

Quantitative Genetics WITH SPECIAL REFERENCE TO Plant & Animal Breeding RALPH E. COMSTOCK



То L. M. Winters, Gertrude Cox, and H. F. "Cotton" Robinson

Ralph E. Comstock, professor emeritus, Department of Genetics, and Biological Sciences Department, University of Minnesota, St. Paul, received his BS, MS, and PhD degrees from the College of Agriculture, Forestry, and Home Economics, University of Minnesota, St. Paul. Dr. Comstock spent his professional career doing research in and teaching animal breeding, applied statistics, and quantitative genetics. He was also a statistical consultant to researchers in agricultural science. Dr. Comstock has published extensively in scientific journals such as Journal of Animal Science, Agronomy Journal, Crop Science, Genetics, Theoretical and Applied Genetics, and Bionetrics and in Proceedings of various national and international conferences.

Quantitative Genetics with Special Reference to Plant and Animal Breeding

First Indian Reprint: 2014

Authorized reprint by Wiley India Pvt. Ltd., 4435-36/7, Ansari Road, Daryaganj, New Delhi – 110002.

Published by John Wiley & Sons, Inc. All rights reserved.

No part of this book, including interior design, cover design, and icons, may be reproduced or transmitted in any form except with the permission John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030.

Limit of Liability/ Disclaimer of Warranty: The publisher and the author make no representations or warranties with respect to the accuracy or completeness of the contents of this work and specifically disclaim all warranties, including without limitation warranties of fitness for a particular purpose. No warranty may be created or extended by sales or promotional materials. The advice and strategies contained herein may not be suitable for every situation. This work is sold with the understanding that the publisher is not engaged in rendering legal, accounting, or other professional services. If professional assistance is required, the services of a competent professional person should be sought. Neither the publisher nor the author shall be liable for damages arising here from. The fact that an organization or Website is referred to in this work as a citation and/or a potential source of further information does not mean that the author or the publisher endorses the information the organization or Website may provide or recommendations it may make. Further, readers should be aware that Internet Websites listed in this work may have changed or disappeared between when this work was written and when it is read.

TRADEMARKS: Wiley, the Wiley logo, and related trade dress are trademarks or registered trademarks of John Wiley & Sons, Inc. and/or its affiliates, in the United States and other countries, and may not be used without written permission. All other trademarks are the property of their respective owners. John Wiley & Sons Inc., is not associated with any product or vendor mentioned in this book.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Copyright © 1996 by Iowa State University Press.

This edition is authorized for sale in the Indian Sub-continent only.

Printed at: Sanat Printers, Kundli, Haryana

ISBN: 978-81-265-4529-2



Contents

Preface, xiii

Introduction, 3

- 1.1. Frame of reference, 3
- 1.2. Quantitative genetics, 4
- 1.4. Total value and value traits, 5
- 1.5. The critical role of theory, 6
- 1.6. General purposes, 7
- 1.7. Content of Appendix 1, 7

Genetic Background, 9

- 2.2. Populations, 11 2.2.1. Random mating, 12 2.2.2. Migration, 13 2.3. Allele frequency, 13
- 2.4.1. Single-locus genotypes, 16
- 2.4.3. Two-locus genotypes, 18

- 2.8.1. Selection, 24
- 2.6.2. Mutations, 28
- arose, 29

1.3. Breeding, eugenics, and selection, 5 1.8. Some aspects of book organization, 7 1.8.1. Symbol system for variances and covariances, 8

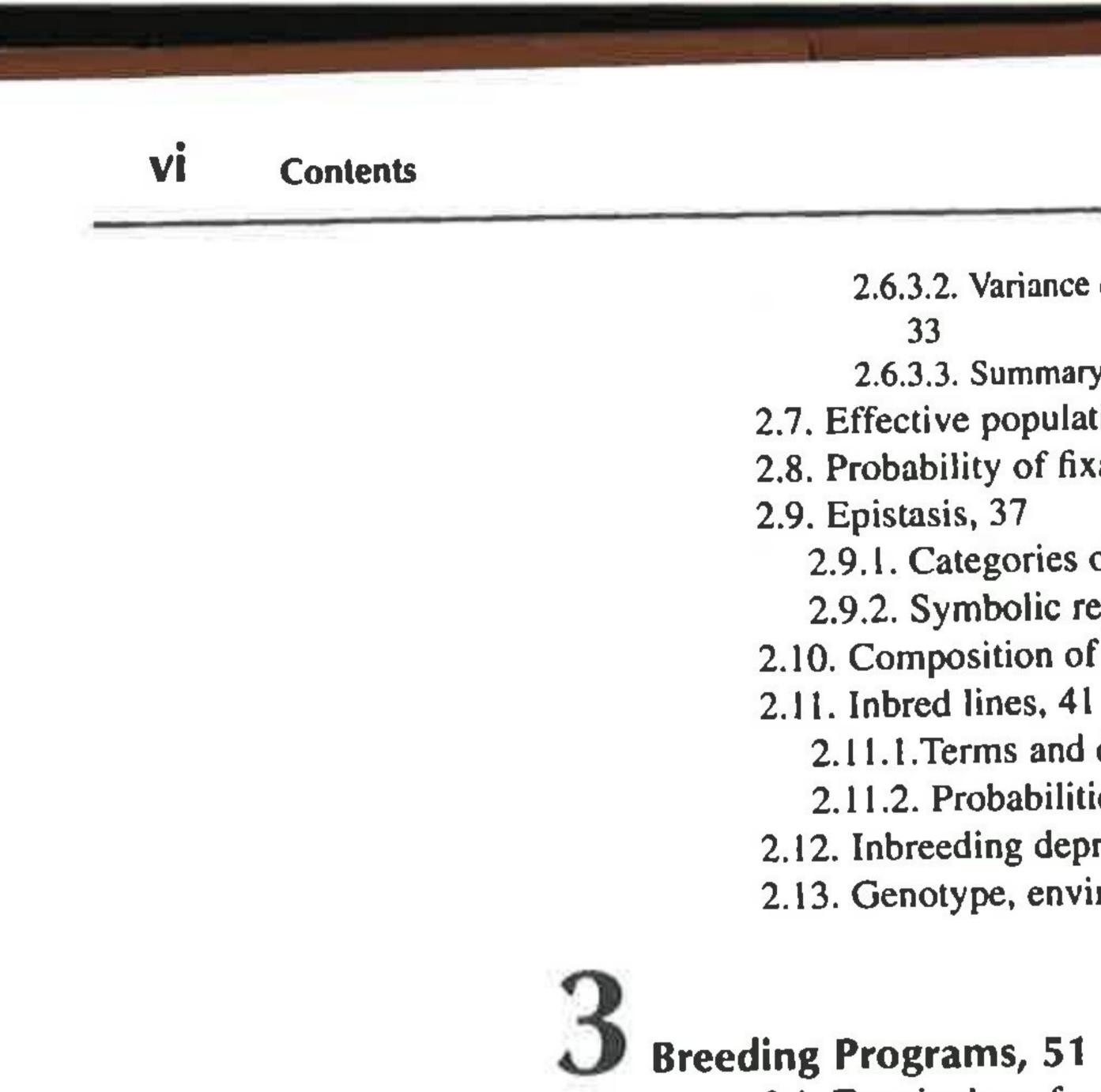
2.1. Genetic model—the assumptions, 9 2.1.1. Summary relative to models and assumptions employed, 11

2.4. Genotype frequencies in random mating diploid populations, 16 2.4.2. Probabilities vs. frequencies, 17 2.5. Inbreeding and its effects on expected frequencies of genotypes,

2.5.1. Computing the coefficient of inbreeding, 22 2.6. Temporal change in allele frequencies, 23 2.6.1.1. Alternative symbolism, 27 2.6.2.1. Deleterious mutations, 28 2.6.2.2. Mutant alleles superior to the ones from which they

2.6.3. Chance and random drift, 29 2.6.3.1. Variance from the sampling of individuals, $\sigma^2(d_c)$, 31





33

- 59

- **Responses to Artificial Selection, 65**
 - - sions, 66

Mass Selection, 77

2.6.3.2. Variance due to the random nature of mutation, $\sigma^2(d_m)$, 2.6.3.3. Summary, 34 2.7. Effective population size, 34 2.8. Probability of fixation, 34 2.9.1. Categories of epistasis, 39 2.9.2. Symbolic representation of genotypic value, 39 2.10. Composition of variance among genotypes, 40 2.11.1. Terms and definitions, 41 2.11.2. Probabilities of single locus genotypes, 42 2.12. Inbreeding depression and heterosis, 42 2.13. Genotype, environment, and phenotype, 46

3.1. Terminology for description, 52 3.2. The breeder's goal-ideal genotypes, 54 3.3. Recurrent selection, 55 3.4. The logic of recurrent selection, 56 3.5. Complete dominance and the utility of systems for exact reproduction of genotypes, 58 3.6. Special issues relating to potential success via recurrent selection,

3.6.1. Overdominance, 60 3.6.2. The selection criterion, 61 3.6.3. Population size, 62 3.6.4. Epistasis, 62 3.6.5. Change in the values of genotypes, 62

Comparisons of Breeding Procedures, 63

5.1. Change in average value of genotypes—a preliminary form, 65 5.2. Primary assumptions in development of more analytic expres-

5.3. The composition of value of genotype, 67

5.4. The derivative of Ÿ with respect to q_i, 68

5.5. The expected change in allele frequency, 69

5.6. The expected change in average value of genotype, 72

5.7. Genotypic superiority of selections, 73

5.8. Summary of assumptions, 74

6.1. Response expectations, linkage equilibrium assumed, 77 6.2. Response expectations given linkage disequilibrium, 79 6.3. Information and insights provided by response expectations, 82 6.3.1. Effects of linkage disequilibrium, 82 6.3.2. Rates of response, 83 6.3.2.1. Allele frequency changes, 83

6.3.2.2. Genotypic mean of the selection criterion, 87 6.3.3. Total response possible, 89 6.3.3.1. Infinite effective population size, 89 6.3.3.2. Finite effective population size, 91 6.3.4. Correlated responses in the absence of linkage disequilibrium, 93 6.4. Reminders concerning assumptions, 95

- tion to $\Delta \ddot{\mathbf{Y}}_{c}$, 97 7.3. The no epistasis assumption, 104 7.3.1. Simple epistasis, 105
 - 7.3.2. Multiple-peak epistasis, 106

Progeny Test and Family Systems of Recurrent Selection, 109

- inbred, 115 8.2. Family systems, 117 8.2.1. Half-sib families, 119 on units, 119 ent individuals, 121 8.2.2. Full-sib families, 122 on units, 122 ent individuals, 123 8.2.3. S_n families, 123 families, 125

 - among families, 125
- 8.3. Summary and comments, 126

Selection for Performance in Crossbreds, 129

- 9.1. Relevance of overdominance, 130 9.3. Reciprocal recurrent selection (RRS), 132 9.3.1.1. Overdominance loci, 133 9.3.1.2. Complete dominance loci, 134 9.3.1.3. Partial dominance loci, 135 9.3.3. RRS using pure line testers, 137
- 9.4. Selection based on performance in S populations (RSP), 138

Mass Selection—Assumptions and Validity of Theory, 97 7.1. The assumption that $\sum_{i}(\Delta q_{i})(\partial \dot{Y}_{c}/\partial q_{i})$ is an adequate approxima-

7.2. The assumption that the regression of \hat{q} on \hat{X} is linear, 98

8.1. Progeny test selection systems, 109 8.1.1. Justification for using $E(\hat{y})$ in derivation of $\sigma(\hat{q}_i, \hat{y})$, 111 8.1.2. Response expectations when selection unit individuals are not inbred (no assumption concerning linkage equilibrium), [1] 8.1.3. Response expectations when selection unit individuals are

8.2.1.1. Identity or partial identity between selection and criteri-

8.2.1.2. Selection units and criterion units composed of differ-

8.2.2.1. Identity or partial identity between selection and criteri-

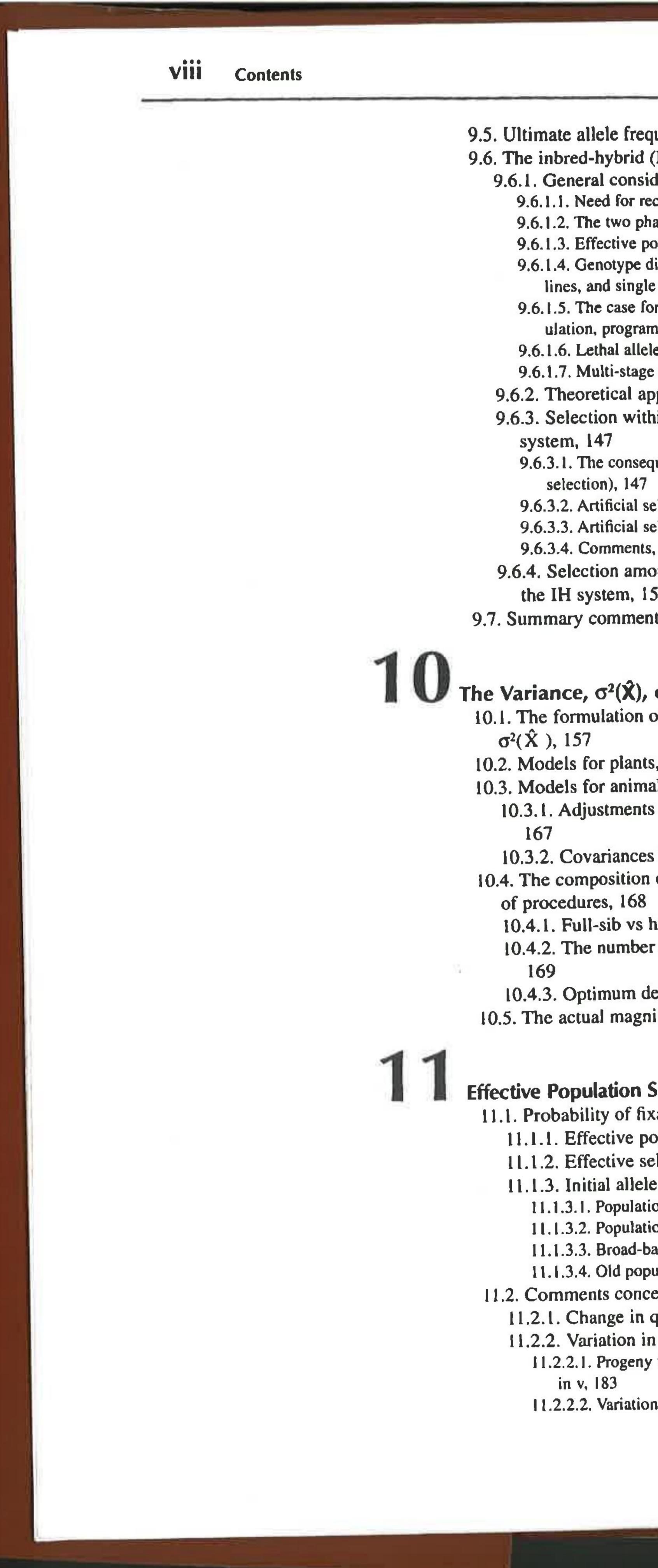
8.2.2.2. Selection units and criterion units composed of differ-

8.2.4. Selection among individuals within families, 124 8.2.4.1. Intrafamily selection in the absence of selection among

8.2.4.2. Intrafamily selection as a supplement to selection

9.2. Selection for specific combining ability (RSSC), 131 9.3.1. Allele frequency changes promoted by RRS, 133 9.3.2. Full-sib reciprocal recurrent selection, 135





9.5. Ultimate allele frequencies and genotypes, 139 9.6. The inbred-hybrid (IH) system, 142 9.6.1. General considerations, 143 9.6.1.1. Need for recurrent selection, 143 9.6.1.2. The two phases of the IH system, 144 9.6.1.3. Effective population size, 144 9.6.1.4. Genotype distributions in the source population, pure lines, and single crosses, 145 9.6.1.5. The case for two-population, as opposed to single-population, programs, 145 9.6.1.6. Lethal alleles and natural selection, 145 9.6.1.7. Multi-stage selection, 145 9.6.2. Theoretical approach, 146 9.6.3. Selection within and among lines—the first phase of the IH 9.6.3.1. The consequence of eliminating lethal alleles (natural selection), 147 9.6.3.2. Artificial selection among lines, 150 9.6.3.3. Artificial selection within lines, 152 9.6.3.4. Comments, 153

9.6.4. Selection among line crosses—the cultivar search phase of the IH system, 154

9.7. Summary comments, 155

The Variance, $\sigma^2(\hat{\mathbf{X}})$, of the Selection Criterion, 157 10.1. The formulation of statements concerning the composition of

10.2. Models for plants, 158

10.3. Models for animals, 163

10.3.1. Adjustments for tangible sources of non-genetic variation,

10.3.2. Covariances between effects, 167

10.4. The composition of $\sigma^2(\hat{X})$ and comparisons

10.4.1. Full-sib vs half-sib reciprocal recurrent selection, 168 10.4.2. The number of random parents in progeny test selection,

10.4.3. Optimum design of field trial comparisons, 170 10.5. The actual magnitudes of variances, 171

Effective Population Size in Recurrent Selection Programs, 173

11.1. Probability of fixation, P_f, 174

11.1.1. Effective population size, 175

11.1.2. Effective selective values in artificial selection, 176

11.1.3. Initial allele frequency (q_o), 178

11.1.3.1. Populations from the cross of two gure lines, 178

11.1.3.2. Populations formed by intercrossing n lines, 178

11.1.3.3. Broad-based foundation populations, 179

11.1.3.4. Old populations, 179

11.2. Comments concerning non-validity of assumptions, 180

11.2.1. Change in q when $-1.0 \le a_x \le 1.0$, 181 11.2.2. Variation in s' not from change in q, 183

11.2.2.1. Progeny test selection-variation in s' from variation in v, 183

11.2.2.2. Variation in s' from variation in test environments, 184

- 11.2.3. Overdominance, 187
- 11.2.4. Independent assortment, 188
- 11.2.6. Summary, 189
- 11.3. E($\Delta \ddot{Y}$) as a function of N_e, 190
 - 11.3.1. General formulas, 198

 - 201

Choice of the Selection Criterion, 203 12.1. Expected change per cycle in genotype values, 203 12.2. The Smith-Hazel selection index (criterion) that maximizes genetic improvement per cycle, 205 12.3. Definition of total value, 207 12.4. The selection criterion that maximizes the total genetic improvement that can be made via recurrent selection, 209 12.5. The decrease in $E(\Delta \ddot{Y}_w)$ associated with using total value as the selection criterion, 212 12.5.1. When $\sigma_{mm} = AG_{mm}$ and $\sigma_{mm'} = AG_{mm'}$ for all values of m

- and m', 212
- 12.5.2. Other situations, 214
- 12.7. Summary and practical problems, 219

/ The Design of Breeding Programs, 223

- 13.1. Introduction, 223
- rent selection programs, 224
- 13.2.1. Primary criteria, 224
- 13.2.2. Secondary criteria, 224
- 13.2.3. Procedures, 225
- 13.2.3.1. Long term programs, 226
- 13.2.3.2. Short term programs, 228
- 13.3. Foundation populations, 228

Comparison of Selection Systems, 231

- 14.1. Long term programs, 232

 - 14.1.1. An example, 233
 - 14.1.2. Comparison of programs, 236
 - 14.1.3. Discussion, 243
- 14.2. Short term, single population programs, 246
- 14.2.1. Impact of effective population size, 250
- 14.2.2. Variations of parameter magnitudes, 258

- 14.3.1.1. When there is no dominance (A = 0), 263
- (A > 0), 264
- 14.3.2. RSP vs. RRS programs when a \leq 1.0, 268 14.4. Discussion and summary, 269

IX

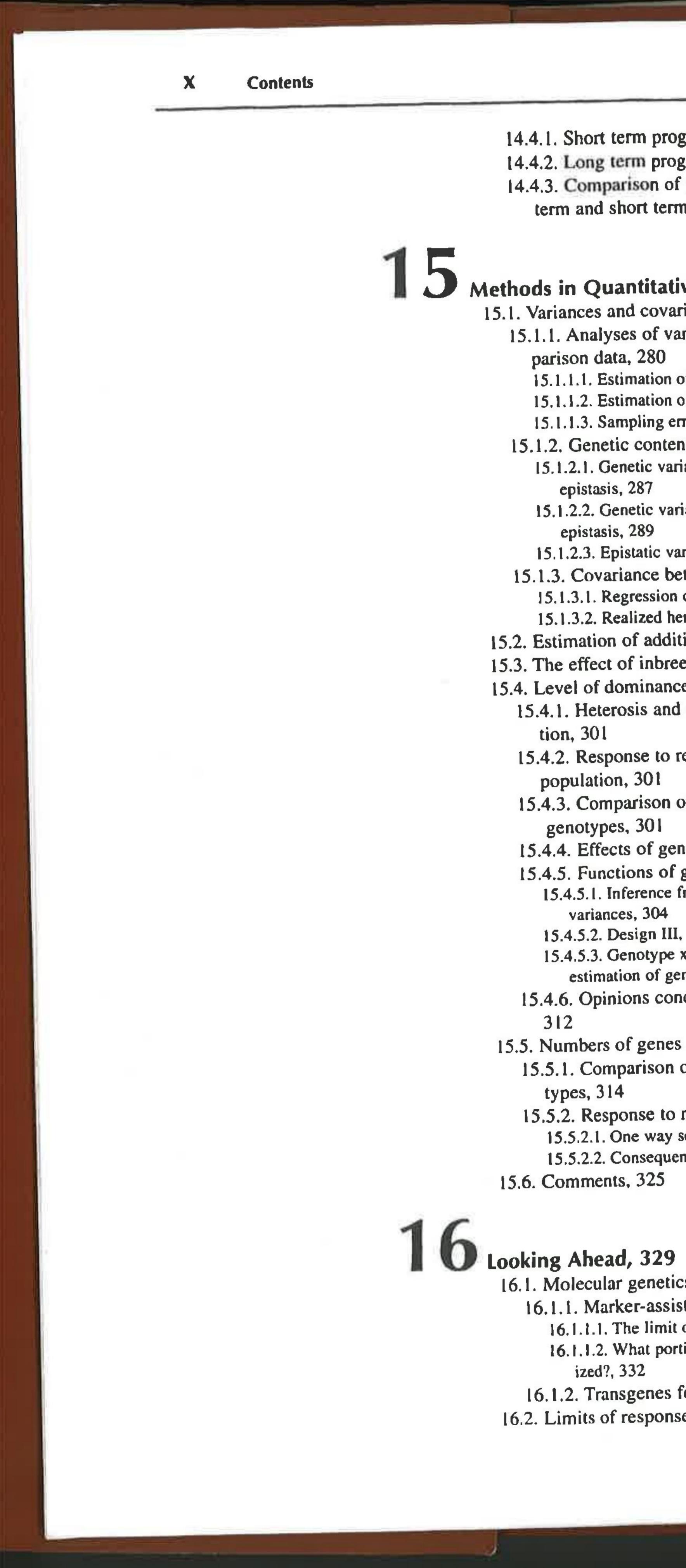
11.2.5. Epistasis and multiple alleles, 189

11.3.1.1. $E(\Delta \ddot{y})_{t}$, in the target population when T=S, 199 11.3.1.2. $E(\Delta \ddot{y})_1$, in the target population when $T=S_1 \times S_2$, 199 11.3.2. Discussion and summary, 200 11.3.3. Applications—choice and design of short term programs,

12.6. Phenotypic information from two or more sources, 217

13.2. Criteria and procedure for the comparative evaluation of recur-13.4. The target population of environments, 229

14.3. Short term, two population programs in which $T = S_1 \times S_2$, 262 14.3.1. Single population (T = S) vs. RSP programs, 262 14.3.1.2. When the favorable allele is in some degree dominant



14.4.1. Short term programs, 270

14.4.2. Long term programs, 273

14.4.3. Comparison of probabilities of fixation and $E(\Delta q)$ in long term and short term programs, 278

Methods in Quantitative Genetics, 279

15.1. Variances and covariances, 279

15.1.1. Analyses of variance and covariance-plant family comparison data, 280

15.1.1.1. Estimation of variances, 280

15.1.1.2. Estimation of covariances, 283

15.1.1.3. Sampling errors of estimates, 284

15.1.2. Genetic content of family variances and covariances, 286 15.1.2.1. Genetic variances among families when there is no

epistasis, 287

15.1.2.2. Genetic variance among S_n families when there is no epistasis, 289

15.1.2.3. Epistatic variance within family genetic variances, 292

15.1.3. Covariance between parent and offspring, 294 15.1.3.1. Regression of offspring on parent, 297

15.1.3.2. Realized heritability, 297

15.2. Estimation of additive genetic variances and covariances, 298 15.3. The effect of inbreeding, 299

15.4. Level of dominance, 300

15.4.1. Heterosis and effect of inbreeding as sources of informa-

15.4.2. Response to recurrent selection applied to an F₂ source population, 301

15.4.3. Comparison of phenotypes associated with single-locus genotypes, 301

15.4.4. Effects of genotypes at marked and linked loci, 303 15.4.5. Functions of genetic variances, 304

15.4.5.1. Inference from estimates of additive and dominance variances, 304

15.4.5.2. Design III, 308

15.4.5.3. Genotype x environment interaction variance and the estimation of genetic variances, 311

15.4.6. Opinions concerning heterosis and levels of dominance,

15.5. Numbers of genes and the magnitudes of their effects, 314 15.5.1. Comparison of groups with different single-locus genotypes, 314

15.5.2. Response to recurrent selection, 316

15.5.2.1. One way selection, 323

15.5.2.2. Consequences of epistasis, 324

15.6. Comments, 325

16.1. Molecular genetics and breeding methodology, 330 16.1.1. Marker-assisted selection (MAS), 330

16.1.1.1. The limit of increased response via MAS, 330

16.1.1.2. What portion of the conceptual promise of MAS can be realized?, 332

16.1.2. Transgenes for improvement of gene pools, 333 16.2. Limits of response, 333

- 16.3. Large recurrent selection programs in the context of world pop
 - ulation growth, 334

- 16.4.1. High priority research, 341

- arising by mutation, 341
- 16.4.1.3. Plateaus, 342

Appendixes, 345

- A1.1. Terminology, 345
- A1.2. Distributions, 346

- A1.5. Expectations, 348
 - A1.5.1. Linear Functions, 349
 - A1.5.2.1. Applications, 350
- 2.1. Wright's Coefficient of Inbreeding, 353

- 6.1. Algebra in Derivation of 6.14, 359
- Among S_n Families, 361 A8.1.1. Progeny Test Selection, 361
- A8.1.2. Selection among S_n Families, 362

- A11.1.2. Special Cases, 366
 - - cycles), 366
 - - cycles), 367

 - tion, 368

16.3.1. Potential for genetic improvements, 336 16.3.2. Considerations—practical and philosophical, 336 16.3.3. Program dimensions, 337 16.4. Quantitative genetics in relation to genetic improvement of agricultural species—looking ahead, 339 16.4.1.1. Tests of theory for comparison of selection systems, 341 16.4.1.2. Assays of the genetic improvement potential of new alleles 16.4.2. Personnel, training programs, and cooperation, 343 Terminology, Symbols, and Elements of Statistics, 345 A1.3. Symbols and Statistics—Univariate Distributions, 348 A1.4. Symbols and Statistics—Bivariate Distributions, 348 A1.5.2. Variance and Covariance of Linear Functions, 350 2.2. Δ_s in the Case of Autosomal Genes in Dioecious Species, 356 5.1. The Effect of Test Environment on $E(\Delta q)$, the Expectation of Allele Frequency Change in Response to Selection, 357 6.2 The Rate at which Linkage Disequilibrium Decreases in Large Random Breeding Populations, 359 8.1. The Covariance between \hat{q} and \hat{y}_{xj} (A) in Progeny Test Selection when Selection Unit Individuals Have Been Produced by One or More Generations of Self-Fertilization and (B) in Selection 9.1. Probabilities of Two-Locus Genotypes in Pure Lines Derived by Successive Self-Fertilizations and without Selection from a Random Mating, Linkage Equilibrium Source Population, 362 9.2. Linkage Disequilibrium within S_n Families, 363 11.1. Variations of Effective Population Size (Ne), 364 A11.1.1. Variance of Allele Frequency (Random Mating Diploid Populations), 365 A11.1.2.1. Selection among half-sib families (two-generation A11.1.2.2. Selection among full-sib families (two generation A11.1.2.3. Selection within full-sib families, 367 All.1.2.4. Selection among families produced by self-fertiliza-A11.1.3. Cycles Extended by One or More Extra Generations of Random Mating in the Population, 369 11.2. Recent Mutations and Superior Alleles at Low Frequencies, 369

XI

24

- XII Contents
- 11.3. Derivations of $E(\Delta q)$ and $E(\Delta y)$ as Functions of N_e. 372 A11.3.1. Generalizations from Appendix 1, 372 A11.3.2. Expected Change in Frequency of the B Allele, 373
 - A11.3.2.1. When selection units are S population individuals or families com
 - posed of on-inbred S population individuals, 373
 - A11.3.2.2. When selection is among S_n families on the basis of their own per
 - formance, 373
 - A11.3.3. Expected Change in the Average Value of Single-Locus Genotypes When the T Population Is the S Population, 373

 - A11.3.3.1. When selection units are non-inbred individuals or families of noninbred individuals, 375
 - A11.3.3.2. When selection is among S_n families on the basis of their own per
 - formance, 375
 - A11.3.4. Expected Change in the Average Value of Single-Locus Genotypes when
 - the T Population is the Cross between Two S Populations, 375
 - A11.3.4.1. When selection units are non-inbred individuals or families of non
 - inbred individuals, 376
 - A11.3.4.2. When selection is among S_n families on the basis of their own performance, 377
 - A11.3.4.3. When $T = S_1 \times S_2$ and selection is based on performance of test cross progenies, 377
 - A11.3.5. Reciprocal Recurrent Selection, 378
- 12.1. Selection Criterion Weighting Coefficients That Maximize Genetic Improvement
- per Cycle, 378
- 12.2. Total Value Discussed in Terms of Maize and Swine, 380
- 14.1. Allele Frequency (q) and the Magnitude of q(1-q), 383
- 14.2. Algebra, 385
- 15.1. Total Genetic Variance, 385
- 15.2. Effects of Genotypes at Marked and Linked Loci-Theory, 387
- 15.3. The Genetic Variances of Design III Data, 389
- 15.4. Biased vs. Unbiased Estimates of Genetic Variances from Design III Data, 393 15.5. Average Genotype Value Difference between the F1 and F2 Generations from a
- Cross of Pure Lines, 396
- 15.6. The Standard Error of $[\Delta \ddot{Y}_x E(\Delta \ddot{Y}_x)]$, 397 A15.6.1. Additive Genetic Variance, 397 A15.6.2. The Estimate of $\Delta \ddot{Y}_x$, 398

 - A15.6.4. Discussion, 399

Notes, 401 References, 413

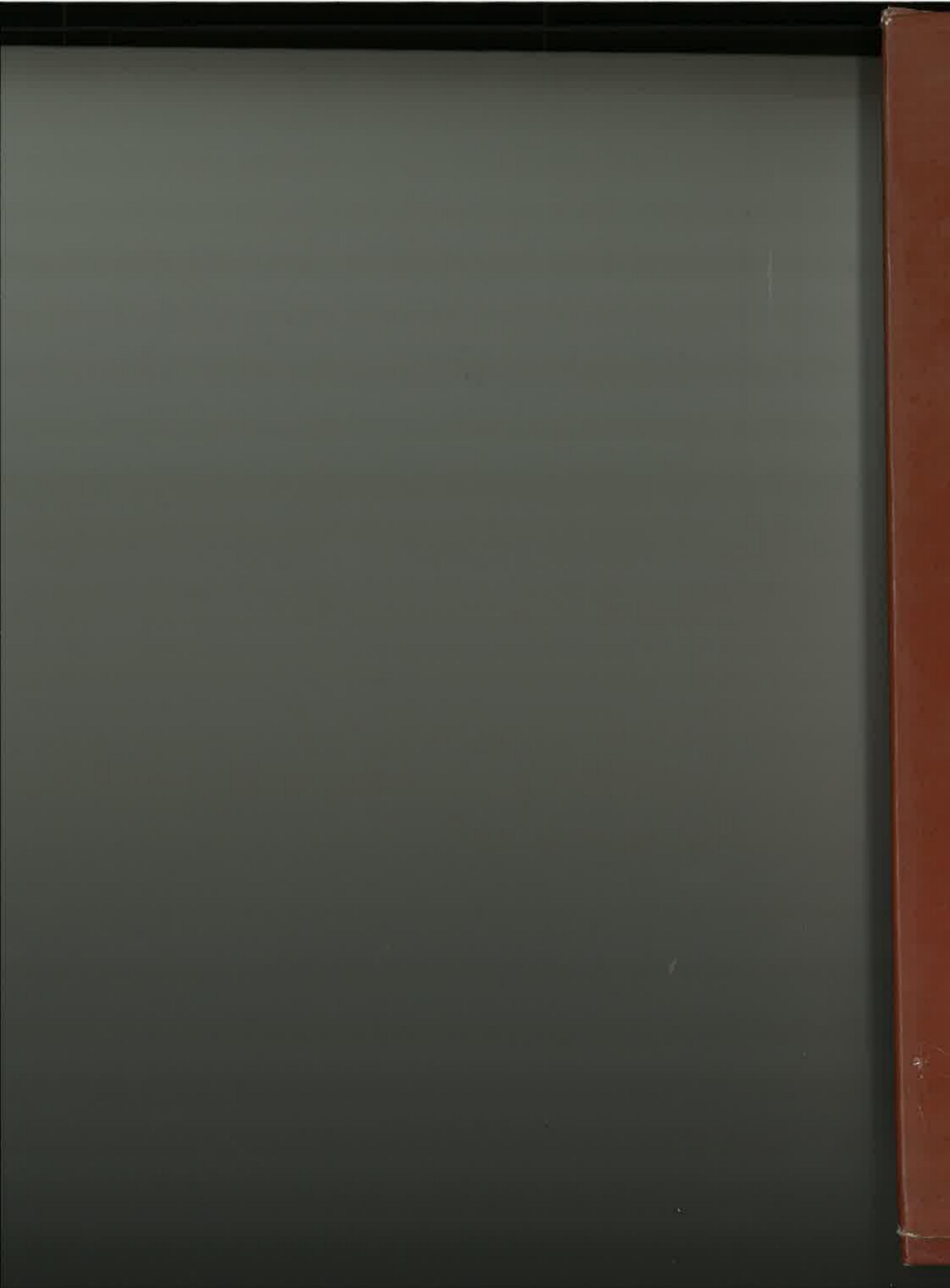
- A15.6.3. The Variance of $[\Delta \ddot{Y}_x E(\Delta \ddot{Y}_x)]$, 399

Preface

The content of this book reflects in many ways the background and experiences that shaped my enduring special interests. I was raised on small farms in southern Minnesota. In the period between high school graduation and enrollment at the University of Minnesota I was an apprentice on our home farm, and during those four years I was a 4H Club member with swine and maize projects. My 4H experience kindled a beginning awareness of (a) the contributions of research relating to the husbandry of agricultural species and (b) opportunity inequalities associated with economic stratification. The former motivated the choice of agriculture as my major field at the university.

Undergraduate and graduate courses that most excited me were Principles of Genetics, Animal Breeding, Principles of Economics, Biometry, and Applied Statistics. It was my good fortune to be influenced by both L. M. Winters and Jay Lush-two of the early leaders in Animal Breeding. I worked for and later with Professor Winters during the 1934-43 years, first as an abstracter of literature pertaining to animal breeding and genetics and as a caretaker of research project animals and later with responsibility for records and analysis of data from his extensive swine breeding investigations. My contacts with Professor Lush derived from the Minnesota and Iowa participations in the U.S.D.A. Regional Swine Breeding Laboratory in the years when I worked as an assistant to Professor Winters. I well remember critiques by Dr. Lush of drafts of my earliest literature contributions.

A later era very significant for me were the ten years, 1947-57, in which as a member of the Department of Experimental Statistics of the North Carolina State University I was charged by Gertrude Cox with statistical consultation in the area of genetics. This wonderful opportunity provided the open door through which I learned about plant breeding methods and problems from H.F. "Cotton" Robinson, Walton Gregory, Paul Harvey, E.B. Morrow, and T.J. Maken among others. It was during those years that I was senior author of the papers that described Design III for investigation of levels of dominance and reciprocal recurrent selection as a system of choice if overdominance was found to be an important feature of the genetics of any economically important quantitative trait. It was also during those years that I began teaching "Statistical Concepts in Genetics," the embryo from which this book emerged.





Exclusively Distributed by STAR Educational Books Distributor Pvt. Ltd. 24/4800, Bharat Ram Road, Darya Ganj New Delhi - 110 002 (India) Ph.: 41562819, 23264462. Fax: +91-11-23264451 Email: sales@star-bk.com Website: www.star-bk.com

This edition is authorized for sale in the Indian sub-continent only.



