

Heterosis

HETEROSIS

*A record of researches directed toward explaining
and utilizing the vigor of hybrids*

Edited by

JOHN W. GOWEN

Professor of Genetics

Iowa State College



IOWA STATE COLLEGE PRESS

AMES • IOWA

Copyright 1952 by The Iowa State College Press
All rights reserved. Composed and printed in the
United States of America

Preface

Heterosis grew out of a desire on the part of Iowa State College to gather together research workers from marginal fields of science, each with something to contribute to a discussion of a central problem of major national interest. The problem of heterosis, as synonymous in large part with that of hybrid vigor, formed a natural theme for discussion. As the reader will note, many fields of science have contributed or stand to make significant contributions to the subject. Major steps in the advance have led to divergent views which may be rectified only through joint discussions followed by further research. The conference of students of this problem was held June 15 to July 20, 1950.

In furnishing the opportunity for these discussions by active research workers in the field, Iowa State College hoped: to facilitate summarization and clarification of the accumulated data on the subject, to encourage formulation and interpretation of the observations in the light of present day biological information, to stimulate further advances in the controlled successful utilization and understanding of the biological processes behind the phenomenon of heterosis, and to increase the service rendered by this discovery in expanding world food supply.

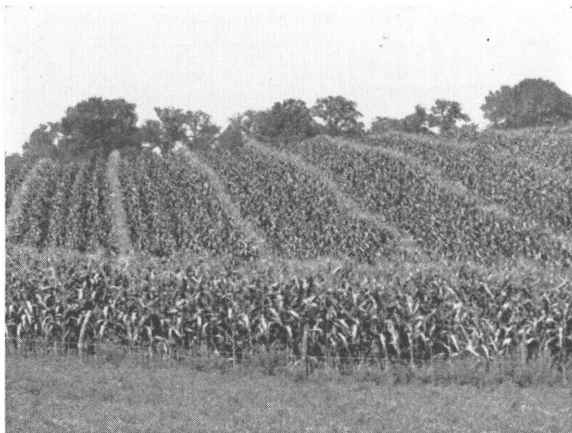
Iowa has a direct, vested interest in heterosis. Today the agricultural economy of the state is based upon hybrid corn. The scene portraying a hybridization block of corn, shown here, is familiar to all who travel within the state as well as to those in surrounding regions, for this method of corn breeding has been shown to be surprisingly adaptable and useful in producing more food per acre over wide areas of the world's agricultural lands.

Iowa's indebtedness to heterosis, generated through crossing selected and repeatedly tested inbred strains, is well known. Few outside the workers in the field realize the full magnitude of this debt.

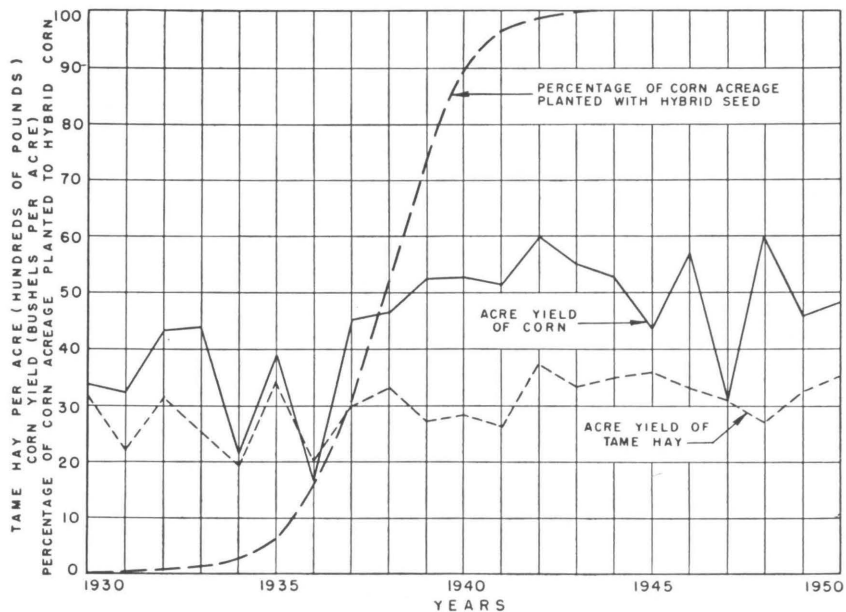
With the progressive introduction of hybrid corn in 1936 there came a steady increase in corn yields over both the former yields and over the yields of other agricultural crops, as that of tame hay, which were not subject to this genetic method of yield improvement. It seems likely that in no other period of like years has there been such an increase in food produced over so many acres of land. The return from hybrid corn has been phenomenal, but it is now evidently approaching an asymptotic value. It behooves us to find out as much as possible about the techniques and methods which

made these advances possible. Even more we should determine what is going on within the breeding and physiological systems through which heterosis finds expression, if further increases in yields are to be obtained or better systems of breeding are to be developed.

Toward this end the conference topics were arranged under four major



Controlled heterosis in the making through pollinations and fertilizations of selectively purified genetic strains of corn (maize). (From G. F. Sprague.)



Trends in acre production of maize before and after heterosis was in use and tame hay over which there has been no such breeding control 1930-1950. (From G. F. Sprague.)

headings. The early history and development of the heterosis concepts and the cytological aspects of the problem occupied the first week. The contributions of physiology, evolution, and specific gene or cytoplasmic effects to the vigor observed in hybrids were dealt with the second week. The third week's meetings covered postulated gene interactions, as dominance, recombination, and other possible gene effects. During the fourth week breeding systems and methods of utilizing and evaluating heterosis effects were considered. In the final week the students considered the problems that lie ahead and recent methods of meeting them.

At each daily conference the speaker of the day presented a formal morning lecture covering his subject. In the afternoon, he led a conference session on the subject of the morning lecture. At this time, all present had an opportunity to participate.

Accompanying, and as a supplement to the Heterosis Conference, a Methods Workshop was held from July 3 to July 13. The Workshop was devoted to recent techniques for evaluating the kinds of data which occur frequently in animal breeding experiments. Workshop meetings were organized by Professor R. E. Comstock of North Carolina State College and Professor Jay L. Lush of Iowa State College.

The meetings were led by men from several institutions besides Iowa State College. Professors Oscar Kempthorne, Jay L. Lush, C. R. Henderson, G. E. Dickerson, L. N. Hazel, F. H. Hull, A. E. Bell, A. M. Dutton, J. Bruce Griffing, C. C. Cockerham, F. H. W. Morley, R. M. Koch, and A. L. Rae contributed much to this phase of the program. It is with regret that it is impossible to present the meat of the methods presented and developed in the Workshop and the afternoon discussions. To many, this material contributed much to the merit of the conference and the use to which the results were put later.

In the field of worth-while living, as well as to see heterosis in operation, conferees were guests, on various weekends, of three nearby companies putting heterosis to the practical test of commercial seed stock production in crops and live stock—the Ames Incross Company, the Farmers Hybrid Corn Company, and the Pioneer Hi-Bred Corn Company.

Finally, the organization of the conference was the product of the joint effort of the genetic group of Iowa State College. This group transcends all departmental lines having as the common interest what goes on in inheritance. They were Jay L. Lush, G. F. Sprague, Oscar Kempthorne, S. S. Chase, Janice Stadler, L. N. Hazel, A. W. Nordskog, Iver Johnson, W. A. Craft, J. Bruce Griffing, and John W. Gowen.

In last analysis it was the interest of the audience and their participations in the discussions that made the Conference worth while. The papers covering material presented by the leaders of these discussions follow.

Table of Contents

1. Early Ideas on Inbreeding and Crossbreeding	CONWAY ZIRKLE	1
2. Beginnings of the Heterosis Concept	GEORGE HARRISON SHULL	14
3. Development of the Heterosis Concept	H. K. HAYES	49
4. Preferential Segregation in Maize	M. M. RHOADES	66
5. Inbreeding and Crossbreeding in Seed Development	R. A. BRINK	81
6. Physiology of Gene Action in Hybrids	W. GORDON WHALEY	98
7. Hybrid Nutritional Requirements	WILLIAM J. ROBBINS	114
8. Origin of Corn Belt Maize and Its Genetic Significance		
	EDGAR ANDERSON <i>and</i> WILLIAM L. BROWN	124
9. Heterosis in Population Genetics	ADRIANO A. BUZZATI-TRAVERSO	149
10. Fixing Transgressive Vigor in <i>Nicotiana Rustica</i> . . .	HAROLD H. SMITH	161
11. Hybridization in the Evolution of Maize	PAUL C. MANGELSDORF	175
12. Biochemical Models of Heterosis in <i>Neurospora</i> . . .	STERLING EMERSON	199
13. Nature and Origin of Heterosis	TH. DOBZHANSKY	218
14. Plasmagenes and Chromogenes in Heterosis	DONALD F. JONES	224
15. Specificity of Gene Effects	M. R. IRWIN	236
16. Genetics and Cytology of <i>Saccharomyces</i>	CARL C. LINDEGREN	256
17. Genetic Implications of Mutations in <i>S. Typhimurium</i> . .	H. H. PLOUGH	267
18. Dominance and Overdominance	JAMES F. CROW	282
19. Gene Recombination and Heterosis	LEROY POWERS	298
20. Gene Interaction in Heterosis	A. J. MANGELSDORF	320
21. Inbred Lines for Heterosis Tests?	GORDON E. DICKERSON	330
22. Specific and General Combining Ability	C. R. HENDERSON	352
23. Rotational Crossbreeding and Heterosis	L. M. WINTERS	371
24. Gamete Selection for Specific Combining Ability		
	E. L. PINNELL, E. H. RINKE, <i>and</i> H. K. HAYES	378
25. Monoploids in Maize	SHERRET S. CHASE	389
26. Early Testing and Recurrent Selection	G. F. SPRAGUE	400
27. Heterosis in a New Population	E. J. WELLHAUSEN	418
28. Recurrent Selection and Overdominance	FRED H. HULL	451
29. Hybrid Vigor in <i>Drosophila</i>	JOHN W. GOWEN	474
30. Estimation of Average Dominance of Genes		
	R. E. COMSTOCK <i>and</i> H. F. ROBINSON	494
Bibliography		517
Index		537

