designs, and this information—combined with information about the relative costs of additional replications within each macroenvironment, additional years of evaluations, and additional locations for evaluations—can be used to design optimal breeding strategies (Milligan et al. 1990). Where genotype-by-environment (GE) interactions cause significant rank changes among families evaluated in different environments, heritability estimates corresponding to response to selection based on means over all environments can be compared with heritability based on means within subsets of local environments to determine the optimal selection strategy (Atlin et al. 2000). Similarly, heritabilities based on different family structures derived from the same base population can be compared to determine which family structure is best for maximizing genetic gain over units of time (Burton and Carver 1993). Heritability may vary among populations, thus, heritability estimates from different populations can be useful for choosing appropriate base populations in which selection will be most effective (Goodman 1965). Because heritabilities vary among traits within a population, heritability estimates of different traits, in addition to genetic correlation estimates among the traits, can be used to identify indirect selection schemes that may be more effective than direct selection schemes (Diz and Schank 1995; Banziger and Lafitte 1997; Rebetzke et al. 2002).

B. Theoretical Basis of Response to Selection

An understanding of the response to selection is needed in order to apply Hanson's (1963) definition of heritability as the fraction of the selection differential expected to be gained when selection is practiced

on a defined selection unit. One way to conceive of the response to selection is as a response or change in the mean of progeny phenotypic values due to a change in the mean value of selection units brought about by selection. The selection differential referred to by Hanson (1963) is the difference between the mean of selected selection units and the overall mean of the initial population. We introduce the notation $S = \mu_s - \mu_0$, where S is the selection differential, μ_s is the mean of the selected selection units, and μ_0 is the overall initial population mean. From elementary statistics, the expected response in any variable, Y, due to a change in a related variable, X, is given as $\Delta Y = b(\Delta X)$, where b is the coefficient of regression of Y on X, ΔY is the change in Y, and ΔX is the change in X (Steel et al. 1997). This general formula can be applied to response to selection by considering X as the variable representing selection unit phenotypic values, and Y as the variable representing phenotypic values of random members of the response units. Thus, ΔX is the selection differential, $\mu_s - \mu_0$, and ΔY is R, the expected response to selection: $\mu_1 - \mu_0$, where μ_1 is the mean (or expected value) of the response unit phenotypes in the first cycle resulting from selection within the initial population. Summarizing, $R = Sb_{YX}$. Therefore, the expected proportion of the selection differential to be achieved as a gain from selection, or heritability, is $R/S = h^2 = b_{YX}$.

The generality of this concept of heritability is very useful for plant breeding, because it is applicable to all plant breeding situations, including selection within randomly-mating cross-pollinated populations, as well as selection among self-fertilized lines (with or without subsequent random-mating), selection among clones, and selection among testcross progenies in hybrid crops. The generality of this concept is also a weakness, because it can have many different genetical meanings, depending on the circumstances and type of selection to which it is applied. We agree with Hanson (1963) and Nyquist (1991, p. 313) that the only remedy for this situation and the possible confusion arising from it is that researchers clearly indicate the basis of their heritability estimates—what is the defined reference unit for selection, and to what method of selection does it refer? Furthermore, we suggest that the reference unit for measuring response also be indicated along with heritability estimates, as this also impacts the interpretation of heritability.

The application of the heritability formula to specific breeding situations is discussed in Section VIII. To specify an appropriate heritability function for any breeding situation, the coefficient of regression of the value of the response unit on the value of the selection unit is required. Mathematically, the regression coefficient is the covariance of the phenotypes of selection and response units divided by the selection unit

phenotypic variance (Nyquist 1991, p. 249). Specifying the response unit phenotypic value as Y, the phenotypic value of the selection unit related to the response unit through its female parent as X_f, and the phenotypic value of the selection unit related to the response unit through its male parent as X_m, we obtain:

$$b_{YXf} = \mathrm{Cov}(X_f, Y)/\mathrm{Var}(X_f),$$
$$b_{YXm} = \mathrm{Cov}(X_m, Y)/\mathrm{Var}(X_m).$$

If selection is practiced on selection units related to both female and male parents, the total expected response to selection is the sum of the two expected responses (Nyquist 1991, p. 272):

$$R = b_{YXf}S_f + b_{YXm}S_m,$$

where S_f and S_m are the selection differentials on female and male sides of the pedigree, respectively.

As shown by Nyquist (1991, p. 272), if selection units related to female and male parents have the same expected value and population variance (i.e., no sexual dimorphism), then $b_{YXf} = b_{YXm}$, $\mathrm{S}_f = \mathrm{S}_m = \mathrm{S}$, and the total response to selection is:

$$R = [2\mathrm{Cov}(X_f, Y)/\mathrm{Var}(X_f)]S = [\mathrm{Cov}(X, Y)/\mathrm{Var}(X)]S$$

where $\mathrm{Cov}(X, Y) = 2\mathrm{Cov}(X_f, Y) = \mathrm{Cov}(X_f, Y) + \mathrm{Cov}(X_m, Y)$. Therefore, the heritability equation that refers to response to selection when selection is practiced on both male and female sides of a pedigree is:

$$h^2 = \mathrm{Cov}(X, Y)/\mathrm{Var}(X). \quad [1]$$

To apply this formula to a specific breeding method, the selection and response units must be specified because their relationship determines the numerator of the equation. For example, response units can be related to the selection units as clonal (asexual) offspring, first-generation progeny of random-matings of the selection units, progeny resulting from self-fertilization of the selection units, or they can be indirectly related to the selected units, such as offspring of relatives of the parents (called "recombination units" by Hallauer and Miranda [1988, p. 170]), rather than direct offspring of the selection units actually evaluated. Each of these situations results in unique covariances between selection and response units. Nyquist (1991, pp. 272–277) presented the selection

pedigree diagrams and covariances between selection units and response units for many commonly used selection schemes.

Specification of the selection unit is also necessary because the denominator of the heritability equation is the variance among selection unit phenotypic values. The variance among the selection units depends on whether individuals or families are evaluated. If families are evaluated, the experimental design used to estimate family means, such as the number of replications and environments in which selection units are evaluated, will impact the variance of selection units, which are family mean phenotypic values in this case.

C. Reference Populations, Assumptions, and Model Definitions

Heritability estimates must refer to a defined population of genotypes (Comstock and Moll 1963; Dudley and Moll 1969). Reference populations are generally assumed to be random-mating populations in Hardy-Weinberg and gametic phase equilibria, although for self-pollinating crops, sometimes the reference population is taken to be completely inbred genotypes derived from a Hardy-Weinberg and gametic phase equilibria reference population by inbreeding without selection. Diploid inheritance is assumed throughout this chapter. To estimate the heritability of the reference population, individuals or families should be sampled at random for measurement. Also, heritability estimates must refer to a specified population of environments (Comstock and Moll 1963; Dudley and Moll 1969; Nyquist 1991, pp. 239–243). Defining the reference population of environments is often more difficult than defining the reference population of genotypes, and reference populations of environments are rarely explicitly defined by researchers. Generally, however, a reference population of environments is defined geographically. For example, public plant breeders often are assigned to develop improved cultivars for a specific state or province of a country, in which case the reference set of populations that is of interest to such a breeder is their state. In contrast, international agricultural research centers are often explicitly concerned with developing germplasm that is broadly adapted to a loosely-defined ecological zone throughout the world. Their reference set of environments may include, for example, all subtropical zones throughout the world. Having defined the target set of environments, the researcher should attempt to sample test environments at random from this population. This is also difficult, because evaluations are often performed on experimental research stations, limiting the plant

breeder's ability to sample target production fields. Similarly, it is rarely feasible for researchers to evaluate material for more than a small number of years, thus limiting the sample of potential climatic variations under which the germplasm of interest can be evaluated. These problems are close to insurmountable, although recent research focused on better defining target production environments may help researchers to better sample the reference population of environments (Gauch and Zobel 1997). We can only emphasize that researchers attempt to sample a range of environments that represent the target production environments for the germplasm, and that at a minimum, this should include a sample of several locations and several years.

Defining and adequately sampling the reference population of genotypes and environments is important for estimating heritability because this provides the context to which the heritability estimate refers. The genotypic values of the individuals in the population may depend on the environment or the conditions under which the experiment was performed (Comstock and Moll, 1963). For example, a drought-tolerant genotype of wheat (*Triticum aestivum*) will most likely be more vigorous under drought conditions compared with a normal genotype, whereas under higher moisture conditions, the normal genotype may be superior. Thus, when the experiment is performed in only a single environment, the estimated genotypic values cannot necessarily be used to make inferences beyond the original environment. The scope of inference of any experiment is an important issue that is often overlooked, but should be as well-defined as possible to avoid any confusion regarding interpretation of the results. The genotypic values refer specifically to the conditions under which the experiment was performed, and it cannot be assumed that the values would be the same in another reference set of environments. Therefore, genetic variance depends on the reference environments as well as the genotypes evaluated. Furthermore, the genetic variance component estimated in the experiment refers only to the population which was sampled for the experiment.

A clear definition of the population being sampled is also important for the estimate of genetic variance to have any meaning. One population of any species will not necessarily have the same amount of genetic variation as another population even from the same species, which can be due to many factors, such as selection, mating behavior, random drift, migration, and mutation. Thus, for example, there is no reason to expect that the genotypic variance estimated for a particular trait for one population of alfalfa (*Medicago sativa*) will have any relevance to another population of alfalfa. Furthermore, the variation observed for any one trait in any population may not hold for another trait in the same

population. For example, a maize (*Zea mays*) population that has been under selection for resistance to a particular disease may eventually become fixed for the resistant phenotype, but it may still have genetic variation for other traits, such as yield or flowering time.

Heritability estimates must be made from data collected in multiple locations and during multiple years representing the target set of environments or else the estimates will be biased unless genotype-by-environment interaction is negligible, which is rarely true for quantitative characters of agronomic importance (Nyquist 1991, pp. 239 and 312). This bias arises because the genotype-by-environment interaction variance is confounded with the genotypic variance component if the genotypic variance component is estimated from a single environment or from a sample of multiple locations or from a sample of multiple years only (Nyquist 1991, pp. 288–289). Another bias can arise if researchers ignore the cross-classified nature of years and locations during the statistical analysis of their experiment. For example, if families are evaluated at three locations across three years, the environments can be classified by year and location, leading to variance components estimates for years, locations, year-by-location interaction, families, and family-by-year, family-by-location, and family-by-year-by-location interactions. Or the analysis can proceed by classifying each year and location combination as one of nine environments, leading to variance component estimates of environments, families, and family-by-environment interaction. The latter choice leads to a simpler statistical model, but also creates bias in the resulting estimate of heritability, because the estimate of family-by-environment interaction variance is smaller than the sum of family-by-year, family-by-location, and family-by-year-by-location variances (Comstock and Moll 1963; Nyquist 1991, pp. 289–290). Throughout this chapter, the model that ignores the cross-classification of families and environments is used only to simplify the presentation of mathematical formulas. This should be avoided if possible in analysis of cross-classified data sets, and formulas for estimating heritability are provided with both approaches to handling environmental classification (Table 2.1, pp. 86-101) at the end of the chapter.

Having defined the reference populations of genotypes and environments, we can define the effects of the statistical model that will be used to estimate heritability. First, assume that the genotypes are sampled at random from the reference population, meaning that the genotypic effects (G_j's) are independent with expected value of zero and a common variance, σ^2_G. Assume also that the environments are sampled at random from the reference population of environments. Further, distinguish between the effects of macroenvironments (which generally refer to a

combination of a geographical location and unique weather pattern, that is, a single year and location combination) and the effects of microenvironments (which refer to environmental variations within macroenvironments). Therefore, we introduce a term for the effect of macroenvironments, E_i, and a term for the effect of microenvironments, ε'_{ijk}. Each is distributed around a mean of zero with variance σ^2_E for macroenvironments and $\sigma^2_{\varepsilon'}$ for microenvironments. We also introduce a term $R_{(i)k}$ for the mean effect of replications (complete blocks) within environments. This leads to a common form of the linear model for data observed on genotypes replicated in multiple blocks within multiple environments on a plot basis:

$$Y_{ijk} = \mu + E_i + R_{(i)k} + G_j + GE_{ij} + \varepsilon'_{ijk}. \quad [2]$$

This type of model assumes that genotypes can be replicated; in Section V.A we demonstrate how to generalize the model to nonclonal material. The model also assumes that only one phenotypic value is recorded on each plot. If data are taken on individual plants within each plot, the error variance can be partitioned into variance due to random plot effects and within-plot variance. If not, then plot effects and plant-within-plot effects are confounded in the residual effect, which is denoted as ε'_{ijk} in Equation [2], to maintain consistency with Nyquist (1991, p. 258). See Nyquist (1991, pp. 252–259) for details on the definition of residual variances in this model and more complex statistical models. Other than the overall mean effect, μ, all effects in this model are random.

If selection is based on the mean phenotypic value of genotypes evaluated in multiple replications and macroenvironments (r replications within each of e macroenvironments), then the values of interest are mean values of genotypes:

$$\begin{aligned}\overline{X}_{.j.} &= \mu + \frac{\sum_{i=1}^{e} E_i}{e} + \frac{\sum_{i=1}^{e}\sum_{k=1}^{r} R_{(i)k}}{er} + G_j + \frac{\sum_{i=1}^{e} GE_{ij}}{e} + \frac{\sum_{i=1}^{e}\sum_{k=1}^{r} \varepsilon'_{ijk}}{er}. \\ &= \mu + \overline{E}.. + \overline{R}.. + G_j + \overline{GE}.. + \overline{\varepsilon}'_{.j.} \end{aligned} \quad [3]$$

Similarly, if the genotypes of the next base population are evaluated in replicated, multiple environment trials, their mean phenotypic values ($\overline{Y}_{.j.}$) are the response unit values. We assume that the set of environments in which selection units are evaluated and the set of environ-