INHERITANCE OF AND INTERRELATIONSHIPS OF TRYPTOPHAN, NIACIN, PROTEIN, AND KERNEL WEIGHT IN CORN

by

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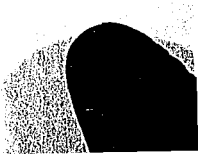
A THESIS

Submitted to the School of Graduate Studies of Michigan State College of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Farm Crops
1953



ACKNOWLEDGMENT

The writer wishes to express his sincere thanks and appreciation to Dr. E. C. Rossman for his guidance in outlining this research and for his advice in the preparation of the manuscript. Grateful acknowledgment is also due to Dr. R. W. Luecke and Dr. E. J. Benne for their valuable assistance and to Mrs. Jean Vincenzi for helping with the assays reported herein. The writer is also indebted to the Michigan Certified Hybrid Seed Corn Producers Association for granting the funds which made this study possible.

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INTRODUCTION

Improvement in nutritive value of corn for human and animal consumption is one of the objectives in some corn breeding programs. Approximately eighty-five percent of the total corn production in the United States is used for livestock feeding. In other parts of the world, millions of people depend upon corn for a principal part of their diet.

Corn protein is low in tryptophan and lysine, two of the essential amino acids for normal growth. Corn is also low in niacin content. Lack of niacin is mainly responsible for pellagra in the high corn diet areas.

Since the early work of Hopkins (21), a number of investigations have shown that the chemical composition of the corn is under the control of genetic factors. Therefore, improvements in protein, tryptophan and niacin contents of corn are possible by plant breeding techniques.

Protein, tryptophan and niacin contents in corn are all quantitatively inherited. The success of a breeding program to improve the quantity of these constituents may be improved with more information concerning the mode of inheritance and the interrelationships of these constituents. The objectives of this study were:

(1) To survey sixty inbreds as source materials for

breeding high niacin and high tryptophan corn.

(2) To study the interrelationships of tryptophan, niacin, protein and kernel weight in corn.

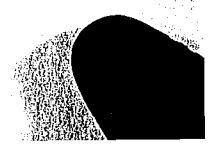
(3) To obtain information on dominance relationships, nature of gene interactions, gene numbers and degree of heritability of tryptophan, niacin, protein and kernel weight in corn.

REVIEW OF LITERATURE

Feeding experiments with corn (2, 7, 26, 29) showed that its protein was of low biological value, due principally to its low tryptophan content. In their metabolic study of amino acids, Wilcock and Hopkin (48) demonstrated that tryptophan was directly utilized as the normal precursor of some specific hormone or other substances essential to growth. Matsuyama and Mori (28) in their quantitative study of tryptophan in various proteins found only traces of tryptophan in corn protein as compared to 0.83%, 1.33%, and 1.00% of tryptophan in the proteins of soybean, rice and wheat, respectively.

Mishler et al. (32) and Powick et al. (38) stated that corn diet was low in niacin content. Supplementing the corn diet with synthetic niacin cured the deficiency and increased growth in their feeding experiments with chickens and pigs, respectively.

Burkholder (4) reported that corn meal contained 10 to 15 micrograms of niacin per gram. An adult would have to eat 1,000 grams of corn meal per day in order to meet the daily niacin requirement of 15 milligrams per day. He suggested breeding a strain of corn which contained at least 35 microgram per gram for use by people whose dietary is pellagra producing.



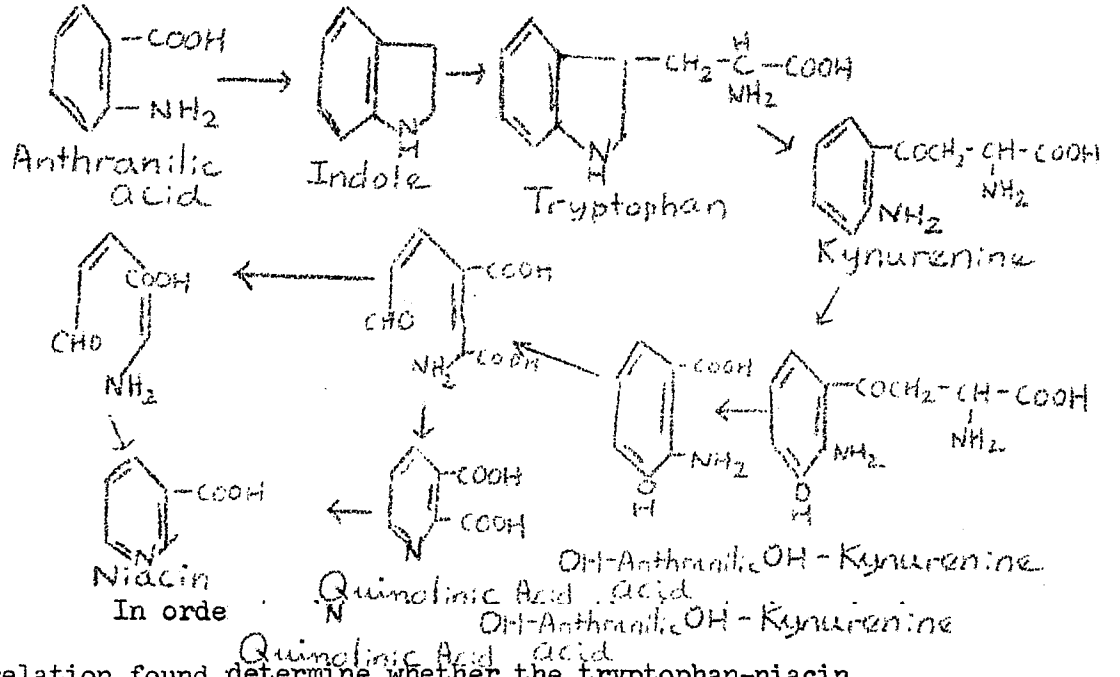
Krehl et al. (24) showed that either 50 mg. of tryptophan or 1.0 mg. of niacin per 100 gram of ration completely counteracted the niacin deficiency caused by the inclusion of 40% corn grits in a low protein ration. In their studies of significance of tryptophan in human niacin metabolism, Holman and DeLange (20) gave evidence that protein deficiency and particularly tryptophan deficiency might play a significant role in pellagra.

Elvehjem (13) found an increase of niacin and niacin metabolite excretion when rats were fed tryptophan. He stated that the long recognized relationship between the consumption of corn and pellagra was mainly due to the deficiencies of tryptophan and niacin in corn.

In their survey of Guatemalan corn varieties for tryptophan and niacin, Aguirre and Bressam (1) found that quantities of tryptophan supplied by corn provided 50 to 118% of that required for adult human maintenance, while the same corn only supplied an average of 73% of the required niacin. They concluded that the conversion of some tryptophan into niacin and the release of unavailable or bound niacin in "Tortillas" prepared by soaking corn meal in lime water, accounted for the low incidence of pellagra in Guatemala.

Bonner and Yanofsky (3) using mutant strains of Neurospora studied the biosynthesis of tryptophan and niacin. They stated that tryptophan appeared to serve as precursor of

niacin and also proposed the following hypothesis.



In order to determine whether the tryptophan-niacin relation found by Nason (33) demonstrated it by studying the mature excised corn embryo grown in sterile culture. He found that the addition of tryptophan to the nutrient solution resulted in a significant increase of niacin in the mature excised corn embryo.

Flynn et al. (14) analyzed individual selfed ears from an open pollinated variety for crude protein and niacin. As the percentage of crude protein increased, they observed a marked decrease in niacin. The kernels of medium protein corn contained 34.1 micrograms of niacin per gram and those of high protein corn contained 27.3 micrograms per gram.

Sarkar (42) found a significant negative correlation between protein and niacin content. Rodriguez et al. (41)

also reported a small negative correlation ("r" = -0.249) between protein and niacin content of 39 inbred lines of corn in Ohio. Frey (17) found highly positive correlation between protein and tryptophan in two crosses of corn.

Earley et al. (11) reported that a heavy application of nitrogen to the soil resulted in an increase in the concentration of protein and a decrease in niacin.

Miller et al. (31) reported that niacin content appeared to be essentially independent of the protein and protein components studied.

In 1899, Hopkins (21) showed that it was possible to influence the composition of corn by proper ear-row selection. The first extensive protein selection in corn was inaugurated by the Illinois Agricultural Experiment Station at that time. After fifty years of selection, Woodworth reported (49) that the high protein strain contained 19.45% and the low protein strain had 4.91%. The shift was rapid at first but became slower in succeeding generations.

East and Jones (12) also reported that the protein content of corn was an inherited characteristic. They listed a number of other factors, such as temperature, moisture, and fertilizer, that might also affect protein content.

Previous investigations (10, 12, 34) have shown the effects of non-genetic factors influencing protein content of corn. Seasonal effects, location effects and stage of maturity

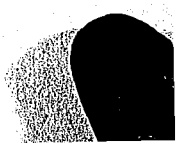
caused variations in protein content.

Inheritance studies of protein content in corn grain (15, 19) have shown that the number of hereditary factors affecting protein content must be large, and low protein was found to be dominant in most cases. Chemical composition of the entire kernel was influenced by heterosis since hybrid vigor increased the carbohydrate fraction of corn more than the protein fraction, thus tending to lower the protein percentage.

Osborne et al. (35) and Showalter and Carr (43, 44) reported that zein, which constitutes approximately one half of corn protein, was deficient in tryptophan.

It has also been proven (21, 30) that selection of corn kernel having large germ size would give both superior quality and quantity of corn protein and tryptophan since the germ portion of corn kernel contains a high protein percentage and a lower zein percentage than that of the endosperm portion.

For improvements in protein quality, Frey (17) suggested that it might be more desirable to select directly for increased percentage tryptophan in corn grain. He found complete dominance for low tryptophan in Illinois high x Illinois low, while Hy x 1198 showed no dominance. Protein percentage in the Illinois high x Illinois low followed the assumptions of arithmetic gene interaction while tryptophan,



leucine, isoleucine and valine inheritance followed either interaction. Protein percentage and tryptophan were conditioned at least by 22 and 15 genes, respectively.

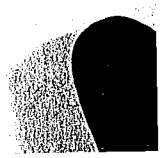
In one cycle of recurrent selection, Frey (16) found that the percentage of tryptophan was raised 0.013%, which was an increase of 12.79% over the original F_2 population.

Several workers (20, 25, 39, 45) have shown that the niacin concentration in corn was a function of the genetic constitution with very limited influence of environment. They reported that starch corn exhibited a wide range of niacin content when the different varieties grew on the same soil in the same locality during the same season.

Mather and Barton-Wright (27) noted that the starchy Su gene was dominant for lower niacin content over its su allele. They found that sweet corn had twice as much niacin as starchy corn. Gorfinkel (18) also reported practically a complete dominance of Su gene for low niacin. He found the niacin content of early varieties to be higher than the medium and late varieties.

Teas et al. (46) found tryptophan and niacin were consistently higher in sugary than in starchy in the late development period of kernel, but they were essentially equal in the two genotypes at earlier stages of kernel development.

Richey and Dawson (40) showed that the mode of inheritance for niacin content was multiple factor inheritance

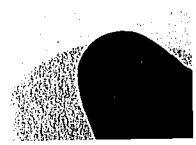


involving the joint action of many genes of small individual effects with dominance lacking. They found that single and double cross hybrids tended to be intermediate between the parental inbreds in niacin content.

In a series of high and low niacin crosses, Gorfinkel (18) observed that where the parents had a content of 22 micrograms per gram or less, the niacin content of the hybrids appeared to be additively determined and exceeded that of both parents. When the parental inbreds had more than 22 micrograms per gram the niacin contents of the hybrids were intermediate between the parents. Hybrids high in niacin came from crosses of high niacin inbreds.

Investigations by the Ohio Station (8, 22, 23) have shown that genetic and environmental factors, such as soil and season, influenced the niacin content of corn hybrids. Ditzler et al. (9) found that high and medium niacin contents were dominant in all the crosses studied and the niacin values of the hybrids fell between the limits established by the parental inbreds.

Richey and Dawson (40) found that the seed parent had twice the influence of the pollen parent on niacin content. Miller et al. (30) in their oil inheritance study also showed that the genotype of the ear bearing parent had a predominating influence on the oil percentage of the grain produced. Source of pollen had a consistent though relatively small effect.



Norden (34) found no relationship between kernel weight and protein contents. However, he found that the kernel weight was significantly affected by season, hybrids, maturities and location.

Leng (25) and Richey and Dawson (40) found no close relationship between kernel size and niacin concentration.

MATERIALS AND METHODS

Sixty inbreds were analyzed for tyrtophan and niacin contents. Two crosses, W23 x Oh 51A and W23 x R53 were available for inheritance studies of tryptophan and niacin. F_2 and backcross seeds were produced in the greenhouse during the winter 1951-1952. The patterns of these two crosses were:

(1) High niacin-low tryptophan (W23)
x
Low niacin-medium tryptophan (R53)

(2) High niacin-low tryptophan (W23)
x
Medium niacin-high tryptophan (Oh51A)

The symbols, P_1 and P_2, refer to the two parental inbreds; Bc_1 designates the backcross to P_1, and Bc_2 refers to the backcross to P_2.

Two rows each of the P_1, P_2 and F_1 and four rows each of F_2, Bc_1 and Bc_2 were planted on May 19, 1952 in the corn breeding nursery. Each row consisted of twenty plants spaced one foot apart. The plants were hand pollinated to eliminate possible effects of source of pollen on the immediate generation. Eight plants of one single cross were outcrossed with sweet corn pollen.

All ears were mature at harvest. They were dried in a seed corn drier at 100 degrees F. One hundred kernels of each

ear were counted and weighed. About two thirds of the kernels on each ear were ground in a Weber's hammer mill using a 20 mesh sieve. Random samples of the ground corn were taken for moisture determination. These were found to be quite uniform in moisture content, approximately 10% moisture. All the values reported are on the air-dry basis.

Protein Analysis--One gram of the ground corn was taken for protein determination. Nitrogen was determined by the standard Kjeldahl-Gunning Method as described by the Association of Official Agricultural Chemists (50). Protein values are Kjeldahl nitrogen x 6.25. One determination was made on each sample.

Microbiological Analysis--Microbiological methods are based on the observation that certain microorganisms require specific amino acids and vitamins for growth. Using a basal medium complete in all respects except for the amino acids and vitamins under test, growth responses of the organism are compared quantitatively in standard and unknown solutions. The acid produced by the organism is measured to determine the amount of growth which indicates the amount of vitamin or amino acids in the test solution. The procedure is briefly summarized as follows:

Test organism: Lactobacillus arabinosus 17-5(8014) was used for both tryptophan and niacin determinations. The

composition of inoculum and stab for culturing this organism is shown on Table 1.

Table 1. Composition of medium for inoculum (Lactobacillus arabinosus)

Ingredients	Proportion	Amount required for 200 ml.	500 ml.
Bacto-peptone	0.8%	1.6 gm.	4.0 gm.
Yeast extract	0.1%	0.2 gm.	0.5 gm.
Sodium acetate (anhydrous)	0.1%	0.2 gm.	0.5 gm.
Glucose	1.0%	2.0 gm.	5.0 gm.
Salt A	0.5%	1.0 ml.	2.5 ml.
Salt B	0.5%	1.0 ml.	2.5 ml.
For making stab, add 1% Bacto agar		2.0 gm.	5.0 gm.

Standard curve: The standard stock solutions for tryptophan and niacin were prepared with 2ug/ml. and 0.1ug/ml, respectively. Triplicate tubes were set up for each of the eight levels for the standard curves. Table 2 shows the amount of standard stock solution in each tube and Figures 1 and 2 show sample standard curves when the various levels of standard solutions were titrated with 0.1N sodium hydroxide. A new standard curve was prepared for each new group of assays.

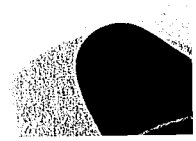


Table 2. Amount of standard tryptophan and niacin on the eight different levels

ml. of standard	ug./ml. trypt.	ug./tube N.A.	ml.H_2O	ml.B. medium
0.0	0.0	0.00	5.0	5.0
0.5	1.0	0.05	4.5	5.0
1.0	2.0	0.10	4.0	5.0
1.5	3.0	0.15	3.5	5.0
2.0	4.0	0.20	3.0	5.0
2.5	5.0	0.25	2.5	5.0
3.0	6.0	0.30	2.0	5.0
3.5	7.0	0.35	1.5	5.0

*Each test tube is thus filled up to 10 ml. mark.

Basal medium: The composition of basal medium for both tryptophan and niacin determinations is given in Table 3.

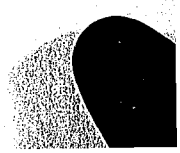


Table 3. Composition of 100 ml. of basal medium for tryptophan and niacin determinations

Ingredients	Amount
Casein hydrolysate 100mg./ml.	10 ml.
l -cystine 4mg./ml.	10 ml.
Biotin 0.1ug./ml.	0.4ml.
p-aminobenzoic acid 100ug./ml.	0.2ml.
Thiamine, calcium panthothenate pyrodoxine 100ug./ml.	0.2ml.
Riboflavin 100ug./ml.	0.4ml.
Adenine, Guanine, Uracil 1mg./ml.	2.0ml.
Salts A	1.0ml.
Salts B	1.0ml.
Glucose	4.0gm.
Sodium acetate (anhydrous)	4.0gm.
d-l tryptophan 4mg./ml. (for niacin determination)	10.0ml.
Niacin 100ug./ml. (for tryptophan determination)	14.0ml.

*The mixture is adjusted to pH 6.6 -6.8 and diluted to 100 ml. with distilled water.

Figure 1 Sample standard curve for tryptophan assay

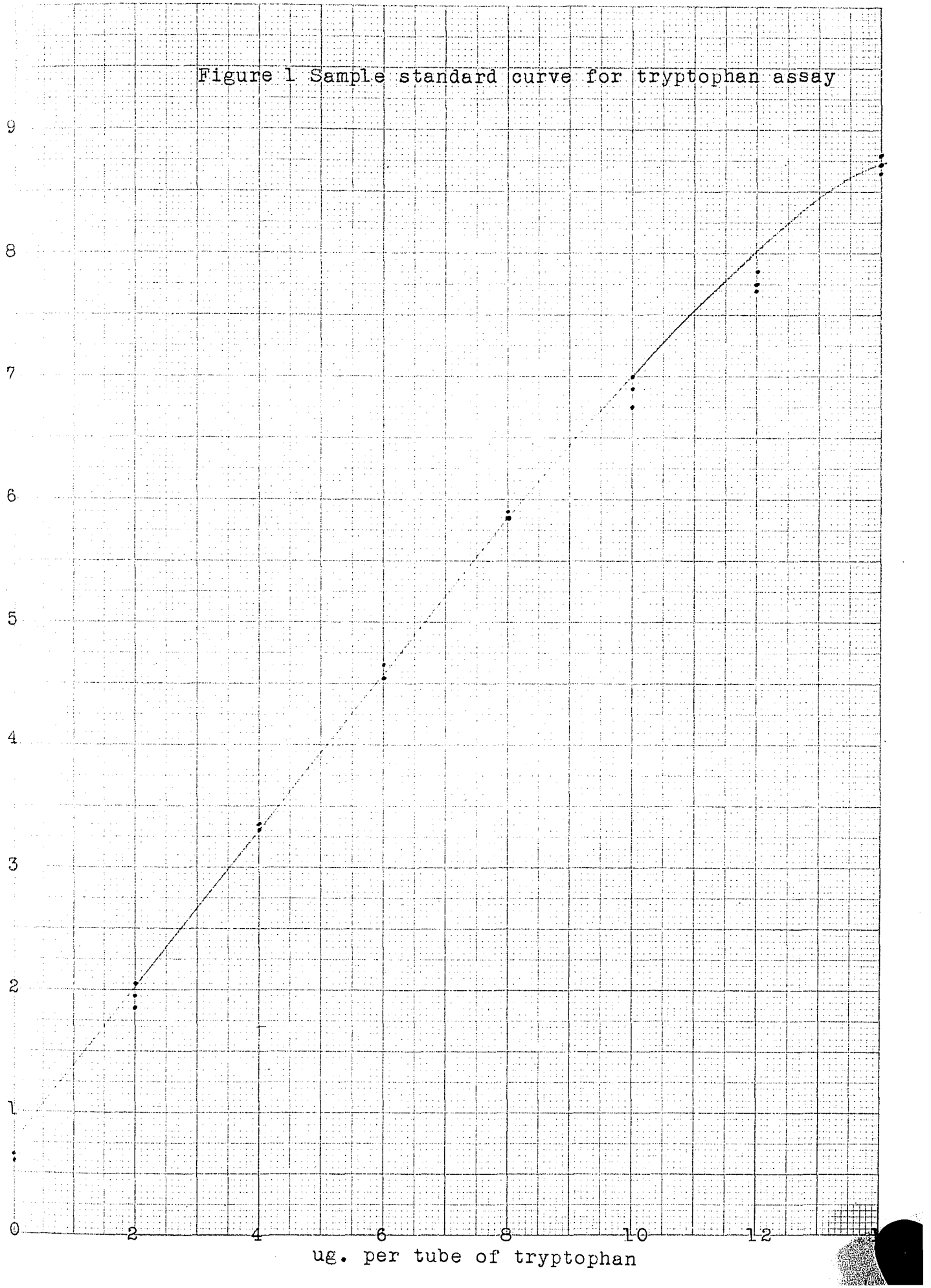
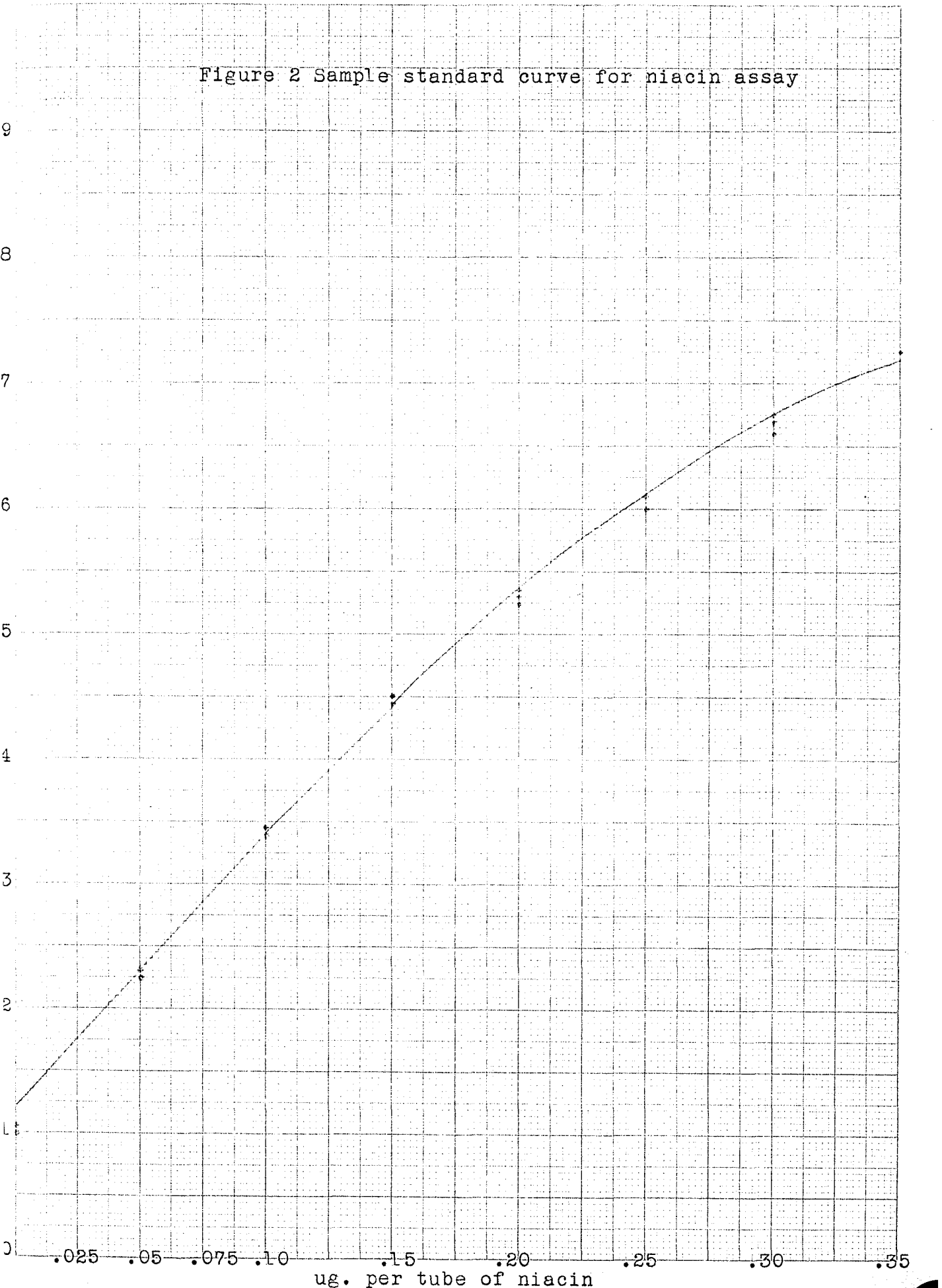


Figure 2 Sample standard curve for niacin assay



Tryptophan analysis: Since the unnatural D-forms of certain of the essential amino acids are not utilized in nutrition, the values expressed in this study are for L-tryptophan. Tryptophan values are given as the percentages in the whole corn kernel. Sixteen milliters of 4N NaOH were added to 0.5 grams of the ground sample and the material was autoclaved at 250° F. with 15 pounds of pressure for eight hours to insure complete digestion. Concentrated hydrochloric acid was used to adjust the sample to pH 7 and distilled water was added to dilute the sample to 100ml. After filtering, the sample was covered with a few drops of toluene and stored in the refrigerator until assayed.

Niacin analysis: Values for niacin are expressed in micrograms per gram of grain. One gram of the ground sample mixed with 50 ml. of 0.1N HCL was hydrolyzed in the autoclave for 30 minutes at 15 pounds of pressure with a temperature of 121° C. After the sample had been digested, it was centrifuged for 15 minutes at 3500 R.P.M. Twenty-five ml. of the supernatant was drawn, adjusted to pH 4.6 with NaOH, and diluted to 50 ml. After filtering, the sample was covered with a few drops of toluene and kept in refrigerator until assayed.

Tryptophan and niacin assays: When the prepared samples reached room temperature, dilutions were made to get the proper concentration. Duplicate samples of 1, 2, and 3 ml. were pipetted into test tubes and 4, 3, and 2 ml. of distilled water

were added to bring the tubes to the 5ml. mark, respectively. Five milliters of the basal medium were added to each tube of both unknown and standard samples. The tubes were covered with metal caps and sterilized in an autoclave for 12 minutes at 15 pounds of pressure at 121° C. The tubes were then inoculated with one drop of Lactobacillus suspension which had been transferred from the stab culture about 18 hours previously and had been treated with a series of dilutions by sterile saline solution. After incubating 72 hours at 37° C., the tubes were titrated to pH7 with 0.1N NaOH. A standard curve was prepared, from which the concentrations of the unknown samples were determined. The same procedure was applied for both tryptophan and niacin determinations except that the basal medium used for tryptophan assay contained no tryptophan and the basal medium for niacin assay contained no niacin.

Methods of Inheritance Study:

(1) Heterosis and dominance relationships: The interpretation of the data for heterosis and dominance relationships was based on the patterns outlined by Powers (36, 37). Genic variances and means of the population were used to determine whether heterosis, phenotypic dominance, genic dominance, or no dominance existed.

(2) Nature and interactions of genes: The formulas by Powers (37) were used for estimating the expected means on

the assumption of arithmetic and geometric gene interactions. These formulas are shown in Table 4.

Table 4. Formulas for estimating the expected means on the assumption of arithmetic and geometric gene interactions

Population	Arithmetic Mean	Geometric Mean
F_2	$\frac{\bar{P}_1 + 2\bar{F}_1 + \bar{P}_2}{4}$	antilog of $\frac{\log\bar{P}_1 + 2\log\bar{F}_1 + \log\bar{P}_2}{4}$
Bc_1	$\frac{\bar{F}_1 + \bar{P}_1}{2}$	antilog of $\frac{\log\bar{F}_1 + \log\bar{P}_1}{2}$
Bc_2	$\frac{\bar{F}_1 + \bar{P}_2}{2}$	antilog of $\frac{\log\bar{F}_1 + \log\bar{P}_2}{2}$

* $\bar{P}_1$, $\bar{P}_2$ and $\bar{F}_1$ are the means of two parents and F_1 populations, respectively.

(3) Gene numbers: The formula by Castle and Wright (6) was used for estimating gene numbers.

$$N = \frac{(F_2 \text{ range})^2}{8\,(SF_2^2 - SF_1^2)}$$

N = the number of gene pairs

F_2 range = the highest F_2 individual minus the lowest F_2 individual

SF_2^2 = the variance of the F_2

SF_1^2 = the variance of the F_1

The assumptions underlying this formula are:

1. All gene effects are additive.
2. All genes are equally important and have equal effects.
3. No dominance is present.
4. The F_1 variance represents only environmental variances.
5. One parent contains only plus genes and the other parents contain only minus genes for the characters in question.

(4) Heritability: Warners method (47) was used to estimate heritability. In this method, heritability estimates are based on the variances of the three segregating populations, the F_2 and the summed backcrosses to each parent. The method has the advantage of not requiring an estimate of environmental or of total genetic variances, but uses only total within population variances.

Heritability is calculated as:

$$\text{Heritability} = \frac{(1/2)\ D}{V\ F_2}$$

where $(1/2)\ D$ = the additive genetic component of the F_2 variance,

VF_2 = total within F_2 variance, and

$(1/2)D = 2(VF_2) - (VBc_1 + VBc_2)$ where

VBc_1 and VBc_2 are the total within variances

of the backcrosses of the F_1 to the respective parents.

The assumptions underlying this formula are:

1. Genic effects are additive, locus to locus (no epistasis).
2. Genotypic and environmental variances are independent.
3. The environmental components of F_2 and backcross variances are of comparable magnitude.

EXPERIMENTAL RESULTS AND DISCUSSION

A Survey of Tryptophan and Niacin Contents for Sixty Inbred Lines

Tryptophan and niacin contents for sixty inbred lines are shown in Table 5. The averages were 23.54ug./gm. for niacin and 0.072% for tryptophan. Niacin contents ranged from 13.45ug./gm. to 33.54ug./gm. a difference of 149.7%. Tryptophan contents ranged from 0.050% to 0.089%, a difference of 78%. Kernel weights for these inbreds averaged 24.04 grams per 100 kernels and ranged from 13.10 grams to 35.00 grams.

Considerable differences in niacin and tryptophan contents were evident among inbred lines that had no previous selection for these characteristics. Analysis of individual ears of the parental lines used in the following inheritance studies showed considerable variability for tryptophan and niacin contents within long-time inbred lines of corn (Table 7). Since these inbreds had no selection for tryptophan and niacin, it is possible that the inbreds might be quite variable for these characteristics.

Table 5. A Survey of Niacin and Tryptophan Content of 60 Inbred Lines Grown in Michigan Experiment Station, 1950

* (The weight in grams per 100 kernels of each inbred is also recorded)

Inbreds	Niacin ug./gm.	Tryptophan 0/0	Kernel Weight gm./100	Inbreds	Niacin ug./gm.	Tryptophan 0/0	Kernel Weight gm./100
R53	18.11	.060	30.88	MS42	20.41	.087	28.10
W9	28.78	.056	18.10	L317	16.93	.082	14.00
ND230	27.53	.072	20.30	WR3	18.58	.082	22.50
49	24.73	.064	24.00	MS4	27.02	.073	20.80
W-D	18.19	.066	19.40	R9-2-1-1-1	22.20	.077	29.30
M13	31.09	.067	25.20	MS113	27.68	.069	25.70
Ial53	26.56	.082	21.10	MS1	24.97	.089	22.50
W25	27.66	.065	28.90	P44-4-2-6-2	14.73	.076	32.30
WF9	27.46	.073	22.80	MS24A	20.13	.089	27.10
Ohio 51A	27.67	.063	27.39	MS64	33.54	.081	17.80
M14	25.90	.072	16.80	F14-3-3-7-2	16.82	.075	25.50
W23	32.14	.050	20.61	P44-4-6-1-1	26.84	.063	26.50
Hy2	23.05	.066	19.40	P44-4-3-6-1	14.89	.066	30.70
W10	19.91	.074	24.70	D95-4-6-1-1	25.76	.078	22.90
L289	26.56	.076	19.80	P87-6-14-1	32.88	.064	22.80
C105	21.78	.074	27.40	F14-3-8-5-1	17.97	.076	19.20
MS14	25.32	.062	28.60	D95-4-5-1-1	21.45	.073	27.00
A385	14.86	.076	21.90	P44-2-1-5-1	28.91	.069	25.80
MS17	20.65	.062	23.10	G11-1-2-2-3	20.39	.072	23.70
Oh43	23.72	.067	28.30	D95-4-5-6-1	24.77	.080	27.60

Table 5. (continued)

Inbreds	Niacin ug./gm/	Tryptophan 0/0	Kernel Weight gm./100	Inbreds	Niacin ug./gm.	Tryptophan 0/0	Kernel Weight gm./100
W146	22.70	.070	24.40	F50-2-3-2-1	13.43	.070	33.80
MS40	28.34	.078	23.50	F13-3-5-6-1	25.83	.074	22.00
Oh45	20.41	.064	24.30	P44-2-4-8-1	25.01	.071	35.00
SD105	19.31	.080	18.80	F16-2-4-2-2	20.85	.077	23.90
187-2	23.28	.070	31.80	P7-1-3-3-3	26.75	.069	25.90
W8	28.05	.082	18.50	P7-1-1-4-1	19.18	.069	24.0
MS206	17.55	.083	19.80	G100-5-2-7-1	28.56	.069	15.8
MS50	16.12	.078	23.60	Kan K R	25.68	.063	24.0
MS12	21.38	.079	24.20	M15-58-3	24.42	.080	24.6
MS15	26.53	.081	30.70	N	30.56	.073	13.10

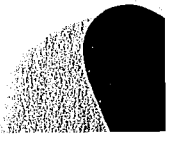
Correlation coefficients for tryptophan, niacin, and kernel weight are presented in Table 6.

Table 6. Correlation coefficients "r" for tryptophan, niacin and kernel weight of the sixty inbred lines

Correlation between	"r" value
Tryptophan and niacin	-0.2438
Tyrptophan and kernel weight	-0.1098
Niacin and kernel weight	-0.2653*

*Significant at 5%

All the "r" values were negative, but only the correlation between niacin and kernel weight was significant at 5% level of probability and it was too small to be of any importance in selection. However, there was a slight trend toward higher niacin in small kernels and vice versa. There was no relationship between tryptophan content and kernel weight for the 60 inbreds studied. Even though the negative correlation between tryptophan and niacin contents was not significant, there were several inbreds that were above average for both tryptophan and niacin, and some lines were low in both. Thus, it appears possible to develop lines with higher than average contents of both tryptophan and niacin.



Interrelationships of Tryptophan, Niacin, Protein and Kernel Weight

Two crosses, W23 x R53 and W23 x Oh51A, were used in studying tryptophan and niacin. W23 x R53 was a cross of high niacin-low tryptophan x low niacin-medium tryptophan. W23 x Oh51A was a cross of high niacin-low tryptophan x medium niacin-high tryptophan. Protein percentages were determined only for W23 x R53 populations. Kernel weights were determined for both crosses. Means, standard deviations of means and ranges for protein, tryptophan, niacin and kernel weight are presented in Table 7.

Large differences in tryptophan, niacin, protein and kernel weight were observed within the non-segregating P_1, P_2 and F_1 populations of both crosses, Coefficients of variations of all the characteristics for each population were calculated (Table 8). Despite the small number of individuals in the P_1, P_2 and F_1 populations, it appeared that the non-segregating populations were as variable as the segregating populations in all the characters studied. Variability in the non-segregating populations, P_1, P_2 and F_1, is commonly attributed to environmental factors. Inbred lines of corn tend to be more susceptible to non heritable factors than the more vigorous F_1, F_2 and backcross populations. Since these inbreds had not been previously selected for these characteristics, it is also possible that there was some genetic variation among individuals within a line.

Table 7. Means and Ranges of Niacin, Tryptophan and Kernel Weight for each population in the Cross of W23 x R53 and W23 x Ohio 51A

		W23 x R53				
		Niacin ug./gm.	Tryptophan 0/0	Protein 0/0	Kernel Weight gm./100	Number of Samples
P_1*	Mean	32.14	.050	10.00	20.61	
	Range	23.73-41.39	.042-.059	7.63-12.81	16.36-25.50	15
	S.D. of Mean	1.35	.0011	0.31	1.00	
P_2*	Mean	18.11	.060	12.57	30.88	
	Range	13.25-25.64	.053-.069	10.44-14.06	22.90-36.64	15
	S.D. of Mean	0.86	.0015	0.26	1.05	
F_1	Mean	27.97	.056	11.23	24.11	
	Range	21.77-34.01	.051-.062	8.69-14.13	13.65-30.15	15
	S.D. of Mean	1.03	.0008	0.39	1.30	
F_2	Mean	24.88	.060	12.24	24.16	
	Range	16.48-41.75	.049-.070	9.06-15.38	13.76-30.45	47
	S.D. of Mean	0.76	.0007	0.22	0.52	
Bc_1	Mean	30.28	.053	11.06	25.56	
	Range	21.82-42.72	.045-.061	8.63-13.69	15.00-32.15	43
	S.D. of Mean	0.82	.0006	0.21	0.58	
Bc_2	Mean	21.78	.059	11.95	26.83	
	Range	12.81-34.90	.049-.069	9.50-15.19	17.47-38.85	49
	S.D. of Mean	0.76	.0007	0.20	0.56	

*P_1 = W23 P_2 = R53

Table 7. (continued)

W 23 x Ohio 51A

		Niacin ug./gm.	Tryptophan 0/0	Kernel Weight gm./100	Number of Samples
P_1*	Mean	32.14	.050	20.61	
	Range	23.73-41.39	.042-.059	16.36-25.50	15
	S.D. of Mean	1.35	.0011	1.00	
P_2*	Mean	27.67	.063	27.39	
	Range	29.81-24.34	.055-.082	23.64-29.32	15
	S.D. of Mean	0.39	.0016	0.95	
F_1	Mean	32.64	.056	29.54	
	Range	27.33-38.66	.049-.065	19.72-36.50	15
	S.D. of Mean	0.81	.0012	1.04	
F_2	Mean	32.94	.056	26.29	
	Range	20.24-49.72	.044-.066	15.85-34.15	58
	S.D. of Mean	0.89	.0008	0.56	
Bc_1	Mean	32.50	.050	23.57	
	Range	22.90-48.43	.041-.060	12.90-31.86	62
	S.D. of Mean	0.68	.0004	0.58	
Bc_2	Mean	30.86	.056	28.81	
	Range	17.90-55.94	.047-.074	16.04-34.07	61
	S.D. of Mean	0.87	.0007	0.47	

* P_1 = W23 P_2 = Ohio 51A

Table 8. Coefficient of Variability of all the characters studied in each populations of the crosses W 23 x R 53 and W 23 x Ohio 51A

Populations	W 23 x R 53				W 23 x Ohio 51A			Average %
	Protein	Tryptophan	Niacin	Kernel Weight	Tryptophan	Niacin	Kernel Weight	
P_1	11.96	8.70	16.61	15.57	8.70	16.61	15.57	13.39
P_2	7.88	7.98	19.02	13.24	10.03	5.53	7.81	10.21
F_1	13.45	5.38	14.70	20.90	8.18	9.56	13.64	12.26
F_2	12.34	7.82	20.86	14.65	10.25	20.38	16.17	14.63
Bc_1	12.75	7.30	18.16	14.91	6.92	16.49	19.98	13.79
Bc_2	11.80	9.14	24.70	14.50	10.09	21.94	12.84	15.00

Long-time inbred lines are commonly assumed to be homozygous, but actually they may be homozygous only for the characters selected and may be variable for unselected characters. Only ears with good seed set were selected for this study so it is not likely that sparse-pollination was a factor in the result obtained.

The frequency distributions tables for tryptophan, niacin, protein and kernel weight are shown in Tables 9, 10, 11, and 12, respectively. The wide ranges covered by parents again indicated that they were relatively heterozygous for the factors affecting these characteristics. The distribution of F_1 individuals for tryptophan, niacin and protein were within the limits set by both parents and the two backcross populations tended to shift toward their respective parental side and few extremes appeared. For all the characters studied, the F_2 population had a wider distribution than that of the F_1. This leads to the conclusion that these characters were quantitatively inherited. Without linkage, the greatest amount of variability should be present in F_2 populations. The range of segregation in F_2 populations for all these characters, almost covered the range of some of the parental lines. This suggests that relatively few genes were responsible for these characteristics. These frequency distribution tables also indicate the presence of dominance relationships of these characters. The detailed study of these appears in

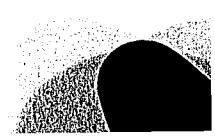


Table 9. Frequency Distribution of Tryptophan Percentage in each Population of Two Corn Crosses

	Class Centers for Tryptophan Percentage												
Population	.038	.040	.042	.044	.046	.048	.050	.052	.054	.056	.058	.060	.062
W23 x R53													
P_1 (W23)			1	1	3	2	2	3	2		1		
$Bc_1(W23xF_1)$				1	2	6	5	8	8	9	2	2	
F_1							1	2	5	1	4	1	1
F_2							2	3	1	4	7	10	11
$Bc_2(R53xF_1)$							3	4	4	5	11	5	4
P_2(R53)									1	2	2	1	
W23 x Oh 51A													
P_1(W23)			1	1	3	2	2	3	2		1		
$Bc_1(W23xF_1)$			2	1	11	12	11	12	11	1		1	
F_1							3	2	1	1	3	3	1
F_2				1	1	4	6	6	7	10	8	3	3
Bc_2(Oh51A x F_1)						8	4	8	9	8	6	5	6
P_2(Oh51A)										2	2	2	1

Table 9 (Continued)

.064	.066	.068	.070	.072	.074	.076	.078	.080	.082	.084	.086	Total
												15
												43
												15
4	1	2	2									47
3	5	3	2									49
2	1		1									10
												15
												62
	1											15
4	2	1	1	1								58
3	2	1			1							61
5	1		1						1			15

Table 10. Frequency Distribution of Niacin Content in each Population of Two Corn Crosses

Population	Class Centers for Niacin Content ug./gm.												
	10	12	14	16	18	20	22	24	26	28	30	32	34
W23 x R53													
P_1(W23)								1	1	3	3	1	2
Bc_1(W23xF_1)							1	7	7	5	6	3	5
F_1							2		6	3		2	1
F_2				1	3	6	8	11	4	6	2	3	1
Bc_2(R53xF_1)		2	2	7	7	4	9	4	5	4	1	2	2
P_2(R53)			2	5	3	2	1	1	1				
W23 x Oh51A													
P_1(W23)								1	1	3	3	1	2
Bc_1(W23xF_1)							1	2	7	8	9	10	2
F_1										2	1	7	2
F_2						1	3	2	6	6	4	7	6
Bc_2(Oh51xF_1)					1	1	1	4	11	11	7	9	5
P_2(Oh51A)								2	2	8	3		

Table 10 (Continued)

36	38	40	42	44	46	48	50	52	54	56	58	Total
	1	1	2									15
3	1	2	3									43
	1											15
	1		1									47
												49
												15
	1	1	2									15
12	4	4	1	1		1						62
1	2											15
9	6	3		2	1		2					58
1	1	4	2	1		1				1		61
												15

Table 11. Frequency distribution of protein percentage in each population of cross W23 x R53

Population	Class centers for protein percentages									
	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5
W23 x R53										
P_1(W23)		1		1	1	3	4	2	1	1
$Bc_1(W23xF_1)$				3	1	5	6	5	2	6
F_1				1		2	2	1	1	3
F_2					2	1	2	2	4	6
$Bc_2(R53xF_1)$						3	3	5	4	6
P_2(R53)								1		3

Table 11 (Continued)

12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	Total
		1							15
3	7	3	2						43
2		1	1	1					15
6	6	8	2	2	3	2	1		47
7	7	6	2	3	2	1			49
1		7	2	1					15

Table 12. Frequency of distribution of kernel weights in each population of two corn crosses

Population	Class centers for kernel weight gm./100 kernels												
	13	14	15	16	17	18	19	20	21	22	23	24	25
W23 x R53													
P_1(W23)			1	1	1				1	3	2		
Bc_1(W23xF_1)			1			2			4		3	4	8
F_1		1			1	1		1	1	1		1	1
F_2		1		1		2		4	1	3	3	6	10
Bc_2(R53x F_1)					1		1		2	1	5	5	1
P_2(R53)											1	1	
W23xOh51A													
P_1(W23)			1	1	1				1	3	2		
Bc_1(W23xF_1)	2	3		2	1	1	1	3	1	7	8	6	9
F_1								1					1
F_2				1			3	1	1	3	5	10	4
Bc_2(Oh51AxF_1)				1					2		2	1	3
P_2(OH51A)											1		

Table 12 (Continued)

26	27	28	29	30	31	32	33	34	35	36	37	Total
1												10
5	3	1	5	5	1	1						43
1	1	1	1	3								15
4	5	3	2	2								47
5	4	8	9	2	1	2				1	1	49
		2	1	3		1		2	2	1	1	15
1												10
3	3	2	2	5	1	2						62
	2	1	2	3			3		1		1	15
3	4	5	3	4	5	2	1	1	1	1		58
2	7	9	7	7	7	5	3	3	1		1	61
	1	1	2									5

the following section on dominance relationships.

Correlation coefficients are shown in Table 13. In W23 x R53, significant positive correlations between protein and tryptophan content, and between protein and kernel weight were found in all three populations, while correlation between protein and niacin were all significantly negative. Correlations between tryptophan and niacin were all negative but only two of the three correlations were significantly negative. There was a slight tendency for niacin to be negatively correlated with kernel weight but the relationship was significant in only one of the three populations. Tryptophan tended to be positively correlated with kernel weight but again only one of the three populations was significant.

In W23 x Oh51A, the negative correlations of tryptophan with niacin was not significant in any of the populations. Kernel weight and tryptophan were positively correlated. Correlations of kernel weight with niacin were significantly negative in two of the three populations.

The positive correlation of protein with tryptophan and the negative correlation between protein and niacin as shown in W23 x R53 were in close agreement with the previous investigations by Frey (17), Flynn et al. (14), Sarkar (42), Rodriguez et al. (41) and Earley et al. (11). Thus, the negative correlation found between tryptophan and niacin in W23 x R 53 seemed possible since the protein with tryptophan and the protein with

Table 13. Correlation Coefficients involving the Protein and Tryptophan Percentages, Niacin Content, and Kernel Weight in each population of the Cross W 23 x R53 and W23 x Oh51A.

	Protein			Tryptophan			Niacin		
	F_2	Bc_1	Bc_2	F_2	Bc_1	Bc_2	F_2	Bc_1	Bc_2
W 23 x R53									
Tryptophan	+.5439**	+.6044**	+.3965*						
Niacin	-.5831**	-.5401**	-.4547**	-.5539**	-.1580	-.3027*			
Kernel Weight	+.3238*	+.3484*	+.3176*	+.3887**	+.0175	+.0898	-.2003	-.2000	-.3439*
W23 x Oh51A									
Tryptophan									
Niacin				-.1287	-.2260	-.0414			
Kernel Weight				+.3236*	+.3360**	+.2208	-.1395	-.7153**	-.2487*

** Significant at 1% level
* Significant at 5% level

niacin were positively and negatively correlated, respectively. This positive correlation of protein with tryptophan and the negative relationships between protein and niacin and between tryptophan and niacin agree with the hypothesis of tryptophan--niacin biosynthesis postulated by Bonner et al.(3) and Nason (33). Tryptophan may be a precursor of niacin (1, 13, 20, 24). Tryptophan is transformed to niacin during growth by means of gene action, thus the larger the amount of niacin formed the smaller the amount of tryptophan remaining. In W23 x Oh51A, the evidence in favor of this biosynthesis hypothesis was not as strong as it was in the cross W23 x R53 since the negative correlations between tryptophan and niacin were not statistically significant.

The biosynthetic relationships of tryptophan and niacin may imply that it would not be possible to obtain a corn variety that is high in both niacin and tryptophan. However, data in Table 5 show that some inbred lines were higher than average in both niacin and tryptophan.

Significant positive correlation was found between kernel weight and protein in all three populations of W23 x R53. In a selection program for high protein in the cross, the plant breeder might take advantage of this small correlation and select the lines with large kernels. Correlations of kernel weight with tryptophan and with niacin showed a slight tendency for high tryptophan to be associated with

large kernel weight and for high niacin to be associated with low kernel weight. While one half of these correlations were significant, the relationships appeared to be small and of little value in breeding for niacin and tryptophan. Presumably, the kernel weight could be easily affected by the environmental factors as reported in the previous investigations (10, 34).

Inheritance Study of Niacin, Tryptophan, Protein and Kernel Weight

The inheritance studies with these characters should be viewed with some reservation. Since these are all quantitative characters affected directly or indirectly by a large number of genetic factors, hundreds of samples of segregating populations should be used to make inheritance studies more effective. Since chemical determinations of tryptophan and niacin are costly and time consuming, a comparatively small number of samples was used.

Dominance Relationships

Means, standard deviations of means, total variances and genetic variances for niacin, tryptophan, protein and kernel weight of each population in the two crosses are presented in Table 14. The total variance of the F_1 population was used as an estimate of environmental variance in the calculation of genetic variance. Genetic variance is equal

Table 14. Means, Standard Deviations of Means, Total Variances and Genetic Variances for Niacin, Tryptophan, Protein and Kernel Weight of each population in the crosses W23 x R53 and W23 x Oh51A

Population	No. of Samples	Mean: Niacin ug./gm.	Mean: Tryptophan %	Mean: Protein %	Mean: Kernel Weight gm/100	Standard Deviation of: Niacin ug./gm	Standard Deviation of: Tryptophan %	Standard Deviation of: Protein %
W23 x R53								
P_1(W23)	15	32.14	.050	10.00	20.61	1.35	.0011	0.31
P_2(R53)	15	18.11	.060	12.57	30.88	0.86	.0015	0.26
F_1	15	27.97	.056	11.23	24.11	1.03	.0008	0.39
F_2	47	24.88	.060	12.24	24.16	0.76	.0007	0.22
Bc_1	43	30.28	.053	11.06	25.56	0.82	.0006	0.21
Bc_2	49	21.78	.059	11.95	26.83	0.76	.0007	0.20
W23 x Oh51A								
P_1(W23)	15	32.14	.050		20.61	1.35	.0011	
P_2(Oh51A)	15	27.67	.063		27.39	0.39	.0016	
F_1	15	32.64	.056		29.54	0.81	.0012	
F_2	58	32.94	.056		26.29	0.89	.0008	
Bc_1	62	32.50	.050		23.57	0.68	.0004	
Bc_2	61	30.86	.056		28.81	0.87	.0007	

Table 14. (Continued)

Mean	Total Variances				Genetic Variances			
Kernel Weight	Niacin ug./gm	Trypto-phan %	Protein %	Kernel Weight gm/100	Niacin ug./gm	Trypto-phan %	Protein %	Kernel Weight gm/100
1.00	28.49	.000019	1.43	10.30				
1.05	11.87	.000023	0.98	16.73				
1.30	16.91	.000009	2.29	25.42				
0.52	26.92	.000022	2.28	12.53	10.01	.000013	-0.01	-12.89
0.58	30.27	.000015	1.98	14.50	13.36	.000006	-0.31	-10.92
0.56	28.91	.000029	1.98	15.15	12.00	.000020	-0.31	-10.27
1.00	28.49	.000019		10.30				
0.95	2.34	.000040		4.58				
1.04	9.75	.000021		16.21				
0.56	45.53	.000033		18.09	35.78	0.000012		1.88
0.58	28.77	.000012		22.18	19.02	-0.000009		5.97
0.47	45.83	.000032		13.68	36.08	0.000011		-2.53

to the total variance minus the F_1 variance.

Niacin content: In the cross W23 x R53, no heterosis for niacin was observed since the F_1 mean did not significantly exceed the mean of either parent of the cross. No genic dominance was indicated since the genetic variances of the two backcross and F_2 populations were of similar magnitude. The F_1 mean fell between the mean of one of the parents and the average of the two parental means, so that partial phenotypic dominance was indicated for high niacin. Epistasis of high niacin dominant genes was not apparent, as evidenced by the fact that the means of the F_2 and Bc_2(to R53) were considerably less than that of the F_1.

In the cross W23 x Oh51A, there was also no indication of heterosis since the F_1 mean did not significantly exceed either parent. Partial genic dominance of genes contributed by W23 for a high niacin value was indicated in that the genetic variance estimated for the backcross to W23 was considerably less than that of the F_2 and the backcross to Oh51A. Evidence for complete phenotypic dominance for high niacin was indicated by the fact that the mean of the F_1 did not differ significantly from the high niacin parent, W23. The relatively small differences between the means of the F_1, F_2, Bc_1, and Bc_2 indicated that epistasis of dominant gene may have occurred. Slight segregation occurred in the F_2 and

Bc to W23 (Table 10) for a high niacin value beyond W23 and the F_1, showing that intra-allelic and inter-allelic gene interaction might be present.

Tryptophan percentage: No heterosis and no phenotypic dominance (Intermediate) for tryptophan percentage was exhibited in the cross W23 x R53 since the mean of the F_1 showed no significant difference from the average of two parent means. Genetic variances of the segregating populations indicated the presence of partial genic dominance for low tryptophan, as evidenced by the fact that the genetic variance of Bc_1 to W23 was considerably lower than that of Bc_2 and F_2. No epistasis was observed since the means of F_2, Bc_1 and Bc_2 differed considerably from the F_1 mean.

In the cross W23 x Oh51A, the mean of the F_1 was also close to the average of the two parent means, indicating no heterosis and no phenotypic dominance. The genetic variance of the backcross to W23 was negative as compared to that of the F_2 and Bc_2 and there may have been complete genic dominance for low tryptophan by genes contributed by W23. Epistasis was probably not present since the mean of Bc_1 was significantly different from that of the F_1.

Protein percentage: In the cross W23 x R53, there was no indication of heterosis and phenotypic dominance since the F_1 mean closely approached the average of the two parent means. Further evidence for no phenotypic dominance was indicated by the fact that the mean of either backcross population did not

differ significantly from the average of the F_1 and the appropriate parent. No genic dominance was indicated since the genetic variances of the two backcross and F_2 populations were of similar magnitude. The means of F_1, F_2, Bc_1 and Bc_2 deviated considerably so that no epistasis was indicated.

Kernel weight: In the cross W23 x R53, no heterosis and no phenotypic dominance (Intermediate) were exhibited as indicated by the relative small difference between the F_1 mean and the average of the two parents. The genetic variances for F_2, Bc_1 and Bc_2 were all negative and of the same magnitude so that no genic dominance was indicated. No epistasis was apparent since no heterosis and no dominance were observed for this character.

The comparison of the F_1 mean of the cross W23 x Oh51A with that of the two parents showed slight heterosis for large kernel weight since the F_1 mean exceeded the mean of Oh51A considerably. Complete genic dominance was possible, since the genetic variance of the backcross to Oh51A was negative as compared with the genetic variance of Bc_1 and F_2. This indicates some degree of genic dominance for large kernel weight by the genes contributed by Oh51A. No epistasis of these dominant genes for large kernel weight was observed since there were wide differences between F_1 mean and the means of the segregating populations.

A summary of the dominance relationships for the characters studied in these two crosses is given in Table 15.

The phenotypic dominance for high niacin found in both crosses was in agreement with the result by Ohio workers (9). This leads to the conclusion that a cross of high niacin x low niacin may be used in a breeding scheme to improve the niacin content of the low niacin parent. Richey and Dawson (40) concluded that niacin value was intermediate between two parents with dominance lacking. This difference in agreement indicates that the behavior of dominance relationships might be different in different inbreds involved in a cross as reported by Gorfinkel (18).

Both tryptophan and protein have shown no phenotypic dominance. However, some degree of intra-allelic gene interaction was observed since there was genic dominance for low tryptophan in both crosses. Frey (17) found that low protein and low tryptophan were dominant characters and others (19) have also found low protein to be dominant over high protein. The difference between their results and those of the present study might be attributed to the small differences of tryptophan and protein values between the parents used in this study and also to considerable variation caused by environmental factors. W23 was found to contribute dominant high niacin genes and the crosses involving it would probably be low in tryptophan since there were negative correlations between tryptophan and niacin.

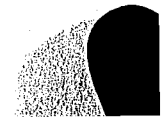


Table 15. Summary of the characters studied with respect to heterosis and dominance relationships.

Character	W23 x R53	W23 x Oh51A
Niacin	No heterosis Partial phenotypic dominance No genic dominance No epistasis	No heterosis Possible complete phenotypic dominance Partial genic dominance Possible epistasis
Tryptophan	No heterosis No phenotypic dominance (Intermediate) Partial genic dominance No epistasis	No heterosis No phenotypic dominance (Intermediate) Possible complete genic dominance No epistasis
Protein	No heterosis No phenotypic dominance (Intermediate) No genic dominance No epistasis	
Kernel weight	No heterosis No phenotypic dominance (Intermediate No genic dominance No epistasis	Slight heterosis Possible complete genic dominance No epistasis

Kernel weight was variable and, therefore, no definite conclusion could be drawn. However, possible heterosis and dominance for large kernel weight was indicated in W23 x Oh51A. This might be due to the fact that the kernels of F_1 and segregating populations tend to be larger than the long-time selfed inbreds.

Among the frequency distribution tables, only the niacin content in W23 x Oh51A deserved some attention. In backcross population to the high niacin parent and in F_2 population, slight segregation for high niacin value beyond that of the parent and F_1 was observed. This probably indicated that intra-allelic and interallelic gene interaction was present. The intra-allelic gene interaction might be of some importance in affecting the complete phenotypic dominance.

Nature of Gene Interaction

The observed means and the calculated mean based on the assumption of arithmetic and geometric gene interactions for niacin, tryptophan, protein and kernel weight in the two crosses are shown in Table 16. It was impossible to determine whether the observed means for these characters fitted either the arithmetic or geometric scheme of gene interaction since the calculated values were similar. Frey (17) found arithmetic gene interaction for protein in one cross but his tryptophan data did not fit either of the calculated values.

Table 16. Observed means and calculated arithmetic and geometric means for Niacin Content, Tryptophan percentage and Protein percentage in three segregating populations of the two crosses.

Population	Niacin ug./gm.			Tryptophan %			Protein Percentage			Kernel Weight gm./100		
		Calculated Mean			Calculated Mean			Calculated Mean			Calculated Mean	
	Observed Mean	Arithmetic	Geometric	Observed Mean	Arithmetic	Geometric	Observed Mean	Arithmetic	Geometric	Observed Mean	Arithmetic	Geometric
W23 x R53												
F_2	24.88	26.55	25.98	.060	.056	.056	12.24	11.26	11.22	24.16	24.92	24.65
Bc_1	30.28	30.06	29.99	.053	.053	.053	11.06	10.62	10.60	25.56	22.36	22.30
Bc_2	21.78	23.04	22.51	.059	.058	.058	11.95	11.90	11.88	26.83	27.50	27.29
W23 x Oh51A												
F_2	32.94	31.27	31.21	.056	.056	.057				26.29	26.77	26.49
Bc_1	32.50	32.39	32.40	.050	.053	.053				23.57	20.08	24.67
Bc_2	30.86	30.16	30.06	.056	.060	.059				28.81	28.47	28.45
Average	28.87	28.91	28.69	.055	.056	.056	11.75	11.26	11.23	25.87	25.02	25.64

Estimated Gene Number

The estimated number of genes affecting niacin and tryptophan in the two crosses are shown in Table 17. No estimation on gene numbers for protein and kernel weight could be made because the variance of the F_1 populations for these two characters were greater than the variances of their respective F_2 population. The estimated number of genes for niacin and tryptophan were low in both crosses. This is evidence that it would be relatively easy to select high tryptophan and high niacin lines in the segregating populations. Since all of the assumptions in the formula for estimating gene numbers may not always be fulfilled, the calculated gene numbers are considered as minimum numbers of genes with major effects and there may be many more genes involved with small effects.

Table 17. Estimated number of genes affecting for niacin and tryptophan in the crosses W23 x R53 and W23 x Oh51A.

Characters	W23 x R53	W23 x Oh51A
Niacin	8	3
Tryptophan	5	5

Heritability Study

Table 18 presents the estimated heritability values for niacin, tryptophan, protein and kernel weight for the two crosses.

Table 18. Estimated percent of Heritability for Niacin, Tryptophan, Protein and Kernel Weight by means of total within variances in each segregating population of the two crosses W23 x R53 and W23 x Oh51A.

Population	Total Within Variances for			
	Niacin	Tryptophan	Protein	Kernel Weight
W23 x R53				
F_2	26.92	0.000022	2.28	12.53
Bc_1	30.27	0.000015	1.98	14.50
Bc_2	28.91	0.000029	1.98	15.15
% of Estimated Heritability	-20	00	26	37
W23 x Oh51A				
F_2	45.53	0.000033		18.09
Bc_1	28.77	0.000012		22.18
Bc_2	45.83	0.000032		13.68
% of Estimated Heritability	36	66		1.7

In W23 x R53, two negative values and a zero value for heritability were found for niacin, kernel weight and tryptophan, respectively. These negative and zero heritability values show that the environmental variances were greater than the F_2 genetic variances. Thus, there was no encouragement for selection for tryptophan, niacin and kernel weight in this cross. Protein percentage in W23 x R53 showed 26% heritability, offering some encouragement for selection.

In the cross W23 x Oh51A, heritability for niacin and tryptophan was 36% and 66%, respectively. Thus, there were possibilities for selection in the F_2 segregating population. Low heritability for kernel weight was again observed in this cross.

Larger populations of segregating material are needed to give more accurate estimates of heritability. From the results of this study, it appears that the magnitude of heritability estimates for a character differed from cross to cross and there was more opportunity for selection for tryptophan and niacin in W23 x Oh51A than in W23 x R53.

Study of the Relative Effect of the Source of Pollen on the Niacin and Tryptophan Content of Corn

Eight F_1 plants of the cross Ial53 x R53 were pollinated with sweet corn pollen and another eight F_1 plants of the same cross were self pollinated. Comparisons of niacin content and tryptophan percentage for the selfed and outcrossed ears are shown in Table 19. The difference in niacin content was not significant and the difference in tryptophan percentage was significant at 5% level. These differences indicate that the high niacin content of sweet corn was recessive to the starchy character, as shown by previous investigations (25, 40). Therefore, the high niacin content of sweet corn does not appear promising for improving the niacin content of starchy corn through breeding.

Lower tryptophan values were observed in the outcrossed plants than the selfed plants. Heterotic dilution might be a possible explanation for that, however, other factors could also affect it since the difference was not highly significant.

Information on dominance relationships, heritability, gene numbers, genetic and environmental variability are important to plant breeders. The type of breeding program, opportunity for selection, and rate of improvement may be determined as more information of this type is accumulated.

Results presented in this study indicate that tryptophan, niacin and protein are not equally amenable to selection.

Table 19. Comparison of the average niacin and tryptophan contents of selfed and sweet corn pollen crossed ears in Ial53 x R53 plants.

Character	Selfed ears Av.	Sweet corn pollen crossed ears Av.	Difference
Niacin, ug./gm.	21.73	21.26	0.47
Tryptophan, %	0.057	0.053	0.004*

* Significant at 5% level

Inheritance of these characteristics appears to differ somewhat depending upon the particular parents used and this fact complicates a breeding program. These chemical constitutents were complex in their inheritance and, in some cases, they were affected more by environmental variation.

Since chemical analyses of the large number of samples needed in a plant breeding program are so expensive and time consuming, any significant relationship that might exist among the characteristics should be of value in reducing the amount of chemical analyses needed in a selection program. Therefore, more effort should be devoted to finding more easily determined characters that may be associated with these chemical constituents.

With the expanded production of synthetic vitamins by chemical industries, it appears that addition of niacin to the feed may beamore practical solution than attempting to correct

the deficiency by plant breeding. However, where a nutritional deficiency can be corrected by improvement in the natural feedstuff, dependence on the human element can be reduced. Cost of adding synthetic tryptophan to feed rations at present is almost prohibitive, so improvement in tryptophan content of corn would be a definite contribution. It was reported by Elvehjem (13) that it would cost 400 times as much to use synthetic tryptophan as to use niacin. Furthermore, the presence of tryptophan in the feed can be converted to niacin by ruminant animals.

Since high niacin was found to be dominant in the present study, it appears possible to obtain both high niacin and high tryptophan contents by backcrossing a high niacin line to a high tryptophan parent as the recurrent parent. Recurrent selection appears to be a promising breeding scheme to improve niacin content of corn in the material since the data indicated partial to complete dominance for niacin. No dominance was indicated for tryptophan and protein and, therefore, recurrent selection does not appear to be a promising procedure to improve these constituents.

SUMMARY

Sixty inbred lines and two crosses, W23 x R53, and W23 x Oh51A, were analyzed for tryptophan and niacin contents. Protein analyses were made for W23 x R53 and kernel weight was determined for both crosses. Interrelationships of these characters were investigated. The inheritance of these characters concerning dominance relationships, nature of gene action, gene numbers and heritability were studied.

Considerable differences in niacin and tryptophan contents were evident among the sixty inbred lines. The differences between high and low for niacin and tryptophan were 149.7% and 78%, respectively. Several inbreds were above average for both tryptophan and niacin and some lines were low in both.

In cross W23 x R53, significant positive correlations were found between protein and tryptophan and significant negative correlations between protein with niacin and tryptophan with niacin. This seemed to agree with the tryptophan-niacin biosynthesis. Negative correlations between tryptophan and niacin were not significant in the cross W23 x Oh51A. In both crosses, there was a slight tendency for high tryptophan to be associated with large kernel weight and high niacin to be associated with small kernel weight. While a few of these

correlations were significant, the relationships were small and of little value in a plant breeding selection program. Significant positive correlations for protein with kernel weight were found.

High niacin was dominant over low niacin on both crosses. Tryptophan and protein showed no phenotypic dominance. Kernel weight was variable. There was no dominance for kernel weight in the cross W23 x R53, while in W23 x Oh51A slight heterosis or complete dominance was indicated for large kernels.

It was not possible to determine whether the observed mean for these characters fitted either the arithmetic or geometric scheme of gene interaction since the values were similar. Probably, both types of gene interaction were involved.

Estimated gene numbers for tryptophan and niacin were low. Heritability of these characters differed in each cross. More encouragement for selection for tryptophan and niacin was present in W23 x Oh51A than W23 x R53.

There was considerable variability in the non-segregating population, P_1, P_2, and F_1 for all the characters studied. Environmental factors might have caused part of this variation. Since these characters had no previous selection, it is possible that there was some genetic variation among individuals within the parents used in these studies.

Niacin content was not affected by sweet corn pollen. Slightly lower tryptophan content was found in the ears of plants outcrossed with sweet corn than in the selfed plants.

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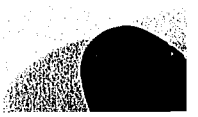

INHERITANCE OF AND INTERRELATIONSHIPS OF TRYPTOPHAN, NIACIN, PROTEIN, AND KERNEL WEIGHT IN CORN

by

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AN ABSTRACT

Submitted to the School of Graduate Studies of
Michigan State College of Agriculture and
Applied Science in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Farm Crops
1953

Approved E. E. Rossman

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ABSTRACT

The success of a breeding program to improve the quantity of the nutritive constituents of corn may be achieved with more information concerning the mode of inheritance and interrelationships of these constituents.

Sixty inbred lines and two crosses, W23 x R53 and W23 x Oh51A, were analyzed for tryptophan and niacin contents, using microbiological assay. Protein analyses were made for W23 x R53 and kernel weight was determined for both crosses. Interrelationships of these characters were investigated. The inheritance of these characters concerning dominance relationships, nature of gene action, gene numbers and heritability were studied.

Considerable differences in niacin and tryptophan contents were evident among the sixty inbred lines. The differences between high and low for niacin and tryptophan were 149.7% and 78%, respectively. Several inbreds were above average for both tryptophan and niacin and some lines were low in both.

In cross W23 x R53, significant positive correlations were found between protein and tryptophan and significant negative correlations between protein with niacin and tryptophan with niacin. This seemed to agree with tryptophan - niacin biosynthesis. Negative correlations between tryptophan and niacin were not significant in the cross W23 x Oh51A. In both

crosses, there was a slight tendency for high tryptophan to be associated with large kernel weight and high niacin to be associated with small kernel weight. While a few of these correlations were significant, the relationships were small and of little value in a plant breeding selection program. Significant positive correlation for protein and kernel weight were found.

High niacin was dominant over low niacin in both crosses. Tryptophan and protein showed no phenotypic dominance. There was no dominance for kernel weight in the cross W23 x R53, while in W23 x Oh51A slight heterosis or complete dominance was indicated for large kernels.

It was not possible to determine whether the observed mean for these characters fitted either the arithmetic or geometric scheme of gene interaction since the values were similar.

Estimated gene numbers for tryptophan and niacin were low, indicating the relatively high possibility of selecting these characters in the segregating populations. Heritability of these characters differed in each cross. More encouragement for selection for tryptophan and niacin was present in W23 x Oh51A than W23 x R53.

There was considerable variability in the non-segregating populations, P_1, P_2, and F_1 for all the characters studied. Environmental factors might have caused part of this variation. Since these characters had no previous selection, it is possible

that there was some genetic variation among individuals within the parents used in these studies.

Niacin content was not affected by sweet corn pollen and slightly lower tryptophan content was found in the ears of plants outcrossed with sweet corn than in the selfed plants.