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Concepts and Breeding of Heterosis in Crop Plants

Proceedings of the Plant Breeding Symposium sponsored by the Crop Science Society of America and the American Society of Horticultural Science, 3 November 1996, in Indianapolis, Indiana.

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Kendall R. Lamkey and Jack E. Staub

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FOREWORD

Heterosis (or hybrid vigor) has been a major factor in the increased production of several important plant species during this century; however, the most dramatic and well-publicized impact on yield and other performance characteristics has probably occurred in maize. From 1933 to 1943 the increased yield of hybrid maize over the traditional open-populated varieties was so evident that approximately 90% of all farmers in the Midwestern portion of the USA switched to planting commercial hybrids.

Two very significant results occurred from the development of hybrid maize in the USA. First was the development of a far superior product for farmers. Second was the rapid increase in the number of researchers working in the private sector to develop improved maize varieties. Prior to 1930, most of the professional researchers, which were few in number, were employed by the public sector. Today, more than 500 researchers in the USA work on maize breeding, and more than 90% of them are employed in the private sector. There is little doubt that the exploitation of heterosis and the growth in number of researchers working on maize were major factors contributing to the increase in average yield in the USA from 1.5 Mg ha^{-1} to more than 7 Mg ha^{-1} during the period 1930 to 1990.

The alarming rate at which the world population continues to grow demands that major cereal production will have to increase by 30 to 40% over current production by the year 2020. One area of research that could prove to be valuable in achieving this increase is the exploitation of heterosis and the development of commercial hybrids in wheat and rice, the two major food cereals. Hybrid rice is now a viable commercial product in countries such as China and India that rely on this plant as their major food cereal. Area devoted to hybrid rice is growing rapidly in each of these countries.

In light of the pressing problem of producing ever-increasing amounts of food on less arable land, this publication on the history and current knowledge of heterosis is most timely. The Crop Science Society of America appreciates very much the hard work of K.R. Lamkey and J.E. Staub in performing the many time-consuming duties associated with editing this book.

Ronald P. Cantrell, President, 1998
Crop Science Society of America

PREFACE

The Joint Plant Breeding Symposia Series is sponsored by the Crop Science Society of America (CSSA) and the American Society of Horticultural Science (ASHS) to provide information and increase the awareness of plant breeders and plant geneticists in important areas of applied genetics. The symposia is held every other year and alternately hosted by the two societies. Concepts and breeding of heterosis in Crop Plants, the third joint plant breeding symposia, was held on Sunday, 3 November 1996 in Indianapolis at the ASA–CSSA–SSSA national meetings. The topic of heterosis grew out of discussions between committee members who had organized the previous symposia held in 1994 and members of the Vegetable Breeders Working Group, ASHS. They felt there was a need to bring together agronomic and horticultural scientists to discuss issues related to heterosis and its application to crop species.

The resulting one-day symposium was organized around three general themes: history and perspective, mechanisms, and detection and exploitation. The intent of the history section was to provide a historical overview of heterosis, its role in business, and to present a summary of the utility of heterosis in agronomic and horticultural crops. The intent of the mechanisms of heterosis section was to examine the underlying genetics and biology of heterosis. Likewise, the intent of the detection and exploitation of heterosis section was to examine how heterosis can be manipulated and utilized in practice.

Heterosis dominated the thinking of plant and animal geneticists in the 1940s and 1950s as evidenced by the now classic book entitled Heterosis edited by John W. Gowen and published by Iowa State University Press. In fact, the entire U.S. hybrid maize industry and much of the world maize industry is founded on heterosis. Despite the importance of heterosis in maize and the plethora of research done on heterosis, little is known empirically about the underlying genetic and related physiological basis of heterosis. In fact, the biological basis of heterosis is considered by some scientists to be inadequately defined. The chasm of unanswered questions regarding heterosis is undoubtedly why it still dominates the thinking of many scientists and was the impetus for the manuscripts published in this volume.

Although heterosis and hybrid vigor are often used synonymously, heterosis and hybrids are not necessarily synonymous. To have heterosis you need hybrids, but producing hybrids does not guarantee heterosis. The development of hybrids is being actively pursued in many agronomic and horticultural crops, but exploitation of heterosis is often not the primary reason. For instance, many horticultural crop species fail to demonstrate inbreeding depression and/or heterosis. Although the production of hybrids from inbred lines allows one to fix heterosis, hybrids also provide many other advantages in a crop production system. For instance, hybrids provide uniformity, require farmers to purchase new seed each year, and create a vehicle for the protection of intellectual property.

One issue that emerged from this symposium is that heterosis can be difficult to measure and define, particularly in crops where there are multiple harvest dates and related quality issues. Moreover, the importance of yield and quality can differ among crop species. The information found herein should give breeders, geneticists, and biologists additional insights into the complexity of heterosis. It is clear from the symposium contents that old questions regarding heterosis and its relative importance resurfaced, and new questions were defined in the light of emerging technologies.

Kendall R. Lamkey and Jack E. Staub

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Conversion Factors for SI and non-SI Units

Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Units	To convert Column 2 into Column 1, multiply by
		Length	
0.621	kilometer, km (10^3 m)	mile, mi	1.609
1.094	meter, m	yard, yd	0.914
3.28	meter, m	foot, ft	0.304
1.0	micrometer, m m (10^{-6} m)	micron, m	1.0
3.94×10^{-2}	millimeter, mm (10^{-3} m)	inch, in	25.4
10	nanometer, nm (10^{-9} m)	Angstrom, Å	0.1
		Area	
2.47	hectare, ha	acre	0.405
247	square kilometer, km^2 $(10^3\ m)^2$	acre	4.05×10^{-3}
0.386	square kilometer, km^2 $(10^3\ m)^2$	square mile, mi^2	2.590
2.47×10^{-4}	square meter, m^2	acre	4.05×10^{3}
10.76	square meter, m^2	square foot, ft^2	9.29×10^{-2}
1.55×10^{-3}	square millimeter, mm^2 $(10^{-3}\ m)^2$	square inch, in^2	645
		Volume	
9.73×10^{-3}	cubic meter, m^3	acre-inch	102.8
35.3	cubic meter, m^3	cubic foot, ft^3	2.83×10^{-2}
6.10×10^{4}	cubic meter, m^3	cubic inch, in^3	1.64×10^{-5}
2.84×10^{-2}	liter, L (10^{-3} m^3)	bushel, bu	35.24
1.057	liter, L (10^{-3} m^3)	quart (liquid), qt	0.946
3.53×10^{-2}	liter, L (10^{-3} m^3)	cubic foot, ft^3	28.3
0.265	liter, L (10^{-3} m^3)	gallon	3.78
33.78	liter, L (10^{-3} m^3)	ounce (fluid), oz	2.96×10^{-2}
2.11	liter, L (10^{-3} m^3)	pint (fluid), pt	0.473

		Mass	
2.20×10^{-3}	gram, g (10^{-3} kg)	pound, lb	454
3.52×10^{-2}	gram, g (10^{-3} kg)	ounce (avdp), oz	28.4
2.205	kilogram, kg	pound, lb	0.454
0.01	kilogram, kg	quintal (metric), q	100
1.10×10^{-3}	kilogram, kg	ton (2000 lb), ton	907
1.102	megagram, Mg (tonne)	ton (U.S.), ton	0.907
1.102	tonne, t	ton (U.S.), ton	0.907
		Yield and Rate	
0.893	kilogram per hectare, kg ha^{-1}	pound per acre, lb $acre^{-1}$	1.12
7.77×10^{-2}	kilogram per cubic meter, kg m^{-3}	pound per bushel, lb bu^{-1}	12.87
1.49×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 60 lb	67.19
1.59×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 56 lb	62.71
1.86×10^{-2}	kilogram per hectare, kg ha^{-1}	bushel per acre, 48 lb	53.75
0.107	liter per hectare, L ha^{-1}	gallon per acre	9.35
893	tonnes per hectare, t ha^{-1}	pound per acre, lb $acre^{-1}$	1.12×10^{-3}
893	megagram per hectare, Mg ha^{-1}	pound per acre, lb $acre^{-1}$	1.12×10^{-3}
0.446	megagram per hectare, Mg ha^{-1}	ton (2000 lb) per acre, ton $acre^{-1}$	2.24
2.24	meter per second, m s^{-1}	mile per hour	0.447
		Specific Surface	
10	square meter per kilogram, m^2 kg^{-1}	square centimeter per gram, cm^2 g^{-1}	0.1
1000	square meter per kilogram, m^2 kg^{-1}	square millimeter per gram, mm^2 g^{-1}	0.001
		Pressure	
9.90	megapascal, MPa (10^6 Pa)	atmosphere	0.101
10	megapascal, MPa (10^6 Pa)	bar	0.1
1.00	megagram, per cubic meter, Mg m^{-3}	gram per cubic centimeter, g cm^{-3}	1.00
2.09×10^{-2}	pascal, Pa	pound per square foot, lb ft^{-2}	47.9
1.45×10^{-4}	pascal, Pa	pound per square inch, lb in^{-2}	6.90×10^3

(continued on next page)

Conversion Factors for SI and non-SI Units

To convert Column 1 into Column 2, multiply by	Column 1 SI Unit	Column 2 non-SI Units	To convert Column 2 into Column 1, multiply by
		Temperature	
1.00 (K −273)	Kelvin, K	Celsius, °C	1.00 (°C + 273)
(9/5 °C) + 32	Celsius, °C	Fahrenheit, °F	5/9 (°F −32)
		Energy, Work, Quantity of Heat	
9.52×10^{-4}	joule, J	British thermal unit, Btu	1.05×10^{3}
0.239	joule, J	calorie, cal	4.19
10^{7}	joule, J	erg	10^{-7}
0.735	joule, J	foot-pound	1.36
2.387×10^{-5}	joule per square meter, J m^{-2}	calorie per square centimeter (langley)	4.19×10^{4}
10^{5}	newton, N	dyne	10^{-5}
1.43×10^{-3}	watt per square meter, W m^{-2}	calorie per square centimeter minute (irradiance), cal cm^{-2} min^{-1}	698
		Transpiration and Photosynthesis	
3.60×10^{-2}	milligram per square meter second, mg m^{-2} s^{-1}	gram per square decimeter hour, g dm^{-2} h^{-1}	27.8
5.56×10^{-3}	milligram (H_2O) per square meter second, mg m^{-2} s^{-1}	micromole (H_2O) per square centimeter second, m mol cm^{-2} s^{-1}	180
10^{-4}	milligram per square meter second, mg m^{-2} s^{-1}	milligram per square centimeter second, mg cm^{-2} s^{-1}	10^{4}
35.97	milligram per square meter second, mg m^{-2} s^{-1}	milligram per square decimeter hour, mg dm^{-2} h^{-1}	2.78×10^{-2}
		Plane Angle	
57.3	radian, rad	degrees (angle), °	1.75×10^{-2}

	Electrical Conductivity, Electricity, and Magnetism		
10	siemen per meter, S m^{-1}	millimho per centimeter, mmho cm^{-1}	0.1
10^4	tesla, T	gauss, G	10^{-4}
	Water Measurement		
9.73×10^{-3}	cubic meter, m^3	acre-inches, acre-in	102.8
9.81×10^{-3}	cubic meter per hour, m^3 h^{-1}	cubic feet per second, ft^3 s^{-1}	101.9
4.40	cubic meter per hour, m^3 h-1	U.S. gallons per minute, gal min^{-1}	0.227
8.11	hectare-meters, ha-m	acre-feet, acre-ft	0.123
97.28	hectare-meters, ha-m	acre-inches, acre-in	1.03×10^{-2}
8.1×10^{-2}	hectare-centimeters, ha-cm	acre-feet, acre-ft	12.33
	Concentrations		
1	centimole per kilogram, cmol kg^{-1}	milliequivalents per 100 grams, meq 100 g^{-1}	1
0.1	gram per kilogram, g kg^{-1}	percent, %	10
1	milligram per kilogram, mg kg^{-1}	parts per million, ppm	1
	Radioactivity		
2.7×10^{-11}	becquerel, Bq	curie, Ci	3.7×10^{10}
2.7×10^{-2}	becquerel per kilogram, Bq kg^{-1}	picocurie per gram, pCi g^{-1}	37
100	gray, Gy (absorbed dose)	rad, rd	0.01
100	sievert, Sv (equivalent dose)	rem (roentgen equivalent man)	0.01
	Plant Nutrient Conversion		
	Elemental	***Oxide***	
2.29	P	P_2O_5	0.437
1.20	K	K_2O	0.830
1.39	Ca	CaO	0.715
1.66	Mg	MgO	0.602