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FACTORS THAT CONTRIBUTE TO LACK OF GENETIC PROGRESS

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Researchers and breeders tend to take credit for periods when yields are increasing. They also tend to blame weather for periods when yields aren't increasing. To do so precludes finding the causes limiting yield increases. This symposium has taken the bold step to address the factors, primarily diseases and nematodes, that might impact the lack of yield increases in the last 10 years. The specific objective of this presentation is to address the genetic factors that contribute to yield stagnation. To do so requires that you also examine the main effects that non-genetic factors have on yield. The approach is to first establish if yields aren't increasing. Following this, the question on what impact weather and pests have had on stagnant yields will be investigated. Finally, factors that influence genetic progress, especially those specific for cotton will be given.

USA Cotton Yield History

The average USA yields from 1866 to 2000 are given in Figure 1. The data are from the USDA Agricultural Statistics for the period indicated. Several yield plateaus are evident. A long period of stagnant yearly yields from 1866 to 1936 shows little increase per year. During this period, the boll weevil (*Anthonomus grandis* Boheman) marched across the Midsouth and limited yields. Initially little knowledge of genetics was known and cotton breeding consisted of mass selections on individual plantations. Problems were productivity, earliness, diseases, and fiber quality (Moore, 1956). Modern plant breeding was initiated in the early 1900s with emphasis on earliness to escape boll weevils. From 1937 to 1964, yields increased dramatically, 10.3 pounds/lint/acre/year. Technology improvements in diseases, insects, weed control, irrigation, mechanization, and breeding all made contributions to yield increases. From 1965 to 1980, yields decreased an average of 1.9 lbs lint/acre/year. During this period no high yielding new varieties were introduced and the available insecticides became ineffective. Beginning in 1981, yields increased for about 10 years due to the introduction of pyretheroid insecticides and new varieties. One new variety type was developed by Dr. Robert Bridge, a Mississippi State University breeder at Stoneville. Another major contribution was the release of Deltapine 90. A general comparison of two new varieties with the two most popular Midsouth varieties grown in the 1970s is given in Table 1. Average yield of two current varieties, 'SureGrow 747' and 'Stoneville 474' was 1032 and 1030 lbs/acre, respectively. That compared to 814 for the average of 'Deltapine 16' and 'Stoneville 213' of 832 lbs/acre. Test data are from two soil types grown in 1998 and 1999 near Stoneville with four environments tested (unpublished data by Meredith). However, beginning in the 1990s, no further yield increases in Mississippi have occurred.

Effect of Non-Genetic Factors on Mississippi Yields

The regression coefficient of year on Mississippi average yield from 1981 to 2001 is non-significant: b = 0.8 lbs lint/acre/year (Figure 2). The average yield for the 21-year period is 734 lbs lint/acre and has a wide range of 571 to 901 lbs lint/acre. The average yields were correlated with monthly weather data from the National Weather Bureau at Stoneville for the same period. The average monthly precipitation, maximum and minimum average temperatures and soil temperature came from 36 weather recording stations and pan evaporation from three stations. Maximum July-August temperatures for 2001 was only from the Stoneville station as a complete data set was not yet available. The only single significant weather factor was average July-August maximum temperature which accounted for 32% of the yield variation; yield = 3219 – 27.2 X; X = maximum July-August temperature. July and August are the periods for cotton flowering and most of the boll maturation period. Adjusting the yields for the 21-year averages reduces the scatter of yearly averages and the range from 330 to 207 lbs lint/acre, Figures 2 and 3. The effect of harvestable acres and losses due to pests show no significant relationships with yield in Table 2. The possible exception is losses due to the bollworm-budworm complex with R^2 of 16% (Prob. = 0.08). However, use of this association with yield would indicate yield should be increasing in the late 1990s. The weather data, harvestable acres, and pests losses show no indication that these factors are the primary cause of the yield plateaus. Similar yield plateaus are evident in other Midsouth states.

Genetic Factors that Influence Yield Progress

Estimating Genetic Progress

Measuring progress of any variable requires comparison of a selected population against a standard. The standard may be increased productivity over time or comparison with a reasonable check. Genetic progress for yield is sometimes measured by the change in variety tests mean yields over time or regression of mean tests yield on year of tests. An analysis of

National Variety test mean yields was made on yields from 15 locations across the USA for the years 1960 to 1996. The locations were in the Eastern, Delta, Central, Plains, West and San Joaquin Regions. The yields followed a similar pattern, Table 3, as the USA's averages given in Figure 1. Trends were similar for all regions, except the Plains which had the lowest yields and showed the most year-to-year variability. The combined analysis for all 15 locations is summarized in Table 3. The average increase in yield for the 37-year period was 6.05 lbs lint/acre/year or 0.64%/year. However, there were two time periods when yields actually decreased. The period from 1960 to 1981 showed an average decrease in yield of 1.8 lbs/acre/year. This period (1982 – 1996) following this plateau also showed a negative slope of 4.5 lbs/acre/year. The increase in yield over the 37-year period was not made in gradual yearly gains, but in a major jump of 173 lbs/acre from the first to second period. As mentioned earlier, the yield increase was made by a combination of better insecticides and varieties. However, the analyses showed that yields peaked in about 1990 followed with another plateau.

A second analysis was made with the average yields from the Regional High Quality Tests. These studies had been conducted for the years 1964 to 1999 and were conducted in 10 states from the Carolinas to East Texas. The combined analysis over all locations indicated a non-significant increase in yield of 2.9 lbs lint/acre/year or 0.32%; Table 4. The analyses also indicated that maximum yields peaked in about 1988.

These two studies covered large geographical areas over 36 and 37 years and produced similar results. They indicate that yields plateaued about 1988. However, variety test means over time are not only influenced by genetic progress, but also by other technology inputs.

A better approach to measuring genetic progress for yield is to compare obsolete and modern varieties. We've conducted five such tests with two to four environments with 12 to 38 varieties per test since 1967 (Bridge et al., 1971; Bridge and Meredith, 1983; Wells and Meredith, 1982; Meredith et al., 1997; and Meredith, 2002, unpublished data). Year of variety release ranges from 1905 to 1999. A summary of the results is given in Table 5. The trend is for decreasing slopes. To summarize all these tests into one study, yields of all varieties were adjusted based on the performance of five varieties which were in all tests and a sixth variety that was in four of the tests. The regression coefficient for yield is 6.0 lbs/acre/year for the years 1905 to 1999 (Figure 4). The combined analysis shows steady progress in the last century. A subset of 23 varieties evaluated in the last tests shows a nonsignificant 3.5 lbs lint/acre/year gain for the 1983 to 1999 period (Figure 5).

Two examples of how new germplasm introduced into breeding programs has resulted in new variety types is the development of 'DES 56' and 'Deltapine Acala 90'. Previously, a general breeding strategy of how to select breeding parents had been to cross the "best" variety with the other best varieties. However, DES 56 and Deltapine Acala 90 were not developed in this manner. Half of the parentage of the new variety types were Stoneville 213 and Deltapine 16. These two varieties were grown primarily in the Midsouth for 20 to 25 years. In 1972, they accounted for over 50% of the USA acreage. Continued use of these two varieties contributed to the yield plateaus from 1965 to 1980 and no new varieties were developed from the cross of Deltapine 16 X Stoneville 213. New varieties began to evolve in about 1981. One variety, DES 56, originated from the cross of Stoneville 213 with AC-FJA 164 (PD2-164). The pedigree of PD2-164 was very complex and involved intercrossing of the triple hybrid (*G. arboreum* X *G. thurberi*) X *G. hirsutum*); AHA 6-1-4 (Acala and primitive Hopi strains): Sealand (introgressions of *G. barbadense*); Earlystaple; and C6-5 (an Acala) (Culp, 1981). None of these germplasms were useable Midsouth cottons. The second breakthrough, Deltapine Acala 90, whose pedigree consists of a University of Arizona germplasm, AZ5909, (25%) John Cotton Polycross (25%), and Deltapine 16 (50%). AZ5909 descended from AXTE which had very complex parentage involving Acalas, triple hybrids, and possibly *G. barbadense*. John Cotton Polycross was the intercross and polycross of four Acalas, 'Auburn 56', Stoneville 213, 'Deltapine Smoothleaf'; and 'Paymaster 111' (Calhoun et al. 1994). Almost all the varieties currently grown in the Midsouth have one or both of these new varieties in the pedigree.

These formulae for success had two components. The first was organized cooperation between states, ARS, and commercial companies. The second was the crossing of an adapted variety with very exotic germplasm to create a population with a large genetic variance.

<u>Experimental Error and Techniques</u>

Another factor, frequently overlooked in practical breeding programs is the large environmental variation that obscures detecting useful genetic variability. Using good experimental designs to account for environmental effects is one method of detecting useable genetic variability. Frequently, the number of replications and environments to account for uncontrollable variation is too small to detect meaningful differences. It requires 41% more replications to detect significant interactions between varieties and treatments than that required for measuring varietial differences with only one treatment. A second method of detecting useful variation is to develop new techniques to measure variation for important components of yield. Two areas where improvements in selection would occur, are (1) improved laboratory and field techniques that accurately measure disease and nematode resistance, and (2) use of genomics to detect useful genes.

Genetic Variability

The simplest model for genetic progress (GP):

$$GP = i\sigma ph$$

where:

i = standardized selection differential
σp = phenotypic standard deviation
h = linear regression of genotype on phenotype

The phenotypic variance is the sum of genetic (G) and environmental (E) factors and their interaction (GE). If G is small or E and GE are large, the selection progress becomes stagnant. Van Esbrock et al. (1999) investigated genetic diversity of USA cultivars from 1970 – 1995. They concluded " our study has shown that genetic uniformity in cotton is greater today than 25 years ago." Further they state that germplasm diversity has not translated to diversity in the field because only a few cultivar genetic types are extensively grown. Kerby et al. (2000) reported that in studies with nine popular varieties grown at nine locations in 1997 and 1998 that 94% of the yield variation was associated with locations, 6% for variety X location, and 1% for varieties. They reported a second series of studies involving 12 varieties grown in 16 cotton growing states for the years 1996, 1997, and 1999; a total of 785 tests for yield. Similar results were obtained and showed that the yield variation for locations, variety X location, and varieties was 90, 9, and 1% respectively. Bowman et al. (1996) studied the genetic base of modern varieties and concluded that the genetic base for cotton improvement was large, but if private breeding programs focused primarily on short-range goals, erosion of genetic diversity in breeding progression could suffer.

Breeding Objectives and Yield Plateaus

While breeding for increased yield is a major objective, there are other characteristics that have to be met for a variety to be successful. Frequently, these other characteristics may be negatively correlated with increased yields. Also, breeding priorities may change. The strong priority placed on yield increases has changed in the last 10 years. Prior to the 1990s, cotton subsidies and profitability were strongly associated with increased yields. The introduction of transgenics introduced a new era with new priorities for cotton breeding. The emphasis was on added value traits. Traits such as Bt, Roundup resistance, and buctril resistance became the primary focus. With this change in priorities came changes in breeding methodology and evaluation procedures. The backcross method became the breeding method of choice and the time and amount of testing spent was reduced so that the new transgenics could be quickly marketed. In 1995, there were essentially no transgenic cotton varieties grown commercially in the world. By 2001, transgenics accounted for 78% of the USA acreage (Table 6), (USDA, Agri. Marketing Service, Cotton, 1996 - 2001). All transgenic cotton varieties have been produced by backcrossing the one or two transgenes into established varieties, such as 'Stoneville 474', 'Deltapine 5415', 'Deltapine 90', 'Deltapine 5690','Deltapine 20', 'Deltapine 50', 'Deltapine 5409', 'SureGrow 125','SureGrow 501', 'Paymaster HS 26', and 'Paymaster 1200'. While using this procedure, there is little opportunity to make improvements in yield, unless the trait itself confers suppression of some pest that affects yield. In a strict backcross procedure selection for one major gene there is little useful genetic variance available for yield. There exists the possibility that the transgene itself might influence yield, but this affect is more likely to be negative than positive. The results in Table 7 show the average yield performance of transgenics and their two conventional recurrent varieties. Initially, there was some increase in yield associated with Bt, which is believed to be associated with control of some insects not controlled by insecticides. The results in Table 8 show 2001 data taken from the reported variety test of Arkansas, Missouri, and Mississippi Delta with a total of 17 locations. The results in Table 8 show little difference in conventional and transgenics with the exception that Roundup Ready varieties yielded 9% less than the other types. Conventional varieties tended to have slightly longer and stronger fiber. Transgenic Bt has resulted in major reductions in losses due to Lepidopterous insects and also reduction in insecticides. The primary benefit to growers has been that transgenics have made management simpler and reduced labor and machinery requirements.

Another breeding priority that is in the process of change is the need to improve fiber quality. There have been serious losses in the USA Textile industry which in turn, has resulted in the cotton grower losing markets. To combat foreign competition and regulatory requirements, USA textile mills have modernized their equipment. Modern faster operating mills require longer, stronger, and finer fiber with fewer short fibers, neps, and trash than what we are producing currently. Improving these fiber traits may result in some losses in yield. The analysis of 36 years of high quality testing has shown (Table 9) that there is a loss of 8 lbs lint for each 1/32 length increase, 15 lbs lint for one HVI strength increase, and a gain of 9 lbs/acre for each unit increase in micronaire.

Summary

There are two ways to end yield plateaus. These are: (1) application of new management technology, such as insecticides, equipment, crop ecology, etc., and (2) new genetic technology, such as varieties. The genetic factors that influence yield improvement are:

1. Useful genetic variance
2. Reduction in confounding effects of environments
3. Development of new techniques to detect genetic variability
4. Basic and developmental programs
5. Breeding objectives
6. Association of other traits with yields

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Table 1. Average[1] lint yield of two obsolete and two modern varieties.

Variety	Year of Release	Yield, lbs lint/acre[2]	
		1st harvest	Total
Stoneville 213	1962	686a	832a
Deltapine 16	1965	685a	814a
Average		685	823
SureGrow 747	1999	844b	1032b
Stoneville 474	1994	844b	1030b
Average		844	1031

[1] Average of two locations each in 1998 and 1999.
[2] Any two means in a column not followed by the same letter are statistically significant by LSD at the 0.1 probability level.

Table 2. Average harvestable acres[f], and % losses due to insects[ff], diseases, nematodes for Mississippi for years 1981 through 2000 and their correlations with yield.

Losses or characteristic	Mean	Correlation (Prob.)	R^2
Harvested acres	1,124.0	0.168 (0.48)	2.8
All pest losses	20.4	0.291 (0.48)	8.5
All insects	8.8	0.337 (0.15)	11.4
All diseases	11.6	0.110 (0.65)	1.2
All nematodes	2.8	0.096 (0.69)	0.9
Worm losses	3.4	0.404 (0.08)	16.3
Lygus losses	1.2	0.124 (0.60)	1.6

[f] Harvestable acres X 10^{-3}; data from USDA Agricultrual Statistics.
[ff] Pest losses obtained from Insect & Disease Losses, Beltwide Prod. Conf. 1982 – 2001.

Table 3. Regression[1] of variety test mean on year of tests (X)[2] for 15 USA locations and average yield for three periods covering 1960 to 1996.

Period 19__	Lint yield on Xi lbs lint/acre	Avg. yield per period lbs lint/acre
60 – 81	$891 - 1.79\ X_1$ (2.38)	870
82 – 96	$998 - 4.51\ X_2$ (5.21)	1043**
60 – 96	$832 + 6.05\ X_1$ (1.25)**	941

[1] Standard error in parentheses.
[2] X = years after the initial year of the period.
** Yield average 1043 significantly (0.0001) higher than 870.

Table 4. Regression of years (X) of test on yearly average of yield and yield components from 1964 to 1999. Data from Regional High Quality variety tests.

Characteristic (Y)	Regression of Y on X: Intercept	$+bx + bx^2$	% b/Mean	R^2%	b prob. Sig. Level
Yield, linear, lbs/ac.	678	+ 2.93 X	0.32	6.5	0.1348
Yield quadratic	- 744	$+38.4\ X - 0.22\ X^2$	--	9.5	0.1918
Lint %	32.8	+ 0.07 X	0.18	45.7	0.0001
Boll weight, g/boll	8.95	- 0.04 Xi	0.71	76.6	0.0001
Seed weight, g/100 seed	16.59	- 0.067 Xi	0.60	82.0	0.0001

Xi = number of years after 1900.

Table 5. Estimated annual yield progress by regression of year of variety release on variety yields (b).

Reference	Years of tests	No. of varieties	Range in years of release	Slope (b)[2] lbs/lint/ac
Bridge, et al., 1971	1967-68	13	1922-62	9.1a
Bridge and Meredith, 1983	1978-79	17	1910-78	8.5a
Wells and Meredith, 1984	1982	12	1905-78	5.7b
Meredith, et al, 1997	1938-93	16	1938-93	5.4b
Meredith, 2002	1998-99	38	1938-93	4.7b
Meredith, 2002[1]	1998-99	23	1983-99	3.5ns

[1] Row 6 of data is a subset of row 5.
[2] Any two bs not followed by the same letter are significant at the 0.05 or lower probability level.

Table 6. Acreage % planted to transgenics.

YEAR	USA	MS	SC
1996	12.0	37.8	16.4
1997	23.0	53.9	32.4
1998	45.0	70.5	59.4
1999	60.0	82.2	96.4
2000	72.1	87.0	85.0
2001	78.0	93.7	90.6

Data from Cotton Acres Planted, 1996 – 2001, Agr. Marketing Service, Cotton.

Table 7. Yield comparisons[f] of transgenic varieties and their recurrent parent.

	Lint yield, lbs/acre	
Type variety	1st harvest	Total
Conventional	718	925
Roundup	712	935
Bt	912*	966
Bt/RR	757	946

[f] Means are from four environments in 1998 and 1999; recurrent parents were Deltapine 5415 and Paymaster 1200.
* Indicates statistical significance at 0.05 probability level.

Table 8. Average yield and fiber properties of transgenic and conventional varieties from three 2001 variety tests in Missouri, Arkansas, and Mississippi Delta.

Variety type	No. of varieties	Lint lbs/ac	UHM length	UNIF.	HVI Str	MIC
Conventional	4	1094	1.13	84.1	30.1	45.4
Bt	2	1081	1.13	83.2	27.9	42.2
Roundup Ready	4	996	1.12	83.7	28.8	44.4
Bt/RR	5	1090	1.10	83.5	28.2	45.5
BXN	1	1065	1.11	83.1	28.6	44.3

Total number of locations = 17.

Table 9. Common regression coefficient[f] of yield, lint/acre^{-1}, on traits for the 20 to 36 years of Regional High Quality Variety testing.

	Common slope (by) of by over years		
Traits (X)	**b**	**R^2**	**Prob.**
Upper half mean (.01 in.)	-2.54	69.7	<0.0001
2.5% span length (.01 in.)	-2.72	74.6	<0.0001
Uniformity	-12.9	68.9	<0.0001
Stelometer strength (T[1])	-2.77	75.2	<0.0001
HVI strength	-14.6	70.9	<0.0001
Yarn tenacity	-3.68	78.0	<0.0001
Micronaire (0.1 unit)	9.0	76.1	<0.0001

[f] Regression coefficient computed assuming all years regression are from the same population and correcting for each year's intercept differences.

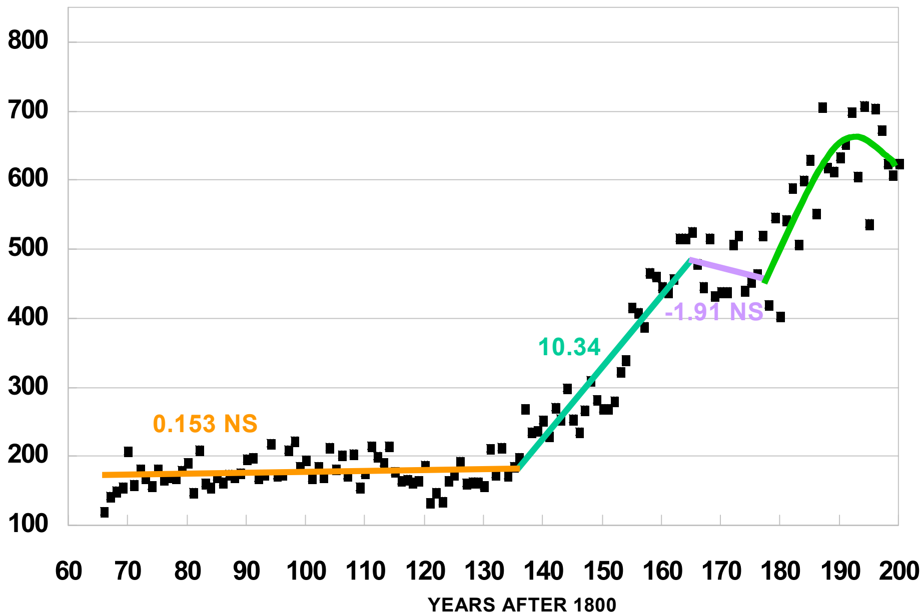

Figure 1. USA average yield (lbsa./acre)from 1866 to 2000.

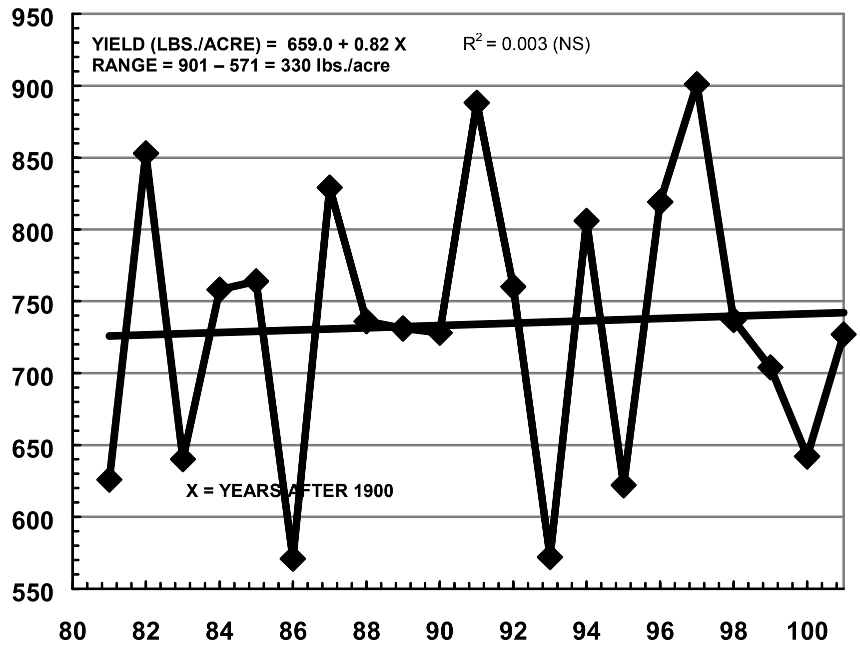

Figure 2. Average Mississippi yield from 1981 to 2001.

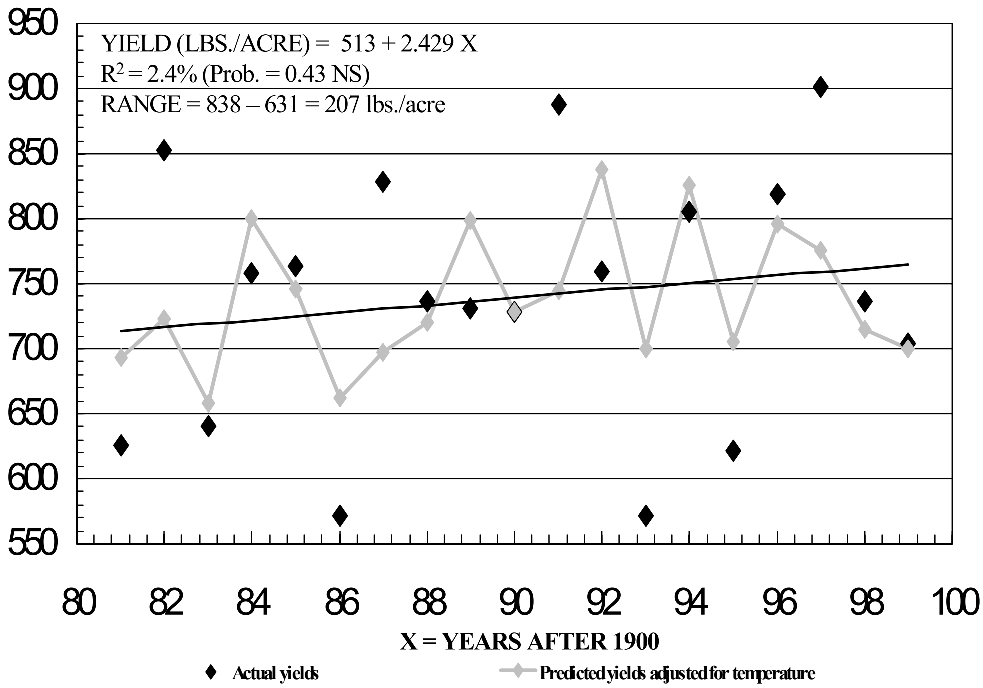

Figure 3. Predicted Mississppi yield assuming each year had an average maximum July-August temperature.

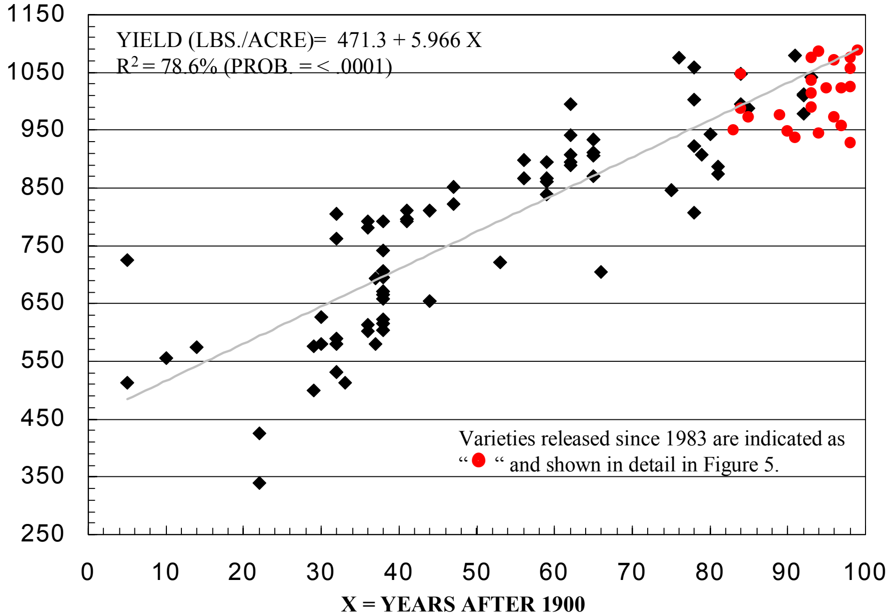

Figure 4. Regression of variety release year on yield as reported in five obsolete vs. modern variety tests.

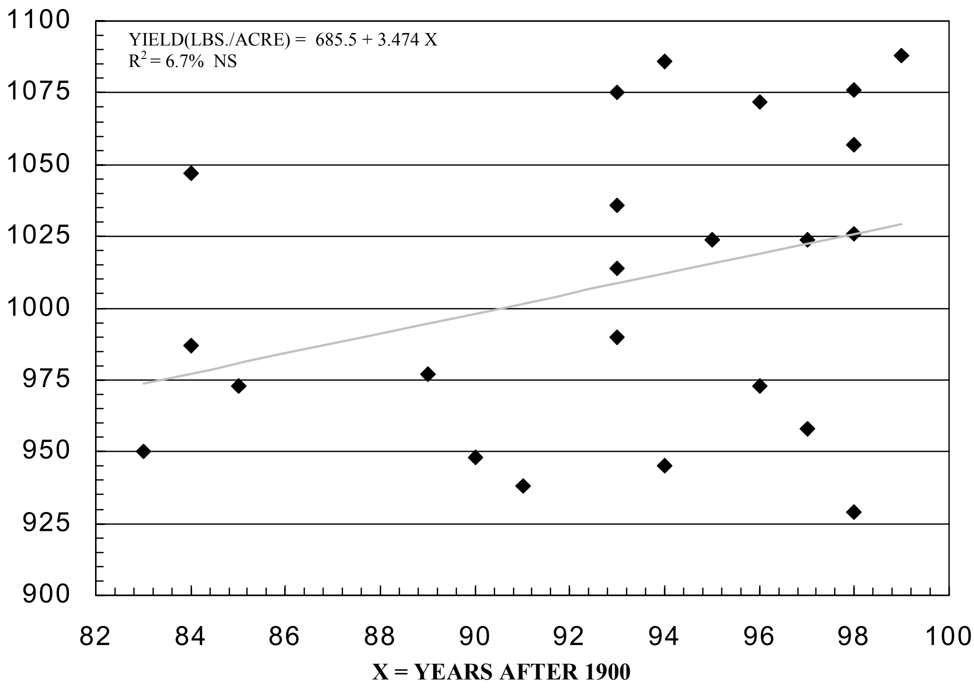

Figure 5. Regression of year of variety release year on varieties' yield as averaged from two locations each in 1998 and 1999.