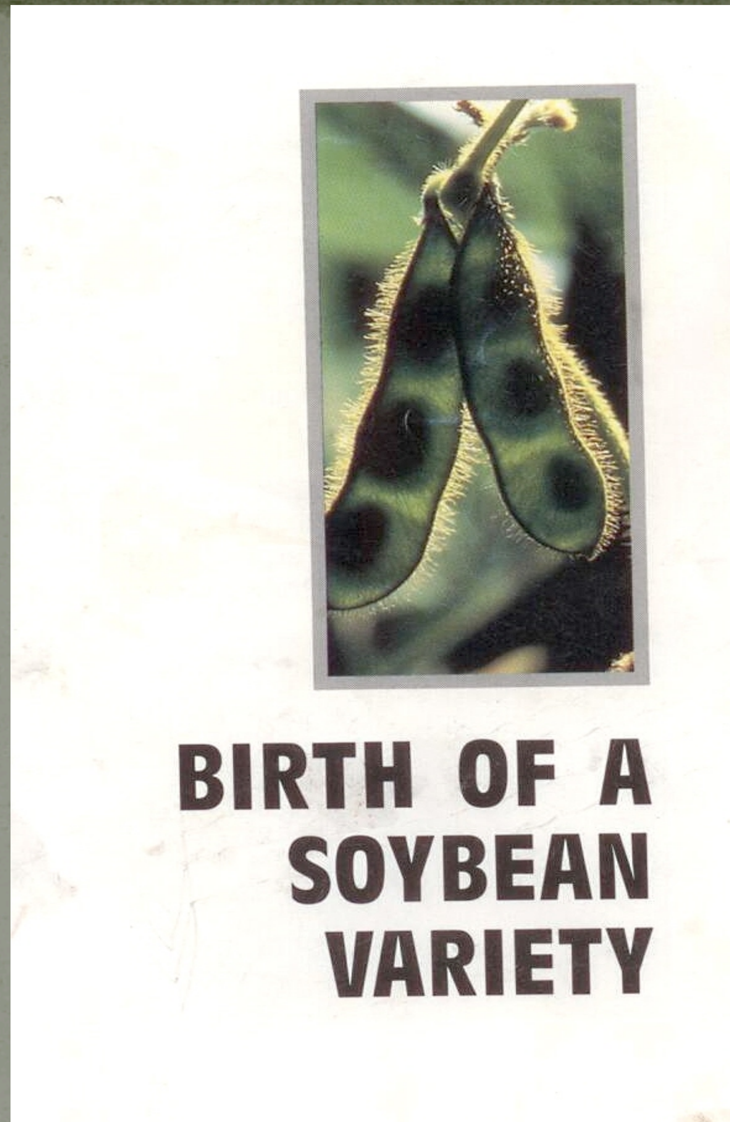
Heterosis in soybean: can it be useful in breeding?

Soybean Varieties

- Derived in the F_3 or later generation
- Highly inbred – probably ≥ F_7
- There is no economical way to produce F_1 hybrid seed.

    unavailability of a good cytoplasmic
        male-sterile/nuclear restorer system.

    unavailability of adequate numbers of
        pollen vectors.

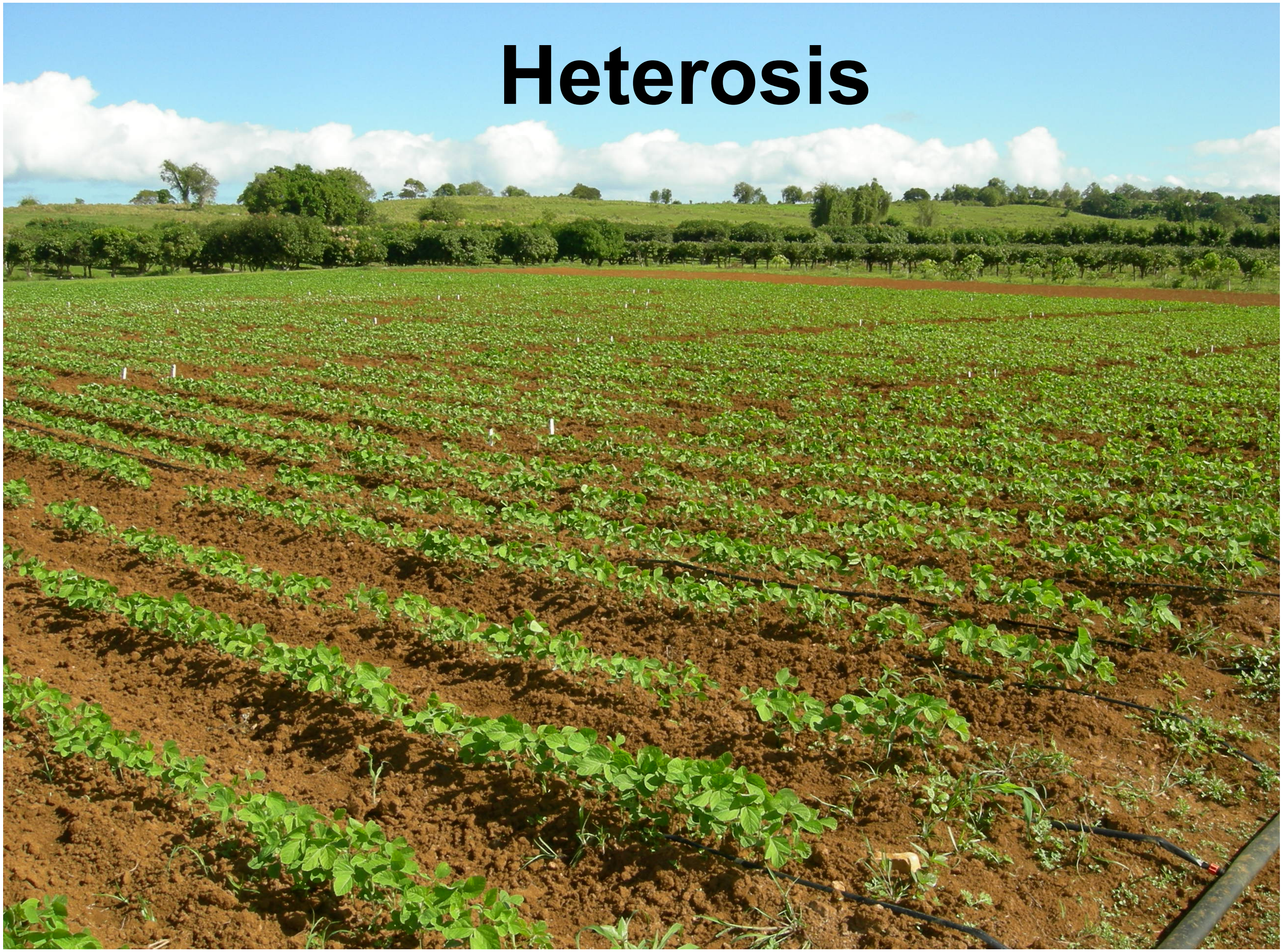


“Soybeans show little heterosis, when they are crossed. Similarly, there is little inbreeding depression when soybeans self-pollinate.” Pioneer Hi-Bred International, Inc.

Heterosis and Inbreeding Depression

- F_1 is rarely compared to the parents or F_2
- Progeny in the F_2 and later generation often look very much like the two parents.
- Mean of the F_5 is similar to the parental mean.

Heterosis



Average F_1 single plant yield heterosis

Number of F_1's	230†	24‡	30§
Average mid parent heterosis	25%	48%	------
Average high parent heterosis	13%	------	8%
% of F_1's mid parent	78%	------	40%
% of F_1's > high parent	55%	------	7%

† 8 experiments
‡ 2 experiments
§ 1 experiment

Average F_2 heterosis in standard yield plots, replicated in 2, 3, 4, or 8 environments

	Loiselle et al. (1990)	Gizlice et al. (1993)	Manjarrez et al. (1997)	Burton (2006)	Burton & Brownie (2006)
Number of F_2 bulks	55	10	24	3	2
Average mid-parent F_2 heterosis	11%	9%	7%	8%	9%
Average high parent F_2 heterosis	-----	-----	3%	-3%	7%

Average F_1 heterosis in standard yield plots, replicated in 2, 4, or 6 environments

	Brim & Cockerham (1961)	Hillsman & Carter (1984)	Nelson & Bernard (1984)	Lewers et al. (1998)	Burton & Brownie (2006)
Number of F_1's	2	8	37	36	2
Average mid-parent heterosis	28%	13%	8%	5%	13%
Average high parent heterosis	20%	6%	3%	-----	11%
% F_1's> mid parent	100%	63%	96%	83%	100%
%F_1's > high parent	100%	50%	68%	----	100%


Is Dominance important?

Two Issues

- Is there significant genetic variation due to dominance in soybean breeding populations?
- If there is dominance, is it of any consequence for soybean breeding?

Dominance would not be expected in an autogamous species.

- Very low frequency of outcrossing
- Highly inbred
- Small genetic load
- Soybeans have been cultivated in Asia for 3000+ years with selection by farmers

Self-fertilization Designs

Coefficients of σ_A^2 and σ_D^2 in the progeny components of variance and covariance

Progeny Component	σ_A^2	σ_D^2	Progeny Component	σ_A^2	σ_D^2
Cov (3c, 3c)	½	1/16	Cov (3, 4)	1	1/8
Cov (3c, 3)	½	0	Cov (3, 5)	1	1/16
Cov (3c, 4)	½	0	Cov (4, 4)	1	1/16
Cov (3c, 5)	½	0	Cov (4, 5)	1	1/32
Cov (3, 3)	1	¼	Cov (5, 5)	1	1/64

Brim & Cockerham (1961)

Self-Fertilization Designs

Reference	No. of populations	Results
Gates et al. (1960)	1	$\sigma^{2**}_{A};\sigma^{2}_{D}(n.s.)$
Hanson and Weber (1961)		$\sigma^{2}_{A}<\sigma^{2}_{AA}$
Brim and Cockerham (1961)	2	$\sigma^{2}_{A}<\sigma^{2}_{D};\sigma^{2}_{AA}<O$
Croissant and Torrie (1971)	2	$\sigma^{2**}_{A};\sigma^{2}_{D}(n.s.)$

Diallel Experiments

Diallel Experiments

F_1 generation (single plant yield)

Significant specific combining ability in 8 of 12 experiments reviewed

F_2 generations (standard plot yield)

Leffel and Hanson (1961)	dominance = 2.4 x additive
Loiselle et al. (1990)	GCA* at 3 locations; SCA* at 1 location
Cho and Scott (2000)	2GCA / (2GCA + SCA) = 0.93†
Gizlice et al. (1993)	GCA** and SCA (n.s.)

*, ** significant at the .05 and .01 level of significance

† 2GCA + SCA = total genetic variance

Inbreeding Depression

Early Generation Testing in Soybean

(Weiss, Weber, and Kalton, 1947)

- **Investigated 17 crosses among 9 parents**
- **Tested the F_1's in field spaced plantings**
- **Tested unselected F_2, F_3, F_4, F_5 bulks together with parents in row plots**
- **Performed selections within F_2, F_3, F_4, and F_5 generations obtain selected F_5 lines**

Mean yield of F_2 bulks and selected F_5 lines

Cross	F_2 Bulk Yield	F_3 Bulk Yield	Mean Yield of selected lines
A31	3620	2580	4074 (10)
B38	3580	2587	4087 (4)
C43	3480	2848	3540 (2)
.	.	.	.
.	.	.	.
D28	2960	2221	3867 (1)
E56	2920	2614	3854 (6)
F47	2873	2314	3814 (2)

Correlation between F_2 bulk and F_5 selected lines for 17 crosses was 0.209.

Inheritance of Quantitative Characters in Soybeans (Brim and Cockerham, 1961)

Investigated 2 crosses: Roanoke x Lee
N48-4860 x Lee

Generated enough F_1 seed by hand pollinations to plant row plots.

Tested F_1, bulks of F_2, F_3, F_4, and F_5, and parents at two NC locations in two years.

Results

	Yield (kg/ha)	
	Cross 1	Cross 2
Mid-parent	3554	2966
F_1	3859	3819
F_2	3477	3385
F_3	3313	3329
F_4	3237	3532
F_5	3273	3050

Heterosis and Inbreeding Depression in Two Soybean Crosses

(Burton and Brownie, 2006)

Objectives

1. Estimate heterosis and inbreeding depression in populations derived from crosses between modern cultivars.

2. Compare the results with those obtained by Brim and Cockerham.

Crosses between modern cultivars.

Hutcheson x Holladay (CP=0.147)

Brim x Boggs (CP=0.173)

Used hand pollinations to generate F_1 seeds, and bulk selfing to generate F_2, F_3, F_4 and F_5

Yields (kg/ha) of Holladay, Hutcheson, F_1, and inbred generations

	1999	2000	2001	2004
Holladay	2461	2927	3130	2804
Hutcheson	2790	2943	3091	2876
F_1	3045	---	3789	---
F_2	2671	3217	3305	3383
F_3	---	2950	3197	2940
F_4	---	---	3442	3036
F_5	---	---	---	2856
$LSD_{.05}$	316	361	357	362

Yield (kg/ha) of Brim, Bogg, F_1, and inbred generations

	1999	2000	2001	2004
Brim	2765	2996	3307	2446
Boggs	2567	2795	3288	2079
F1	2858	---	3511	---
F2	2841	2962	3283	2715
F3	---	2798	3164	2493
F4	---	---	3311	2265
F5	---	---	---	2370
$LSD_{.05}$	471	339	429	858

Coefficients (b x 100) from generation mean yield regressed on the level of inbreeding (F).

	Weiss et al.	Brim and Cockerham	Burton & Brownie
	---------------------kg/ha-------------------		
Average of 17 crosses	-840**		
Cross 1		-650**	-570**
Cross 2		-590	-280

Genetics of Heterosis

Soybean is an ancient polyploid with the at least 2 genome duplications and many homoeologous regions.

(Schleuter et al., 2004)

Gene duplications contribute to the conservation of functional but mildly deleterious genes.

(Husband and Schemske, 1996)

Duplicate favorable alleles may complement each other singly or as linked dominant alleles that are inherited together.

(Bingham, 1998)

- **Overdominance, the interaction of alleles at a single locus – quantitative genetic variation may be due to multiple dosage dependent regulatory loci.**

  (Birchler et al., 2003)

- **Unequal allelic expression has been observed in hybrids due to differences in gene regulation.**

  (Adams, 2007)

- **Duplicate genes in homeologus regions might interact similarly to heterozygous alleles at a single locus.**

  (Mackey, 1970)

All of the genetic causes for heterosis and inbreeding depression can be fixed with inbreeding with the exception of single locus allelic interaction.

F_1 and/or F_2 heterosis as a criterion for selection among crosses

- **F_2 seeds can be easily produced in an off-season nursery in adeqate numbers for yield testing**

- **Select for further inbreeding only those with high yield –**

(Harrington, 1944; Lupton, 1961; Weinhues, 1968)


N99-186
N99-186 X F_2 Graham


N99-186
X F2
Graham

Parental Yields and F2 Heterosis

		Yield (kg/ha)			% High Parent Heterosis
Parent 1	**Parent 2**	**Parent 1**	**Parent 2**	**F_2 Bulk**	
N99-58	**Graham**	**1818**	**1793**	**1641**	**-9.83**
N99-58	**V98-2711**	**1818**	**1704**	**1883**	**3.69**
N98-74	**V98-2711**	**1650**	**1704**	**1859**	**9.24****

$LSD_{.05}$=182

Remake Crosses of Variety Parents

• Essex x Davis	Young
• Young x N73-1102	Brim
• N85-492 x N88-480	Raleigh
• Holladay x Brim	Roy
• Centennial x Young	Dillon
• Braxton x Young	Cook

A Comparison of Variety, Variety Parents, and the F2 Bulk Yield Performance

		Bu/A *		Bu/A**
Variety	**Young**	40.1	**Brim**	42.7
P1	Davis	37.4	N73-1102	36.8
P2	Essex	32.1	Young	37.9
	Mid-parent	34.8	Mid-parent	37.3
	F2	40.2	F2	40.1
Check	NC-Roy	49.3	NC-Roy	42.7
	LSD.05	6.5	LSD.05	2.9

*5 environments
**7 environments

A Comparison of Variety, Variety Parents, and the F2 Bulk Yield Performance

		Bu/A *		Bu/A**
Variety	**Dillon**	41.9	**Cook**	43.2
P1	Centennial	38.6	Braxton	36.7
P2	Young	38.9	Young	41.1
	Mid-parent	38.7	Mid-parent	37.3
	F2	40.6	F2	40.1
Check	NC-Roy	45.2	NC-Raleigh	41.2
	LSD.05	4.1	LSD.05	4.9

*6 environments
**4 environments

A Comparison of Variety, Variety Parents, and the F2 Bulk Yield Performance

		Bu/A *		Bu/A**
Variety	**NC-Roy**	41.8	**NC-Raleigh**	45.4
P1	Holladay	40.8	N85-492	38.3
P2	Brim	42.5	N88-480	41.1
	Mid-parent	41.6	Mid-parent	40.1
	F2	46.7	F2	44.0
Check	Boggs	40.4	NC-Raleigh	45.4
	LSD.05	N.S.	LSD.05	6.2

*4 environments
**6 environments

Testcross a high yielding line to plant introductions as a way of finding those that can bring genetic diversity into a breeding program with no loss in productivity.

(Lewers et al., 1998)

If there is significant dominance, early generation testing may be warranted if an economical and efficient method can be devised- molecular markers may be useful.

Soybean breeding staff who helped with this project

Colleague
- Tommy Carter

Support Scientist
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Technicians
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- Earl Huie
- Bobby McMillen
- Mal Young

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