HEREDITARY VARIATION IN PLANT NUTRITION¹

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INTRODUCTION

PLANT nutrition is here considered from the combined viewpoints of genetics and physiology. Present knowledge concerning plant nutrition as affected by heredity is scanty. STRINGFIELD and SALTER (1934) and LAMB and SALTER (1936, 1937) report a rotation of corn-oats-wheat conducted on four levels of fertility in which corn varieties and hybrids gave significant interactions with fertility levels two years out of five. Wheat showed a significant 'variety $\times$ level of fertility' interaction for the five years while oats did not. GREGORY and CROWTHER (1928) show five barley varieties differed significantly in their response to three levels of N, P, and K in all combinations.

Several established inbred strains of yellow dent corn and certain first generation crosses are reported by DETURK and his collaborators (1933) to differ in response to fertilizer treatments. Thirteen inbred lines of Early Yellow Dent corn and two hybrids gave differential growth when grown on clay and loam soils according to HOFFER (1926). Eight Hogue Yellow Dent inbreds, six White Prize inbreds and certain hybrids varied in their water economy as shown by KIESSELBACH (1926). None of these investigators demonstrated any correlation between the specific behavior of parent inbreds and hybrid combinations.

SMITH (1934) tested a number of corn inbred lines and certain hybrids on several levels of phosphorus and nitrogen. Marked differential responses were found between the inbred lines on low phosphorus levels and to a lesser degree on low nitrogen. Hybrids showed a strong tendency to approach the more efficient parent. Aqueous, sand, or soil-sand cultures all supported similar responses to the phosphorus series. Line responses remained the same whether measured as vegetative plant weight or ear weight. LYNES (1936) also grew inbred strains and hybrids of corn on phosphorus and nitrogen treatments. His results agree well with those of SMITH's. Both workers attribute efficiency in phosphorus utilization to a greater proportion of secondary to primary roots on efficient inbred lines and hybrids.

The larger section of this paper deals with the absorption and utilization of nitrogen ionic forms by corn (*Zea mays*) inbreds and hybrids. The remaining section is concerned with response to limited supplies of nitrogen, phosphorus, and potassium by tomato strains of *Lycopersicum esculentum* and *L. pimpinellifolium*.

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MATERIAL

Twenty-seven yellow dent inbreds, six sweet inbreds, one white dent inbred, one white flint inbred, one yellow flint variety and one white dent variety were tested. These represent inbred strains from Iowa, Illinois, Indiana and New Jersey. The two varieties were obtained from the Florida Agricultural Experiment Station. A brief description of the lines used most extensively is found in table 3, pp. 504-519 of the 1936 Yearbook of Agriculture. The sweet, white dent, and white flint inbred strains have been developed by the Genetics Department, Iowa State College, Ames, Iowa, as have most of the inbred dent corn lines.

Eighteen varieties or strains of *Lycopersicum esculentum* and five strains of *L. pimpinellifolium* were included. Two strains of the former and five of the latter species had been collected from the wild state in South America, chiefly Peru. Two varieties were imported from Italy and one from the Philippine Islands. Strains have all been inbred and purified as genetic stocks in the Genetics Laboratory at Iowa State College. All seeds used were gathered from greenhouse cultures to assure purity.

PROCEDURE

Uniform seed, dusted with Merco to reduce fungus growth, was germinated between paper toweling kept moist by strips of toweling extended into water below hardware cloth supports in granite ware germinating pans. These pans were placed in a germinating chamber for 36 to 48 hours with temperature between 35° and 40°C. At this time radicles were one-half to three-fourths of an inch in length. They were then placed on quarter inch mesh, paraffined hardware cloth supports which were cut to fit the pans so as to rest on the sides about half way up from the bottom. The water level was kept just below the hardware cloth. These pans were held in the dark germinating chamber another 24 hours and then placed in light. After three days the seedlings were large enough to be placed in corks of culture jars. By germinating twice the amount of seed necessary, very uniform seedlings were available for culture studies. The above procedure produced seedlings with very short mesocotyls, an important point in seedlings to be grown in water cultures.

The method of handling corn plants was as follows: Two uniform seedlings were fitted into a two-hole cork (60 mm diameter) with cotton which held the small plants in place and allowed them to expand by compressing the cotton. These corks with seedlings were then placed in quart Mason jars filled with tap water. Later the tap water was replaced by the solutions used. Solutions were changed at intervals of one to two weeks dependent on age of plants and greenhouse growing conditions. Tap water was added between solution changes when required.

Preliminary tests proved that even two brown paper bags slipped over

the jars did not check algal growth. For this reason all jars used were dipped in black screen paint and when dry, redipped in white paint. These containers checked algal growth successfully and did not heat excessively.

Plants were harvested after four to six weeks growth on solution. Green weight of tops was taken in all cases but is not included here. Dry weights of tops and roots were obtained after either thoroughly air drying the plants or oven drying them to a constant moisture percentage. Analysis of variance described by SNEDECOR (1934, 1937) was calculated for total dry weight of plants for all tests. All data represent two plants, that is, one culture jar.

Tomato seeds (for series I, II, and III) were sown in greenhouse flats of two-thirds sand and one-third soil compost mixture. When seedlings were in the two to four leaf stage they were dug, roots washed free of soil particles and plants placed in corks as done with corn seedlings. They were then put in jars of tap water. Five to seven days were allowed to elapse before nutrient solution replaced the water. Tap water partially depleted the nutrient reserve of seedlings and also favored the formation of new roots which were adapted to aqueous media.

Tomato seedlings for series IV were started in flats of sand watered with weak concentrations of a complete nutrient solution. This method proved more efficient in producing uniform seedlings. The nutrient reserve of plants could be controlled easier in sand cultures than in sand-soil mixtures.

The nutrient solutions were modifications of the buffered solution ZINZADZÉ (1933) recommends for constant pH, and the solution used by SMITH (1934). Tap water was used for all cultures making it necessary to add only iron to corn cultures and iron plus boron to tomato cultures in addition to major elements. Iron was added as ferric tartrate in small portions as plants needed it. Boron was added in the form of boric acid at 0.5 p.p.m.

Three modifications of the buffered solution were used in corn studies. These were designated as solutions A, B, and C according to nitrogen form used; NH_4NO_3 , KNO_3 , and NH_4HCO_3 respectively. The salts used and quantities of each were as follows:

Solution	Salt	Grams per liter of solution
A, B, and C	MgSO_4	0.500
A, B, and C	$\text{Ca}_3(\text{PO}_4)_2$	1.000 approximate
A, B, and C	KCl	0.500 “
A	NH_4NO_3	0.286
B	KNO_3	0.714
C	NH_4HCO_3	0.562

The two salts marked ‘approximate’ were added as the buffer which was freshly prepared for each solution change.

In each solution the nitrogen content was calculated to 100 p.p.m. regardless of the form supplied. In test VII one-half strength solutions were used, making nitrogen content 50 p.p.m.

Also three modifications of SMITH's solution were utilized in some of the corn tests. They were designated solutions D, E, and F according to the nitrogen salt used. Nitrogen was again calculated to be approximately 100 p.p.m. Solutions were as follows:

Solution	Salt	Grams per liter of solution
D, E, and F	KCl	0.576
D, E, and F	MgSO ₄	0.864
D, E, and F	KH ₂ PO ₄	0.132
D	(NH ₄) ₂ SO ₄	0.144
	Ca(NO ₃) ₂	0.400
E	Ca(NO ₃) ₂	0.877
F	(NH ₄) ₂ SO ₄	0.708

Solutions for the tomato series were essentially the same as SMITH (1934) used for maize. In making up partially deficient nitrogen solution, CaCl₂ was used in place of CaSO₄. Minus potassium solution was prepared by substituting MgCl₂ for KCl and Ca(H₂PO₄)₂ for KH₂PO₄.

During a preliminary test hydrogen-ion content of solutions was determined electrometrically. Initial pH varied from 7.2 for solutions A and B to 7.4 for solution C. The tap water used in these solutions had a pH of 7.6. After plants had been in solutions seven days, solutions A and B had a pH of 7.3 and solution C still had a pH of 7.4. It may be noted that all solutions were slightly alkaline. This checks closely with SMITH's work using the same source of tap water. Because of the large amount of tap water used the comparatively small amount of salts had little influence on pH. It was not considered necessary for this investigation to follow the pH of solutions more closely since such small differences existed between solutions.

Slight alkaline reaction should favor the absorption and utilization of NH₄-N and at the same time not greatly influence the absorption and utilization of NO₃-N. LOO (1931) found corn seedlings absorbed more ammonia as the acidity of the solution decreased. Nitrate nitrogen was absorbed most rapidly from acid media but was less influenced by reaction of solution than was ammonia.

RESULTS

Corn tests²

Seven inbred strains of corn were cultured on solutions A, B, C, and D from February 6 to March 12, 1936. The test was made in duplicate

² Eight corn tests were made. Those omitted here along with some of the data for tests included may be found in the author's doctoral thesis, #470, Iowa State College Library, Ames, Iowa.

randomized as one unit. Fresh solution was supplied three times. Mean total dry weight data and their analysis of variance summary are presented in tables 1 and 2.

TABLE 1

*Mean total dry weight in grams of plants and coefficient of variability for inbred strains.
Test I (corn).*

INBRED LINES	SOLUTION				C.V.
	A	B	C	D	
Mc	9.5	9.6	6.5	7.4	18.6
La	9.1	8.9	8.5	8.3	4.1
PR	7.5	6.8	8.4	8.5	10.3
K187	8.7	8.8	7.8	8.6	5.4
WCR	10.1	10.2	10.3	9.3	4.6
Ldg(Osf)	11.1	11.0	8.1	10.6	13.9
Idt	7.7	8.1	5.8	8.8	16.9
Mean	9.10	9.06	7.91	8.79	10.5

TABLE 2

Analysis of variance based on total dry weight of plants. Test I (corn).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Between strains	6	8.13**
Between solutions	3	4.38**
Interaction	18	1.71*
strains × B-C	6	2.97**
remainder	12	1.08
Error	28	0.69
Total	55	

** Highly significant. (P less than .01.)

* Significant. (P less than .05.) In all succeeding tables the same custom of using asterisks in the Mean Square column will be used.

Interaction mean square lies between the five percent and one percent levels as measured by its F value and the values given in table 10.2 of SNEDECOR'S "Statistical Methods" (1937). When this source of variation is broken down further the six degrees of freedom attributable to 'strains × solution B-C' are found to contribute a portion of the variance greater than their proportional part. Thus their mean square is highly significant. By comparing strains with solutions B (NO₃) and C (NH₄) a direct measure of the differential response by strains to nitrate only and to ammonium only is obtained. From this it may be stated that these seven inbreds differed in their response to nitrate versus ammonium nitrogen form under the conditions of this test.

Differential strain responses to the two forms of nitrogen are shown in figure 1. Inbreds Ldg(Osf), Mc, and Idt show proportionally less growth on ammonium-nitrogen than do the other four strains.

Top-root ratios of plants were determined since a noticeable discoloration, varying in intensity between strains, was observed on roots grown in solution C. Table 3 presents the mean top-root ratios for three solutions.

FIGURE 1.—Mean total dry weight for solutions B(NO₃-N, solid bars) and C(NH₄-N). Test I.

Differences between means of strains in table 3 are interesting. La and K187 have narrow ratios (2.80 and 2.58) which means that these have proportionally heavier roots than other strains. These differences between strains are highly significant statistically while no significance can be assigned to the variance between solutions or the variance due to the interaction of strains and solutions. Therefore, any toxicity which resulted from solution C must have affected top and root alike so far as dry weight

TABLE 3
Average top-root ratios based on dry weight of plants. Test I (corn).

STRAIN (INBRED)	SOLUTION			MEAN
	A	B	C	
Mc	3.37	3.25	3.28	3.30
La	2.72	3.00	2.68	2.80
PR	3.32	2.99	2.74	3.01
K187	2.40	2.68	2.66	2.58
WCR	3.38	3.42	3.12	3.30
Ldg(Osf)	3.30	3.30	3.32	3.31
Idt	3.22	2.91	2.87	3.00
Mean	3.10	3.08	2.95	3.07

is concerned. Since the interaction variance is very low no important relationship between top-root ratios and response to nitrogen form could have been present.

Percent dry matter in tops was also determined because some plants grown on ammonium nitrogen appeared to be more succulent than plants grown on nitrate nitrogen solution. The analysis of variance summary based on these percentages is given in table 4. Plants grown on ammonium

TABLE 4
Analysis of variance based on percent dry matter of tops. Test I (corn).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Between strains	6	3.45**
Between solutions	2	1.17**
Interaction	12	0.29**
Error	21	0.09
Total	41	

** P less than .01.

nitrogen produced slightly less dry matter than plants grown on other nitrogen forms. The means for solutions exhibit a range of more than twice the standard error (± 0.11 percent). Strains differed significantly in the amount of dry matter they produced. Ldg(Osf), PR, and La have mean percentages of dry matter of tops more than twice the standard error for strains (± 0.17) greater than K187, Idt, WCR, and Mc.

The interaction of strains and solutions (table 4) is highly significant, that is, strains did not all produce the same relative percent of dry matter on the different solutions. Strains, such as PR and WCR, which produced total dry weight on ammonium solution equal or nearly so to that pro-

duced on nitrate solution also had higher relative percentages of dry matter on ammonium solution than did other strains. This differential strain response in percent dry matter would seem to indicate a difference in the utilization of ammonium nitrogen by different inbred strains of corn.

Test II was grown immediately following the harvest of test I. Twenty inbred strains and one variety were grown on three solutions. The same plan was used as in test I. Table 5 contains the data of this test.

TABLE 5
Mean total dry weight in grams and coefficient of variability of strains. Test II (corn).

STRAIN	SOLUTION			C.V.
	A	B	C	
Mc	9.6	8.4	4.8	32.9
La	10.0	9.3	10.3	5.2
PR	9.7	7.5	7.1	17.3
K187	8.5	7.6	6.7	11.8
WCR	9.0	8.6	7.4	10.0
Ldg(Osf)	11.3	10.5	10.9	3.7
Ldg(Blx)	8.5	7.8	4.5	30.8
Ldg	7.1	7.1	5.4	15.0
Bls	8.7	6.7	7.6	13.1
Ose	10.3	10.0	8.1	12.6
Km2	10.6	10.9	8.8	11.2
PR-M	8.9	7.1	7.3	12.7
Sto	7.4	6.5	4.2	27.4
WF9	9.6	8.8	8.2	7.9
Hy	7.6	8.2	4.5	29.3
R4	6.9	7.3	4.7	22.2
LP159	8.3	7.9	4.1	34.2
TR	7.9	8.3	5.5	25.0
A-47	10.0	9.4	6.9	18.8
Tuxpan	10.4	9.1	11.6	12.1
G.B. 797	8.0	6.3	6.0	15.9
Mean	8.97	8.25	6.88	18.02

The coefficient of variability of strains varied greatly in this test. Mc has a large coefficient of variability while La, K187, and WCR have comparatively low values. It may be observed that these coefficient of variability values are large or small mainly because the strain did or did not respond favorably on solution C.

The analysis of variance shows that the variance between strains and between solutions contributes highly significant portions. The interaction, strains with solutions, was likewise highly significant. Inbreds Mc, La, PR, K187, and WCR were consistent in their response in tests I and II. No explanation can be given for the inconsistent results from Ldg(Osf).

TABLE 6
Average top-root ratios based on dry weight of plants. Test II (corn).

STRAIN	SOLUTION			MEAN
	A	B	C	
Mc	2.67	2.39	2.89	2.65
La	2.51	2.35	2.05	2.30
PR	3.17	2.93	2.60	2.90
K187	2.10	1.83	2.01	1.98
WCR	2.87	2.49	2.51	2.62
Ldg(Osf)	3.88	3.04	3.07	3.33
Hy	2.33	2.05	2.44	2.27
R4	3.08	2.98	3.19	3.08
Mean	2.83	2.51	2.60	

Top-root ratios were determined for eight strains (table 6). Inbreds K187, La, Mc, WCR, and Ldg(Osf) have the same ranking of means of strains as they had in table 3. The difference between strains is again highly significant. The difference between solutions is just statistically significant and no significant relationship between strains and solutions was found.

Percent dry matter of tops for eight strains was calculated (table 7). As in the previous test the mean percent dry matter for solution C is lower than for either solutions A or B (standard error for solutions $\pm .15$ percent). Also strains have statistically significant differences between their mean percent dry matter (standard error for strains $\pm .24$ percent). Strains Ldg(Osf), PR, and La have higher percentages of dry matter than K187, WCR, and Mc again agreeing with data in test I. Differential response to

TABLE 7
Mean percent dry matter of tops for eight strains grown in Test II (corn).

STRAIN	SOLUTION			MEAN
	A	B	C	
Mc	9.7	9.6	8.5	9.27
La	12.4	11.7	12.2	12.10
PR	12.4	12.8	10.6	11.93
K187	10.4	10.3	9.5	10.07
WCR	9.6	9.7	8.4	9.23
Ldg(Osf)	14.0	13.7	12.9	13.53
Hy	11.1	10.9	9.4	10.47
R4	11.0	11.2	9.3	10.50
Mean	11.33	11.24	10.10	

treatment by strains was less important in this test than in the previous one. The interaction mean square is just at the five percent level. Only one strain, La, had as high a percent dry matter on solution C as on other solutions.

TABLE 8
Mean total dry weight of plants in grams. Test V (corn).

STRAIN	ZINZADZÉ'S SOLUTION			SMITH'S SOLUTION		
	A	B	C	D	E	F
Hy	7.1	6.4	5.1	8.7	7.8	5.5
R4	7.5	7.4	4.4	6.5	6.0	6.1
Mc	6.7	5.5	4.1	6.9	5.0	6.1
PR	5.9	6.4	5.6	7.1	6.1	6.4
La	8.4	8.5	6.1*	8.8	7.9	6.7
WCR	9.1	7.5	5.4	9.7	8.9	6.2
Mean	7.45	6.95	5.12	7.95	6.95	6.12

* Data were missing because of root rot. Yields filled in by means of missing plot technique given by YATES (1933).

TABLE 9
Analysis of variance based on total dry weight. Test V (corn).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Between blocks	2	0.25
Between solutions†	1	7.02**
Between strains	5	12.80**
Between N-forms‡	2	38.93**
Interactions:		
sol. × strains	5	1.21
sol. × N-forms	2	2.69
strains × N-forms	10	2.19*
sol. × str. × N-forms	10	1.33
Error	67§	0.98
Total	107	

† "Solutions" refers to ZINZADZÉ's and SMITH's type.

‡ "N-forms" refers to ionic forms separately and together.

§ One D/F is deducted for each datum supplied by missing plot technique.

** P less than .01.

* P less than .05.

In order to measure response to nitrogen forms when they are associated with different combinations of other nutrient elements test V was designed. The same buffered solutions (A, B, and C) were used and three modifications (D, E, and F) of SMITH's solution were added. Each solution was triplicated with each of six inbreds; Hy, R4, and Mc shown by earlier

tests to be inefficient in ammonium utilization and PR, La, and WCR shown to be efficient. Randomized block design was first made use of in this test and continued in all later tests. Plants were put into solution March 20 and harvested April 20, 1937 (tables 8 and 9).

The interaction of strains by N-forms is the only one which may be said to have any degree of significance. It also happens to be the one which is of most interest. From the small mean square attributable to the interaction, solutions $\times$ strains, it is evident that these six strains responded similarly to the two solution types.

Inbreds PR, La, Mc, Hy, and R₄ were chosen for hybridization because they represented extreme types in ammonium utilization. Hand pollinated single cross hybrids with endosperms removed were used in both hybrid tests. Endosperms were removed when seedlings were placed in cork supports. In a small side experiment grown in connection with test V it was observed that removing endosperms checked bacterial growth in cultures. No putrefying bacteria were observed in any culture in which endosperms were removed.

Test VII was grown from April 27 to June 2, 1937. Two strengths of each solution were included; 'full' strength was same as in earlier tests and 'half' strength was just one-half concentration for all elements. Results are given in table 10 and statistical data in table 11.

TABLE 10
Mean total dry weight in grams of hybrid plants. Test VII (corn).

HYBRID	SOLUTION					
	A		B		C	
	FULL	HALF	FULL	HALF	FULL	HALF
Mc $\times$ Hy	14.4	10.8	14.9	9.9	11.9	9.9
R ₄ $\times$ Mc	13.2	12.3	13.3	10.4	12.4	10.1
PR $\times$ Hy	13.5	11.3	14.3	11.0	11.6	9.7
PR $\times$ Mc	15.4	13.1	17.2	12.2	14.6	10.7
La $\times$ Hy	15.4	12.0	14.3	10.5	12.6	10.7
R ₄ $\times$ Hy	10.2	9.6	11.6	9.9	6.8	7.6
Hy $\times$ R ₄	13.5	10.9	11.9	10.6	7.8	8.9
Mean	13.66	11.43	13.93	10.64	11.10	9.66

Hybrids responded differentially to nitrogen forms and strengths of solutions. The interaction 'solutions (N-forms) $\times$ hybrids' is highly significant. 'Hybrids $\times$ strengths' is also highly significant. An examination of table 10 shows all hybrids to have made more growth on 'full' than on 'half' strength solutions except the reciprocals R₄ $\times$ Hy and Hy $\times$ R₄ on solution C.

TABLE 11

Analysis of variance based on total dry weight of hybrids. Test VII (corn).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Between blocks	2	13.20**
Between solutions	2	58.84**
Between strengths	1	169.39**
Between hybrids	6	37.84**
Interactions:		
sol. $\times$ hybrids	12	2.56**
sol. $\times$ strengths	2	9.12**
hybrids $\times$ str.	6	7.02**
sol. $\times$ hyb. $\times$ str.	12	1.42
Error	82	1.03
Total	125	

** P less than .01.

Fifteen hybrid combinations of the five inbreds Mc, PR, La, Hy, and R4 were grown from September 4 to October 16, 1937. Only solutions A, B, and C were used with five replications. Statistical data for this test are found in table 12.

TABLE 12

Analysis of variance based on total dry weight of hybrids. Test VIII (corn).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Between blocks	4	1.11
Between solutions	2	325.44**
Between strains	14	26.22**
Interaction	28	1.78
5-7 $\times$ B-C†	1	8.32**
5+7-(2)8 $\times$ B-C	1	0.86
5+7+8-(3)13 $\times$ B-C	1	0.56
5+7+8+13-(4)2 $\times$ B-C	1	11.25**
5+7+8+13+2-(5)11 $\times$ B-C	1	3.85
Remainder	23	1.07
Error	176	1.84
Total	224	

† Numbers 5, 7, 8, 13, 2, and 11 refer to hybrids Mc $\times$ Hy, R4 $\times$ Mc, R4 $\times$ Hy, Hy $\times$ R4, PR $\times$ La, and La $\times$ PR respectively.

** P less than .01.

Total interaction in this test was not significant but this should not be taken to mean that hybrid strains all responded similarly to the treatments. When the majority of strains react similarly as they do here the

variance brought into an analysis by a few strains is overshadowed. If the interaction is broken up into smaller units certain of these comparisons are significant. Two of the five individual comparisons chosen from the 28 interaction comparisons were significant.

The reactions of all hybrid strains grown are given in table 13 as mean differences. The mean differences, $(A+B)/2C$, is a statistical treatment used to isolate strain response by solutions.

TABLE 13
Mean differences, $(A+B)/2C$, of total dry weight of all hybrid strains in grams (corn).

HYBRID STRAIN	MEAN DIFFERENCE		AVE. M.D. FOR GROUP	
	TEST VII	TEST VIII	TEST VII	TEST VIII
Inefficient×inefficient*				
Mc×Hy	1.6	3.7		
R ₄ ×Mc	1.1	5.0	2.30	4.20
R ₄ ×Hy	3.1	4.6		
Hy×R ₄	3.4	3.5		
Inefficient×efficient				
R ₄ ×La		3.0		
R ₄ ×PR		3.1		3.13
Hy×La		3.2		
Hy×PR		3.2		
Efficient×inefficient				
PR×Mc	1.8	2.4		
PR×R ₄		3.9		
PR×Hy	1.8	3.2	1.67	3.78
La×R ₄		4.9		
La×Hy	1.4	4.5		
Efficient×efficient				
La×PR		3.1		2.85
PR×La		2.6		

* Grouped according to the response of inbred parent strains. Maternal parent always written first.

Examination of the average mean differences for groups in table 13 shows an association between hybrid responses and the response of their respective parental strains. A large mean difference represents inefficient utilization of ammonium nitrogen by that hybrid. The large average mean difference for the group 'inefficient×inefficient' (4.20 grams, test VIII) illustrates the inefficiency in ammonium utilization by hybrids of inefficient parent lines. At the same time, the average mean difference for group 'efficient×efficient' (2.85 grams, test VIII) is the smallest group average and demonstrates the relative efficiency of hybrids of efficient parent strains.

Tomato studies

Three series of tomatoes were grown on four solution treatments; full nutrient as used by SMITH, low N, low P, and minus K. Each series was run in duplicate and completely randomized. Air dry weight of plants was obtained. The series were cultured during the periods June 1 to June 27; August 26 to October 1; and October 11 to November 9, 1935 respectively. Solutions low N and low P in series I had one-tenth the amount of the respective element present in full solution. In series II these two solutions were made one-fifth the concentration of full solution for the respective elements. Low N was one-fifth and low P was one-tenth the concentration of full solution in series III.

TABLE 14

Mean differences in grams of total dry weight on low N, low P, and minus K compared with full solution of series I; strains grouped according to fruit size (tomato).

STRAIN	FULL-LOW N	FULL-LOW P	FULL-MINUS K
Small fruit:			
Red Currant	4.2	4.2	2.3
Peru	3.5	3.6	1.9
Lima	3.5	3.5	2.3
Lima II	3.2	3.3	1.6
S. racemigerum†	3.2	3.4	1.8
Mean	3.52	3.60	1.98
Medium fruit:			
Mulua	2.9	3.0	3.1
Guatemala City	2.6	2.9	2.1
Yellow Cherry	3.4	3.9	2.8
Red Cherry	2.9	3.0	1.9
Burbank's Preserving	1.5	2.1	1.3
Mean	2.66	2.98	2.24
Large fruit:			
Philippine	2.7	3.1	1.9
Pizzitelo	2.3	2.6	2.1
Fraschelle	2.6	2.8	2.0
Model Potato Leaf	1.3	1.9	1.4
Yellow Peach	1.8	2.0	1.4
L. Gold Ball	2.3	2.8	2.3
Pritchard	2.4	2.6	1.4
Bonny Best	2.2	2.3	1.5
Livingston's Globe	2.5	3.0	2.2
Sutton's Best of All	2.3	2.8	2.0
Mean	2.24	2.59	1.82

† This is an intermediate form which is here grouped with *L. pimpinellifolium*.

In table 14 mean differences for series I are given with strains grouped according to size of fruit. The small-fruited strains are of the 'wild' species (*L. pimpinellifolium*); medium size strains are small 'cherry type' fruit of the domestic species; and all other strains were large fruited. Table 14 shows an interesting comparison between fruit size and dry weight response to low levels of mineral elements. It appears from this table that large fruited strains were in general more efficient on low N and low P than were small fruited strains. However, it should be again mentioned that all strains in 'small fruit' class are of a different species. Were it not that the 'medium fruit' class is intermediate these relationships could be explained as species differences. It is quite likely that some of the differences should be attributed to species. No relationship is evident between fruit size and dry weight response to minus K.

TABLE 15

Analysis of variance based on total dry weight. Series I, II, and III (tomato).

SOURCE OF VARIATION	DEGREES OF FREEDOM			MEAN SQUARE		
	I	II	III	I	II	III
Between strains	19	7	10	0.79**	5.10**	1.40**
Between solutions	3	3	3	68.84**	39.51**	20.15**
Interaction	57	21	30	0.29**	0.85**	0.43**
strains×N†	19	7	10	0.50**	1.22**	0.66**
strains×P	19	7	10	0.37**	1.19**	0.38*
strains×K	19	7	10	0.22*	0.71**	0.36*
Error	77‡	31	42	0.13	0.12	0.14
Total	159	63	87			

† These are selected groups of comparisons not merely a dividing of the 57 D.F. for interaction into three equal parts. Their sums of squares do not add to equal the sum of squares for interaction because a portion of the variance is repeated in each group of 19 D.F.

‡ One D.F. is deducted for each datum supplied by missing plot technique.

** P less than .01.

* P less than .05.

Because of the similarity of the three series the statistical data are pooled in table 15. The main interactions of strains×solutions are highly significant in each series. Further, when these interactions are broken down to strains by each element separately all three elements are found to contribute a significant portion in each series. Such consistent behavior by tomato strains leaves no doubt of their inherent differences. These strains differ not only in their ability to utilize limited supplies of nutrients as shown by the general interactions but further differ in their ability to use a limited supply of any one of the three elements used.

Five strains were chosen for crossing and further study on the potassium solutions. These are: Lima II, *S. racemigerum*, and 2n ex Haploid as efficient potassium types and Mulua and Yellow Cherry as inefficient potassium types. Table 16 gives the response of each strain used later in hybrids on minus K solution in percentage based on its response on full solution as 100 percent.

TABLE 16
*Percentage response on minus K solution based on each strain's
response on full solution as 100 (tomato).*

STRAIN	SERIES			AVERAGE
	I	II	III	
Lima II	69	79	64	70.7
<i>S. racemigerum</i>	65	62	70	65.7
2n ex Haploid	—	64	73	68.5
Mulua	31	42	—	35.5
Yellow Cherry	48	52	48	49.3

Series IV was grown two years after the three series already reported. Plants were put into solution October 21 and harvested December 3, 1937. Five strains chosen for their potassium response and all but one of their possible hybrid combinations were grown. Because of the high Calcium content of tap water it was difficult to hold iron in solution. Therefore, one-half of $\text{Ca}(\text{NO}_3)_2$ was replaced by the equivalent NO_3 as NaNO_3 in SMITH's solution which helped greatly in maintaining iron in the plants. Five replications of each parent strain and four replications of each hybrid were included. However, root rot (a browning and sloughing off of roots) made it necessary to discard heavily at harvest. Data for this series are presented in table 17 and analysis of variance in table 18. The method of analysis used was that given by SNEDECOR (1934) for disproportionate class frequencies.

The highly significant mean square found for interaction indicates that these strains and their hybrids responded differentially to the two levels of potassium. When mean total dry weight for all parent strains was compared with the corresponding mean for all hybrids the latter were found to have yielded an average of 0.39 grams more per culture on full solutions and 0.84 grams more per culture on minus K solution than had the parents. This is an increase of 5.3 percent over parent mean for full solution and 21.2 percent increase over parent mean for minus K solution by the hybrids. In other words, this group of hybrids made more growth than their parents but this hybrid vigor was four times as pronounced on the deficient level as it was on the higher level of potassium. SMITH (1934) reported a similar increase of maize hybrids on moderately low levels of phosphorus.

TABLE 17

Mean total dry weight in grams, mean differences of full—minus K solutions, and leaf grade. Series IV (tomato).

STRAIN OR HYBRID	SOLUTION		MEAN DIFF.	LEAF GRADE*
	FULL	MINUS K		
Lima II (L)	6.6	4.3	2.3	II
S. racemigerum (S)	8.1	4.4	3.7	II
2n ex Haploid (H)	6.9	4.0	2.9	I
Mulua (M)	7.3	2.6	4.7	V
Yellow Cherry (Y)	8.3	4.0	4.3	IV
Mean	7.44	3.86		
M×Y†	8.3	3.8	4.5	IV
Y×M	7.7	3.3	4.4	IV
M×L	8.8	4.6	4.2	III
Y×L	7.6	4.1	3.5	II
M×S	7.9	5.0	2.9	IV
Y×S	8.6	6.4	2.2	IV
M×H	9.8	4.0	5.8	III
Y×H	6.9	4.0	2.9	III
L×M	7.1	5.0	2.1	III
L×Y	8.8	5.8	3.0	III
S×M	6.5	4.0	2.5	III
H×M	8.9	3.7	5.2	III
H×Y	7.1	5.1	2.0	IV
L×S	7.1	4.7	2.4	II
S×L	7.0	5.0	2.0	II
L×H	6.5	4.3	2.2	I
H×L	7.1	5.7	1.4	III
S×H	8.1	5.2	2.9	II
H×S	8.3	5.8	2.5	II
Mean	7.79	4.70		

* Leaf grades were obtained by observation at time of harvest, after 42 days on minus K solution. Grades are: I—just noticeable paling of leaf margins and occasional necrotic area on oldest leaves; II—noticeable yellowing of leaf margins, few necrotic areas; III—yellow leaf margins, few necrotic areas; IV—striking yellowing of leaf margins, necrotic areas common; and V—yellow leaf margins, necrotic areas very numerous, and old leaves dead.

† Letters represent parent strains, see brackets above.

TABLE 18

Analysis of variance based on total dry weight. Series IV (tomato).

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE
Between strains	23	1.17**
Between solutions	1	113.47**
Interaction	23	0.67**
Error	97	0.13
Total	144	

** P less than .01.

Mean differences (full—minus K) for hybrids follow the same trend as the corn hybrids. Grouped according to their parent strains' response they have group averages as follows: inefficient $\times$ inefficient, 4.45 grams; inefficient $\times$ efficient, 3.58 grams; efficient $\times$ inefficient, 2.96 grams; and efficient $\times$ efficient, 2.23 grams.

Leaf grades of potassium starvation symptoms were taken on this series and are recorded in table 17. Parent strains showed very different symptoms when grown on minus K solution. The dwarf 2n ex Haploid showed no symptoms other than reduced growth after five weeks. On the other hand, Mulua showed numerous small necrotic areas on older leaves after two weeks. By harvest time (six weeks) the lower four or five leaves were dead on all Mulua plants grown on minus K solution. Other strains and, in general, hybrids were intermediate in the degree of symptoms shown. Hybrids M $\times$ Y and Y $\times$ M graded low as did both parents. Hybrids L $\times$ S, S $\times$ L, L $\times$ H, H $\times$ L, S $\times$ H, and H $\times$ S graded fairly high thereby resembling their parents. Other hybrids were generally intermediate in their grade so that no conclusion could be made concerning dominance.

Observation of mean differences of reciprocal crosses in table 17 indicates that there might be some maternal influence acting in these hybrids causing them to respond to potassium deficiency somewhat in the same manner as their maternal parent. A direct comparison of these reciprocals is given in table 19. In each reciprocal pair the hybrid having an inefficient

TABLE 19
Comparison of mean differences of reciprocal tomato hybrids.

INEFF. $\dagger$ $\times$ EFF.		EFF. $\times$ INEFF.		DIFFERENCE OF RECIPROCALLS
HYBRID	M.D.	HYBRID	M.D.	
M $\times$ L	4.2	L $\times$ M	2.1	2.1
Y $\times$ L	3.5	L $\times$ Y	3.0	0.5
M $\times$ S	2.9	S $\times$ M	2.5	0.4
M $\times$ H	5.8	H $\times$ M	5.2	0.6
Y $\times$ H	2.9	H $\times$ Y	2.0	0.9
				Mean 0.9 $\pm$ 0.31

$\dagger$ Maternal parent reaction always given first.

maternal parent gave the greater mean difference. The mean of 0.9 grams is significant since its standard error is ± 0.31 grams. Although the number of comparisons is small it may well be that some maternal influence is involved. SCHLÖSSER (1935) has noted maternal influence for tomato characteristics which carried over into the F₂ generation. Differences in osmotic value of cytoplasm was found for parent stocks and reciprocal hybrids.

Each cross closely resembled its maternal parent. If such differences as osmotic value exist between strains used in the present investigation they might well account for the tendency of hybrids to resemble their maternal parent in low K response.

Chemical analyses for total potassium were made on the parent strains. The chemical method used was that given by the Association of Official Agricultural Chemists (1935). Plants were taken after dry weight was obtained on them and the entire two plants in each sample ashed together. Averages of two samples from each treatment are given in table 20. This table shows a gradient in the amount of total K present in plants grown on

TABLE 20
Chemical analyses for total K of parent strains in grams. Series IV.

STRAIN	SOLUTION	AVERAGE K PER CULTURE	AVERAGE DRY WT. PER CULTURE	AVERAGE K ABSORBED PER GM DRY WT.
Mulua	full	0.2283	5.79	0.0393
Yel. Cherry	full	0.3651	8.60	0.0425
Lima II	full	0.2907	6.27	0.0464
S. racem.	full	0.3073	6.59	0.0507
2n ex Haploid	full	0.3231	7.37	0.0439
Mulua	minus K	0.0263	2.81	0.0094
Yel. Cherry	minus K	0.0252	4.07	0.0062
Lima II	minus K	0.0326	4.24	0.0077
S. racem.	minus K	0.0299	4.43	0.0068
2n ex Haploid	minus K	0.0370	3.96	0.0094

minus K solution. Inefficient varieties (based on dry weight of plants) had less K present than efficient varieties. Of those plants grown on full solution the same holds true except for Yellow Cherry. This one variety not only made the largest growth but had the most K present of any variety grown on full solution. Too much variation is present in the data based on K absorbed per gram of dry weight to tell what really has taken place. A slight tendency for efficient varieties to have absorbed more K per unit of plant is present in plants grown on full solution.

DISCUSSION

Plant species are frequently assumed to be relatively homogeneous physiological populations. Physiological differences between species are well recognized but seldom are such differences considered within a species. The present investigation has brought to light such inherent physiological differences within species. Corn and tomatoes have shown highly significant differential strain behavior when tested for nutritional responses. That is, when strains of a species were grown on several nutritional solu-

tions their rank (measured as total dry weight of plants) was altered from one nutritional treatment to another. This change in rank by strains from one treatment to another was consistent between tests made in different seasons.

Corn inbred strains grown in aqueous mineral cultures having nitrogen either as anion (nitrate nitrogen) or as cation (ammonium nitrogen) consistently responded differentially to the two nitrogen forms. Inbreeding has thus isolated distinct physiological types, each inbred strain being an individual type. Most inbred strains produce more dry weight if supplied anion nitrogen. However, a minority of strains were capable of using the cation equally as well as the anion form provided the former was not too concentrated.

Tomato strains (and varieties) showed consistent, statistically significant, differential strain growth on high and low levels of nitrogen, phosphorus, and potassium solutions. Some strains because of their genetic constitution were capable of making more relative growth on a limited supply of an essential element than were others.

It should be noted that uncontrolled or environmental variation was minimized in this study by using randomized replicated tests and analysis of variance for statistical treatment. Hence the differences found are those resulting from the genetic make-up of the test biotypes and the nutrient treatments. The differential strain responses mentioned above are the interactions of the genetic complex of strains compared with the nutritional treatments. Since the treatments were the same for each strain the significant 'interaction mean square' signifies genetic differences in physiology between strains.

Responses to nutritional tests made by corn and tomato hybrids of varying parentage illustrate the heritability of the nutritional complexes. LYNNESS (1936) and SMITH (1934) reported inheritance of factors for efficient utilization of limited phosphorus and nitrogen by corn inbreds and their hybrids. Both investigators concluded dominance of factors for efficient utilization to be practically complete. In our study tomato hybrids grown on limited potassium gave intermediate responses not equal to their more efficient parent. Corn hybrids also responded intermediately to nitrogen forms when one parent was more efficient in ammonium utilization than the other parental inbred. The intermediate response to all F_1 hybrids having only one efficient parental strain indicates either partial dominance or a mode of inheritance with dominance divided between factors for efficiency and those for inefficiency. The latter interpretation seems preferable since several different strains were involved in the hybrids which all showed similar intermediate responses. If only a few genes were acting it would seem very unlikely that the hybrids of all strains and their

response on two sets of nutritional treatments should possess so nearly the same degree of dominance.

Corn inbred strains grown on solutions supplied with different nitrogen forms varied in dry matter produced per unit of green weight of tops (percent dry matter). In general, plants grown on ammonium nitrogen had lower percentages of dry matter than plants grown on nitrate nitrogen solutions. However, this was not true for all strains. Those strains which made relatively good growth on ammonium nitrogen also had comparatively higher percentages of dry matter than did strains which made relatively poor growth on the cation form. Thus, those strains which made proportionally better growth on cation nitrogen also had higher percent dry matter of tops. In the absence of chemical analyses it seems reasonable to interpret this association between high total dry weight of plants and percent dry matter for efficient ammonium-utilizing strains as indicative of metabolism of ammonium nitrogen more nearly like that of nitrate nitrogen. Empirical observations of plants at harvest agree with this deduction. Ammonium-grown plants of inefficient ammonium-utilizing strains were more succulent (that is, less differentiated) than nitrate-grown plants. However, those efficient ammonium-utilizing strains appeared as differentiated on ammonium as on nitrate solution.

On the other hand, the results from two strengths of solution indicate some toxicity of ammonium nitrogen when supplied at 100 p.p.m. of nitrogen. HOENER and DETURK (1938) report severe toxic symptoms on corn seedlings started in solution at 100 p.p.m. of ammonium nitrogen. STEWART et al (1925) found pineapples made better growth on 40 p.p.m. than on 160 p.p.m. of ammonium nitrogen. The higher concentration was extremely toxic as shown by poor root systems and poor tops. Since most of the corn in this investigation was grown on solutions supplied with 100 p.p.m. of nitrogen and since noticeable discoloration of some root systems grown in ammonium solutions was observed, it seems logical to attribute at least part of the observed differential response to the degree of ammonium tolerance possessed by the strains involved.

ARNON (1937) found that all treatments which favored oxidation in the solution benefited plants grown in $\text{NH}_4\text{-N}$ (ammonium nitrogen). Aeration, copper, manganese, molybdenum, nickel and chromium were the treatments used. Since these treatments were more effective in $\text{NH}_4\text{-N}$ than in $\text{NO}_3\text{-N}$ (nitrate nitrogen) solutions, ARNON believes it is unsound to interpret responses noted in terms of nitrogen source alone. This is very likely true but in the present work tap water was used in all solutions. It scarcely seems possible that all these minor elements would be absent from tap water beyond the trace required. Further, ARNON used a level of $\text{NH}_4\text{-N}$ which was definitely toxic whereas in the present work a level of

NH₄-N was chosen just at the threshold between non-toxicity and toxicity. This is illustrated when certain strains did not show any evidence of injury while others did. Therefore, it seems reasonable to think of the differential strain responses reported here as being measures of ammonium compared to nitrate forms of nitrogen as corn nutrients.

Corn inbred strains differed widely in coefficients of variability, which measured variation in response to nitrogen forms by strains. Inbred strains which utilized both forms equally well have a low coefficient of variability. Other strains have a high coefficient of variability which indicates failure to utilize the nutrient treatments equally. Ammonium nitrogen was generally the poorest nitrogen source and a strain's response on this form accounts for the size of its coefficient of variability. The ranges in coefficient of variability were 4.1 to 18.6 percent, 3.7 to 34.2 percent, and 12.3 to 27.4 percent for three tests. The low values indicate uniformity in nutritional responses equal to that found for morphological characters. KIESELBACH and WEIHING (1933) found the following coefficients of variability in a corn variety: height of plants 10.4 percent, ear height 15.6 percent, stalk diameter 10.7 percent, length of interval from planting to silking 5.3 percent, and grain yield per plant 70.8 percent. LINDSTROM and KOOS (1931) report variations in a genetically pure line of tomatoes, a diploid regenerated from a haploid, as 10.1 percent coefficient of variability for fruit weight. This coefficient of variability should be a fair measure of environmental variation for the character fruit weight, and in comparison, the lower values obtained for corn inbreds on nitrogen forms seem well within the limits of environmental variation expected.

Top-root ratios for corn inbreds showed no relationship with strain response to nitrogen forms. This ratio remained consistent from one nitrogen treatment to another but differed significantly between inbred strains. The significant differences between inbred strains in this ratio clearly illustrates the individuality of these pure genetic strains. Variation in top-root ratio between species has been reported by GOEDEWAAGEN (1937) and CRIST and STOUT (1929).

During the course of this investigation very definite root types were observed in the inbred strains. Such types as the following were characteristic of inbred strains; a thick, heavy, and twisting system; a thick, long, poorly branched system; or a fine shallow system of roots. Such distinct types of root systems are believed to be largely responsible for the differences between strains in top-root ratios.

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SUMMARY

1. Corn inbred strains and single cross hybrids were grown in aqueous mineral solutions supplied with various nitrogen forms. Differential responses by strains and hybrids to ammonium and nitrate nitrogen proved to be statistically significant. Some strains and hybrids made relatively more growth on ammonium nitrogen compared with their growth on nitrate nitrogen than did others.

2. These differential nutritional responses by corn inbreds were due to inherent differences in the genetic constitution of the strains since environmental variation was taken into account. Hybrid responses to nutritional treatments demonstrate the transmissibility of the nutritional complexes present in inbred strains. Partial dominance of the genetic complex for efficient utilization of ammonium nitrogen, or dominance divided between factors for efficiency and for inefficiency is suggested as the mode of inheritance followed by these nutritional characteristics.

3. Percentages of dry matter in tops of corn inbreds grown in solution treatments demonstrate another inherent difference between inbred strains. Not only do strains differ in the percent of dry matter they produce but this factor varies with the nutritional treatment. Those strains which utilized ammonium nitrogen efficiently had little variation in their percent dry matter from one treatment to another. On the other hand, inefficient ammonium-utilizing strains had less dry matter per unit of green weight on ammonium treatment than on nitrate treatment. This is interpreted to signify better metabolism of ammonium nitrogen in efficient ammonium strains than in inefficient ammonium types.

4. Empirical observations of root systems grown in ammonium cultures and dry weight data from two strengths of the ammonium solution agree in showing that strains also differ in their tolerance of ammonium concentration.

5. No association was shown between strains' response to nitrogen form and top-root ratios for strains. Top-root ratios were significantly different between strains. This is in agreement with empirical observations on root systems of inbred strains of corn. Root systems of corn inbreds grown in water cultures are as distinct as are the tops.

6. Tomato strains of two species, *Lycopersicum esculentum* and *L. pimpinellifolium*, were grown on three deficient nutritional solutions (low N, low P, and minus K) and compared with their growth on full nutrient

solution. Significant differential growth was made by strains on each nutritional deficiency.

7. The differential response to potassium levels (full and minus K) by tomato strains was inherited. Hybrid combinations showed equally as striking differential responses as did their parent strains. The genetic complex for efficient utilization of limited potassium supply appears to be complex in nature. At any rate, complete dominance is not present in the F_1 hybrids.

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