

THE CONNECTICUT

AGRICULTURAL EXPERIMENT STATION

NEW HAVEN, CONN.

BULLETIN 171, MAY, 1912.

CORRELATION AND INHERITANCE
IN NICOTIANA TABACUM.

BY H. K. HAYES.

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Connecticut Agricultural Experiment Station.

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CORRELATION AND INHERITANCE IN *NICOTIANA TABACUM*.

BY

H. K. HAYES.

INTRODUCTION.

The objects of this paper are two fold; first, to give some new facts regarding the correlation and inheritance of plant characters in *Nicotiana tabacum*, second, to show how these facts may be applied by plant breeders to the production of new improved forms.

The following facts show that *Nicotiana tabacum* offers special facilities for the study of the correlation and inheritance of plant characters.

1. There are a large number of different varieties which present easily measured quantitative differences in characters.
2. The *Nicotiana tabacum* forms are naturally close pollinated and can be inbred for many years without deterioration.
3. The technique of crossing is very simple and a large number of seeds may be produced by a single cross.
4. The seed is viable for a long time so that a considerable number of generations may be grown on the same field in one year.

As tobacco is one of the principal agricultural crops of the United States it is very important that all of the facts regarding the correlation and inheritance of its characters should be known. For the last nine years many attempts have been made to produce improved forms by hybridization without a very definite knowledge of the underlying principles. It is hoped that this paper may be a contribution to this knowledge.

THE MATERIAL USED.

The material used for the studies reported in this paper, with the exception of the Broadleaf strain, consisted of types which had been inbred for a number of years and which were uniform to type. These were Havana and Broadleaf, which have been grown in Connecticut for cigar wrappers for many years, and three varieties for growing under shade, which had been grown in row selections for a number of years from selfed seed by The Connecticut Agricultural Experiment Station in coöperation with the United States Department of Agriculture.

Following is a short description of the forms used in the experiment. Statistical determinations of special characters are given later.

No. 400. Uncle Sam Sumatra.

This type proved to be of little practical value for growing under shade because the leaves, when cured, had a papery texture. The number of leaves, counting from the fourth leaf from the bottom to the leaf below the bald sucker*, ranges from seventeen to twenty-five and averages about twenty-two.

No. 401. Broadleaf.

A variety which has been cultivated in the open since the early history of the tobacco industry in Connecticut. The number of leaves ranges from sixteen to twenty-two and averages nineteen. The average height is about fifty-five inches and the average leaf area is about 9 sq. dcms. Its leaves are drooping in habit.

No. 402. Havana.

Another Connecticut out-door variety, which averages about twenty leaves per plant, with a range of from sixteen to twenty-five. The average height is fifty-six inches and average leaf area 7 sq. dcms. Its leaves are more erect than the Broadleaf and droop slightly at the tip.

No. 403. Small-leafed Sumatra.

This type was introduced for shade purposes, but did not prove so satisfactory as the Cuban. It averages about twenty-

* The "bald sucker" is a farm name for the last sucker or flowering stem on the top of the plant which has no true leaves.

seven leaves per plant with a range from twenty-three to thirty-one. The average height is about seventy-six inches and the average leaf area is about 3 sq. dcms. The leaves are erect in habit.

No. 405. Cuban.

This type is now used for growing under shade in Connecticut, over two thousand acres being raised in the valley in 1911. It has a range of from sixteen to twenty-five leaves and averages about twenty. The average leaf area is about 5 sq. dcms. and average height about sixty-five inches.

THE METHODS USED.

As shown by the descriptions, each type has been given a number. A cross between No. 405, Cuban, and No. 402, Havana, has been written (405 x 402), the female parent coming first. Whenever later generations have been grown they have been noted by further numbers, as 402-1, (405 x 402)-1, which denote respectively the second generation of Havana and the second generation of the cross between Cuban female and Havana male. The tobacco flower is naturally arranged for self-fertilization. If inbred seed is desired it is only necessary to cover the flower cluster with a Manila paper bag; the 12 lb. size having been found to be most satisfactory for this purpose. It is, however, advisable to take off all but about twenty of the seed pods, as these will produce an abundance of seed.

The technical work in crossing two varieties of tobacco is very simple. The corolla is split up one side, before the blossom opens, and the stamens are removed. Pollen from another variety (taken from its stamens by means of a scalpel or other sharp instrument) is applied to the pistil of the variety from which the stamens have been removed. Those blossoms not used in crossing are removed and the seed-head covered with a Manila paper bag.

The following characters were studied with reference to correlation and inheritance.

1. Number of leaves per plant. The number was counted from the fourth leaf from the bottom of the plant to the leaf just below the bald sucker at the top, which gives about the number that is usually harvested.

2. Height of plant measured from the ground to the last leaf counted.

3. Average area of leaves. After the plants had reached maturity, tracings of the fourth leaf from the bottom, the middle leaf and the last leaf below the bald sucker were made on smooth paper and each was given a series number. The area of each tracing was determined with a planimeter which gives an experimental error of only about 5 sq. centimeters per leaf. The term "average area of leaf" is the average area of these three separate leaves.

4. Average length of midrib, which is the average length of the three leaves used for the area measurements.

5. Average width of leaf, taken in the same manner as the length measurements.

The data, with one exception, which will be mentioned later, were all taken in a uniform manner by the author and Mr. C. D. Hubbell. The planimeter measurements were made by Mr. Hubbell, who has given much efficient assistance in this work. We wish also to express our thanks to Dr. E. M. East for much helpful advice and coöperation.

CORRELATION OF PARTS.

The question of correlation between parts is of great importance when applying the principal of selection to improvement of plants. In our work the usual correlation table has been used and the coefficient of correlation determined. The coefficient of correlation shows the degree of mutual relation, between the characters in question. If it is low (i. e., much below 0.50) it indicates that they do not depend very much upon each other; if high, it indicates that they are closely related and when it rises to unity it shows that both characters depend upon the same cause and are inherited together. If two genes are located in the same chromosome as supposed by Emerson (:11) they could be inherited together but *not* depend on the same cause.

Two types were used to study the correlation between parts. Correlation tables of the results are given at the end of this paper. For convenience in discussing results, the different coefficients of correlation are here grouped in tabular form.

TABLE I.
COMPARISON OF CORRELATION COEFFICIENTS.

No.	Correlation between no. of leaves and hght. of plant	Correlation between no. of leaves and aver. leaf area	Correlation between length and breadth of leaf
No. 401 Broadleaf	+ .368 ± .048	- .165 ± .054	+ .684 ± .029
No. 403 Sumatra	+ .631 ± .033	- .008 ± .055	+ .497 ± .041
(403 x 401)F ₁	+ .406 ± .046	- .226 ± .052	+ .818 ± .018
(403 x 401)-1F ₂	+ .342 ± .058	- .124 ± .065	+ .737 ± .030
(403 x 401)-4F ₂	+ .408 ± .036	- .076 ± .043	+ .761 ± .018

The above table shows that the crosses between the Nos. 401 and 403 have not apparently affected the mutual relationship of the different characters studied. Thus, while there is a positive correlation between the number of leaves per plant and total plant height, this correlation as a rule is somewhat less than +0.5 in our tests. One might expect some correlation between the height and number of leaves because the former is the combined length of the internodes, and the number of internodes depends on the number of leaves. But the correlation is not very large and shows no very close relation between height and number of leaves.

There is a small negative correlation of leaf area and number of leaves but the relation between the two is so small as to have no practical value. That is, number of leaves is not a character distinctly opposed to leaf area.

The high correlation between length and breadth of leaf indicates that both are very closely related, that is, that both are dependent on the same cause or series of causes in inheritance.

INHERITANCE OF CHARACTERS

While all of the characters studied show fluctuating variability they are very differently affected by environment. The most uniform character of all was the number of leaves per plant, which was little affected unless the conditions were so unfavorable as to greatly stunt or dwarf the growth of the plant, as appears in the following table. Each of these four selections was grown at Forest Hills, Massachusetts, Bloomfield, Connecticut, and New Haven, Connecticut, from seeds of a single plant. The Forest Hills plants were grown and the

data taken by Dr. E. M. East. The calculated mean is used to determine the value of the selection.

TABLE II.
NUMBER OF LEAVES PER PLANT.

Selection	Forest Hills	Bloomfield	New Haven	Average Mean
1	25.8 \pm .091	25.7 \pm .081	25.2 \pm .077	25.6
2	30.8 \pm .115	29.6 \pm .078	30.7 \pm .090	30.4
3	25.3 \pm .085	25.2 \pm .074	24.7 \pm .073	25.1
4	25.8 \pm .091	27.4 \pm .079	26.7 \pm .078	26.6

The field at Forest Hills was fairly fertile but in a region where tobacco is never grown commercially. Bloomfield is in the center of the tobacco-growing region and the soil is perfectly adapted to it and heavily fertilized. The soil at New Haven is a thin, poor, sandy loam only moderately dressed with manure and chemicals.

The means of the different selections compared with the average mean show a variation of only ± 0.8 leaves, and as only about one hundred plants were counted for each determination the results seem very uniform.

Three crosses have been studied as to inheritance of characters and for convenience each will be considered separately.

Family (405 x 400) Cuban x Uncle Sam Sumatra.

This cross was made in 1907, the reciprocal F_1 generations and the parents were grown in 1908, and the F_2 generations of the crosses and parents in 1909. In both years the crosses and parents grew on the same plot under shade and therefore under uniform conditions. The data given in Table 3, show the range of variation, the number of plants studied and the usual statistical determinations which consist of the Mean, A, the Standard Deviation, S. D., and the Coefficient of Variability, C. V. The plants were not topped as uniformly in 1908 as with the later generations and therefore the number of leaves per plant cannot be accurately compared with the numbers in later years. This year's work, however, shows that there was no increase in variability as determined by C. V. due to the crossing.

TABLE III.

FREQUENCY DISTRIBUTION OF NUMBERS OF LEAVES PER PLANT OF CROSS (400 x 405)

UNCLE SAM SUMATRA X CUBAN.

No.	Year Grown	LEAF CLASSES														Total	A.	S. D.	C. V.	
		14	15	16	17	18	19	20	21	22	23	24	25							
405, Cuban	1908	2	8	20	51	23	6	110	16.9 ± .066	1.03 ± .047	6.08 ± .276
405-1	1909	3	20	47	51	23	6	150	19.6 ± .059	1.08 ± .042	5.51 ± .215
400, Sumatra	1908	..	1	4	17	53	52	43	18	1	1	190	18.9 ± .062	1.28 ± .044	6.77 ± .234
400-1	1909	1	3	8	13	33	37	14	3	150	21.8 ± .084	1.52 ± .059	6.97 ± .271
(400 x 405)F ₁	1908	1	20	53	55	11	140	18.4 ± .041	0.85 ± .039	4.62 ± .186
(405 x 400)F ₁	1908	..	1	10	44	54	34	7	150	17.9 ± .055	1.01 ± .039	5.64 ± .218
(400 x 405)-1F ₂	1909	..	1	8	18	33	35	29	21	3	1	150	18.9 ± .084	1.53 ± .060	8.10 ± .315
(405 x 400)-1F ₂	1909	..	1	4	14	22	39	40	16	7	5	1	1	150	19.4 ± .091	1.66 ± .065	8.56 ± .333

The second generation of the parents was grown in each case from single inbred plants of the preceding year. The F_2 generations of the crosses were grown from a mixture of seed from several inbred plants of F_1 .

The range of variability as shown by C. V. is considerably greater for the F_2 generation of the crosses than for the parents. As seed from several plants was used for the F_2 generations this increased variability might be considered to be due to gametic differences in the different parent plants, but it seems to us more reasonably explained by a recombination of characters. Although no statistical results can be given, it is only fair to state that the F_2 generations also showed a range of types which were more or less like one or the other parent and intermediates between them.

Family (403 x 401), Sumatra x Broadleaf.

This cross was made in 1910. These same selections and the F_1 and F_2 generations were the types used for the discussion of correlation between parts given above. It should be remembered that the correlation between number of leaves and height of plant was somewhat less than +0.5, that in all cases there was a small negative correlation between average area of leaf and number of leaves but so small as to have little significance, and that there was a large correlation between length and breadth of leaf. It is also important to know that the crossing showed little influence on the correlation coefficient.

In the consideration of inheritance of special characters, each character will be discussed separately.

Tables IV and V give in consecutive arrangement from left to right, the selecting number, the place grown (C. denoting Centerville, Connecticut, and B. Bloomfield, Connecticut), the year grown, in Table IV the parental number of leaves when known, the total number of variates and the usual statistical determinations.

As both tables give results from the same parent plants the following discussion applies equally well to both. The seedlings in all cases were started in sterilized soil and every precaution was taken to prevent mixture of seeds. Seedlings for the Centerville selections were grown in the greenhouse, while the Bloomfield selections were grown under glass in seedbeds at Bloomfield. The F_1 generation and the parent selec-

tions were grown in consecutive rows at Centerville in 1910 and the plants were uniformly spaced on the row.

The range of variation for number of leaves per plant, Table IV, is not transgressive and the F_1 generation shows an intermediate condition. The Mean for number of leaves of No. 403, Sumatra, is $28.2 \pm .082$, for No. 401, Broadleaf, is $19.2 \pm .053$, thus giving an average Mean of 23.7 leaves for the parents. The Mean of the F_1 generation was $23.6 \pm .072$, which is very nearly the same as the average of the parents. The variability, as determined by C. V., is about the same for the F_1 and parent types. The F_1 plants could be distinguished from either parent by anyone who was familiar with the habits of the varieties used.

In 1911 the second generation of the parents and some F_2 generation crosses were grown, the parents at Centerville and the F_2 crosses both at Centerville and Bloomfield. The season was a very dry one, especially near New Haven, and as the Centerville plot was on a poor gravelly soil the plants were somewhat stunted. The range of variation of the parent types was about the same as in 1910, although the Mean of No. 403, Sumatra, was decreased from $28.2 \pm .082$ to $26.5 \pm .106$.

The parents of the F_2 generation crosses No. (403 x 401)-1, No. (403 x 401)-3 and (403 x 401)-4 represented some of the wider ranges of variation of the F_1 generation in number of leaves and plant height. These three selections, were each grown from single inbred plants of the F_1 generation and in 1911 were grown at Bloomfield on a normally fertilized tobacco soil, all giving similar results. The range of variation of these F_2 selections was as great as that of the combined parental and F_1 generations. These results are considered very conclusive, as a total of 5,992 plants were counted. The field was badly infested with cut worms and was reset three different times, thus using seedlings of different ages and rate of development in the bed and giving a high probability that the plants were representative of the whole F_2 generation.

Two of the F_2 generations grown at Bloomfield were also grown at Centerville. Thus we have an opportunity to observe the effects of a normal and of a poor environment on plants grown from seed of single inbred plants. The range of variation at Centerville, considering the number of plants grown, proved to

be about the same as for the F_2 generations at Bloomfield and similar Means for leaf number were obtained. Comparing the variability of the F_2 generations with the parents and F_1 , we find an increase of from 40 to 50%.

Table V, which gives the heights of plants in three-inch classes, shows also an intermediate condition in F_1 for plant height and no increase of variability due to crossing. The Mean of the F_1 generation, $70.8 \pm .250$, is somewhat larger than that of the average of the parents, which is 65.55. This is not due, however, to dominance, but to increased vigor due to hybridization and as this matter has been discussed in a previous publication it will receive no further attention here.

The comparison of the effects of poor and normal environment on plant height gives somewhat different results than for the number of leaves per plant. In number of leaves per plant and also in height of plant there is a slight increase in S. D., in three of the four cases, due to poor environment. In the fourth case, however, in which only 107 plants were grown, there is a large increase in C. V. for plant height due to poor environment. The coefficients of variability for the number of leaves are not appreciably affected. These few data accord with Love's (:11) conclusion that some characters of a species or variety are more variable than others. Our results are given, however, to show to what an extent the statistical determinations can be relied upon when different environmental conditions are used for the different generations. The classes and frequencies are given in our tables for all characters, which affords a much better opportunity to discover the range of variation than where only the statistical determinations are shown. There is no doubt that plant height shows a greater variation in F_2 and that this is due to crossing of different types. While there is room for differences of opinion as to the cause, it seems to the author that segregation of characters supplies the most reasonable interpretation. It is realized, however, that until the F_3 generation is grown we know practically nothing of the purity of these F_2 forms.

Tables VI, VII and VIII give the results of a study of the average leaf area, the average width and average length of leaf respectively of the above cross. In these tables the parents and F_1 were grown in 1910 and the F_2 generations in 1911. These are

TABLE IV.

FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES PER PLANT OF CROSS (403 X 401)

SUMATRA X BROADLEAF.

No.	* Place Grown	Year Grown	Leaves of Parent	LEAF CLASSES																		Total	A.	S. D.	C. V.
				16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33				
403, Sumatra	C	1910	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	35	150	28.2±.082	1.49±.058	5.27±.205
403-1	C	1911	29	2	3	13	23	46	28	27	8	125	26.5±.105	1.76±.075	6.04±.283
401, Broadleaf	C	1910	20	3	13	27	25	21	16	15	4	1	..	150	19.2±.053	0.96±.037	5.00±.194
401-1	C	1911	20	2	9	22	39	22	11	4	108	19.1±.081	1.25±.058	6.54±.300
(403 x 401)F ₁	C	1910	25	2	0	3	21	47	38	29	10	150	23.6±.072	1.30±.051	5.51±.214
(403 x 401)-1F ₂	B	1911	25	9	27	89	214	344	428	462	348	223	132	70	33	12	7	3	1	2402	22.8±.030	2.18±.021	9.52±.111
(403 x 401)-3F ₂	B	1911	24	2	13	58	132	263	323	313	245	150	67	29	14	4	4	2	1	1	1	1632	22.7±.033	2.04±.024	8.90±.106
(403 x 401)-4F ₂	B	1911	21	8	28	92	208	308	359	352	280	171	81	39	16	6	5	3	1	1	1	1958	22.5±.033	2.14±.023	9.51±.102
(403 x 401)-1F ₂	C	1911	25	1	8	10	11	19	16	18	11	6	6	0	1	107	23.8±.146	2.24±.103	9.42±.534
(403 x 401)-4F ₂	C	1911	21	5	16	30	50	52	41	22	15	7	1	1	1	241	22.0±.083	1.91±.061	8.68±.275

* B = Bloomfield, Conn.

C = Centerville, Conn.

TABLE V.
 FREQUENCY DISTRIBUTION OF HEIGHTS OF PLANT OF CROSS (403 X 401)
 SUMATRA X BROADLEAF.

No.	* Place Grown	Year Grown	CLASS CENTERS IN INCHES FOR HEIGHTS OF PLANTS																Total	A.	S. D.	C. V.					
			35	38	41	44	47	50	53	56	59	62	65	68	71	74	77	80					83	86	89	92	95
		
403, Sumatra	C	1910					
403-1	C	1911					
401, Broadleaf	C	1910					
401-1	C	1911					
(403 x 401)F ₁	C	1910					
(403 x 401)-3F ₂	B	1911					
(403 x 401)-4F ₂	B	1911					
(403 x 401)-1F ₂	C	1911					
(403 x 401)-4F ₂	C	1911					
			3	3	3	8	11	19	20	11	16	7	4	3	0	1					
			9	23	38	28	49	34	27	22	7	4					
			150	107	150	150	100	150	150	1656	1733	1090	107	241					
			76.1±	59.3±	55.0±	49.8±	70.8±	72.6±	72.6±	72.6±	71.1±	53.1±	49.9±					
			4.55±	5.08±	3.85±	4.48±	4.54±	6.28±	6.47±	6.60±	7.22±	6.36±					
			5.98±	8.57±	6.99±	9.07±	6.41±	8.65±	8.92±	9.28±	13.40±	12.75±					

* B = Bloomfield, Conn.

C = Centerville, Conn.

the same plants which were used to study the plant height and number of leaves shown in the previous tables.

The tobacco plot at Centerville in 1910 was on a fairly good soil and the plants made a normal growth. The tables show that the mean of the F_1 generation is somewhat larger than the average of the parents. This is believed to be due to increased vigor from crossing and to have nothing to do with the matter of inheritance.

The F_2 generation consisted of two selections. The range of variation was somewhat larger in most cases than in F_1 . Three variates in average width of leaf were obtained, which were as small as the extreme small variates of No. 403. In F_2 there were no variates in average length of midrib and average leaf areas as small as the extreme small variates of No. 403, although several very closely approached this size. The possible increase due to heterozygosis seems a probable explanation for the non-appearance of smaller variates. No variates were obtained in a higher class than the extremes of the F_1 generation. The season was very unfavorable which, without doubt, decreased the average size of the leaves. It is regretted that no data were taken for leaf characters on the parent varieties in 1911, but from observation it is safe to say that no variates would have been produced in as large classes as in 1910. Another fact which may partially explain the small variation in F_2 is the small number of plants grown (three hundred and forty-eight).

Results obtained from a few plants saved from the F_2 Bloomfield crosses are given in the tables under the heading, "seed plants." The purpose of giving the data on these few plants is to show that nearly as large average leaf areas were produced in the F_2 crosses as in the larger parent and that the reason that no such extreme variates appeared in our Centerville cultures is, in a large measure, due to the unfavorable environment.

A consideration of the different types of leaves found in the Bloomfield and Centerville fields convinces the writer that there is a greater variation of leaf area and dimensions in F_2 than in the parental or F_1 forms.

TABLE VI.

FREQUENCY DISTRIBUTION OF AVERAGE AREA OF LEAVES OF CROSS (403 X 401) SUMATRA X BROADLEAF.

No.	Year Grown	CLASS CENTERS IN SQ. DCMS. FOR AVERAGE AREA OF LEAVES														Total	A.	S. D.	C. V.
		2	3	4	5	6	7	8	9	10	11	12	13	14					
403, Sumatra	1910	9	100	39	2	8	31	30	33	27	7	9	1	1	150	3.23 ± .031	0.57 ± .022	17.59 ± .706	
401, Broadleaf	1910	3	8	44	19	4	150	8.65 ± .093	1.70 ± .066	19.66 ± .789	
(403 x 401)-F ₁	1910	5	46	32	6	1	150	6.35 ± .062	1.13 ± .044	17.72 ± .709	
(403 x 401)-1F ₂	1911	..	2	24	29	32	13	6	1	107	5.58 ± .080	1.23 ± .057	22.04 ± 1.064	
(403 x 401)-4F ₂	1911	..	9	47	79	72	27	7	241	5.34 ± .048	1.11 ± .035	20.79 ± .687	
(403 x 401)-F ₃	1911	3	8	8	7	1	
Seed Plants															

TABLE VII.

FREQUENCY DISTRIBUTION OF AVERAGE WIDTH OF LEAVES OF CROSS (403 X 401) SUMATRA X BROADLEAF.

No.	Year Grown	CLASS CENTERS IN CM. FOR AVERAGE WIDTH OF LEAVES										Total	A.	S. D.	C. V.
		WIDTH OF LEAVES													
		12	15	18	21	24	27	30	33						
403, Sumatra	1910	21	90	35	4	57	34	5	150	15.4 ± .111	2.03 ± .069	13.18 ± .521	
401, Broadleaf	1910	8	44	40	2	150	23.8 ± .164	2.97 ± .116	12.48 ± .493	
(403 x 401)F ₁	1910	..	5	37	66	40	2	150	20.9 ± .138	2.51 ± .098	12.09 ± .477	
(403 x 401)-1F ₂	1911	1	23	41	32	9	1	107	18.8 ± .186	2.85 ± .131	15.16 ± .714	
(403 x 401)-4F ₂	1911	2	33	121	73	12	241	18.8 ± .102	2.34 ± .074	12.48 ± .402	

TABLE VIII.

FREQUENCY DISTRIBUTION OF AVERAGE LENGTH OF LEAVES OF CROSS (403 X 401) SUMATRA X BROADLEAF.

No.	Year Grown	CLASS CENTERS IN CM. FOR AVERAGE LENGTH OF MIDRIB OF LEAF										Total	A.	S. D.	C. V.								
		24	27	30	33	36	39	42	45	48	51					54	57	60	63				
403, Sumatra	1910	10	55	72	12	1	150	28.8 ± .125	2.27 ± .088	7.88 ± .307
401, Broadleaf	1910	5	12	34	38	33	16	7	4	1	150	48.7 ± .258	4.69 ± .183	9.63 ± .375
(403 x 401)F ₁	1910	1	6	26	50	46	17	4	150	40.0 ± .187	3.39 ± .132	8.48 ± .330
(403 x 401)-1F ₂	1911	7	17	26	33	15	5	4	107	37.4 ± .275	4.22 ± .195	11.28 ± .526
(403 x 401)-4F ₂	1911	..	1	9	33	62	83	37	15	1	241	37.9 ± .160	3.69 ± .117	9.73 ± .309

Family (402 x 405), Havana x Cuban.

This cross was made in 1909, the parent varieties and the F_1 generation were grown under shade at Bloomfield, Connecticut, in 1910, and the F_2 generation with the parents were again grown in 1911 on the same shaded field. In both years the season was favorable for shade tobacco, and the results were not impaired by unfavorable environmental influences. The usual precautions were taken to prevent mixture of seed and the plants were evenly spaced on the rows. Only a few seedlings were destroyed by insects or other causes and these were reset about a week after the first setting.

The F_1 generation consisted of reciprocal crosses, but as the data from each gave similar results and as only 75 plants of each cross were grown the combined results are given under one head. In our experience with tobacco, reciprocal crosses have always yielded like results.

Table IX gives the results of the study of the inheritance of number of leaves per plant for this family.

The F_1 generation showed about the same range of variation as the parent types, the Mean for the parents and for the F_1 generation being nearly the same. Thus, No. 405 Cuban gave a Mean of $19.9 \pm .082$, No. 402 Havana gave a Mean of $19.8 \pm .076$, while the cross (402 x 405) had a Mean of $19.8 \pm .067$. The variability as determined by either S. D. or C. V. was a little less for the cross than for either parent.

The F_2 generations of the cross and the parent generations were grown in 1911. The parent types in each case had an increase in the Mean over the previous year of from .5 to .7 of a leaf per plant, respectively. As only 150 plants were grown, however, it is impossible to tell whether this is due to a slight impurity in the parent plants or to some other factor. The coefficient of variability was greater for the parent No. 402-1 than in 1910, and less for the parent No. 405-1. The second generation of the cross was very variable, showing a range of from 14 to 33 leaves per plant and an increase of approximately 100% in variability as determined by either S. D. or C. V. The Mean for the number of leaves per plant was also greater in F_2 than in F_1 .

Table X gives the results of the study of plant height. The Mean is larger in F_1 than in either parent. The Mean of No.

TABLE IX.
 FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES PER PLANT OF CROSS (402 x 405) HAVANA X CUBAN.

No.	Year Grown	Leaves of Parent	LEAF CLASSES																Total	A.	S. D.	S. V.				
			14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29					30	31	32	33
405, Cuban	1910	..																				150	19.9 ± .082	1.50 ± .059	7.53 ± .283	
405-1	1911	21	1	7	16	37	36	35	12	4	1	1	124	20.6 ± .066	1.09 ± .047	5.29 ± .227	
402, Havana	1910	150	19.8 ± .076	1.38 ± .054	6.98 ± .272	
402-1	1911	20	143	20.3 ± .101	1.80 ± .072	8.87 ± .354	
(402 x 405)F ₁	1910	150	19.8 ± .067	1.21 ± .047	6.10 ± .237	
(402 x 405)-1F ₂	1911	..	3	4	8	8	20	18	30	24	25	17	16	5	4	3	1	1	1	1	2	192	20.9 ± .161	3.31 ± .114	15.84 ± 5.44	

TABLE X.

FREQUENCY DISTRIBUTION OF HEIGHTS OF PLANTS OF CROSS (402 X 405) HAVANA X CUBAN.

No.	Year Grown	CLASS CENTERS IN INCHES FOR HEIGHT OF PLANTS												Total	A.	S. D.	C. V.				
		41	44	47	50	53	56	59	62	65	68	71	74					77	80	83	86
405, Cuban	1910	1	2	3	16	28	37	35	21	3	4	150	65.4 ± .264	4.80 ± .187	7.34 ± .286
402, Havana	1910	..	1	1	11	36	40	37	20	3	1	150	56.5 ± .218	3.96 ± .154	7.01 ± .273
(402 x 405)F ₁	1910	2	3	18	27	44	23	19	11	3	150	65.5 ± .270	4.90 ± .191	7.48 ± .291
(402 x 405)-IF ₂	1911	4	1	5	6	22	19	19	27	28	15	12	17	8	4	3	2	192	62.9 ± .449	9.23 ± .318	14.67 ± .505

405 Cuban was $65.4 \pm .264$, of No. 402 Havana was $56.5 \pm .218$, while the F_1 had a Mean for height of $65.5 \pm .270$. This, however is no doubt due to increased vigor from crossing and has no significance in inheritance. The variability was a very little larger for the F_1 generation than for either parent and well within the probable error of the determinations.

The F_2 generation showed an increased variability and a considerable degree of correlation between height of plant and number of leaves. Thus, a correlation table gives a correlation coefficient of $+.786 \pm .023$ for number of leaves and plant height.

As Table XI proves, selection No. 405 Cuban has a smaller leaf than No. 402 Havana, although the range of variation is very much the same. The F_1 generation showed the same range of variation as the parent No. 402, although the Mean was lower for the cross. The variability in F_1 was also greater than that of either parent, but within the probable errors.

The F_2 generation produced some leaves with as small average size as the smaller parent and some leaves which averaged larger than either parent. The variability as determined by C. V. was also materially greater than that of the parents.

The correlation coefficient for the average area of leaves and number of leaves per plant was $-.092 \pm .048$, which shows conclusively that there is very little correlation between number of leaves and leaf area and that these two characters are inherited independently.

Tables XII and XIII show that the difference of the parents in size characters of the leaf is chiefly a difference in average length, as the average width of leaves of both parents is very nearly the same.

Table XII shows that the range of variability of the F_2 generation for length of midrib is as great as the combined variability of the F_1 generation and the parents. One variate had a smaller average length of leaf than the lower class of the lower parent, and seven variates had a longer average midrib than the larger parent.

The abrupt ending of the parent classes, however, and the fact that a larger number of variates occurred in F_2 than in the parents makes it probable that the variability for average

TABLE XI.

FREQUENCY DISTRIBUTION OF AVERAGE AREA OF LEAVES OF CROSS (402 X 405) HAVANA X CUBAN.

No.	Year Grown	CLASS CENTERS IN SQ. DCM. FOR AVERAGE AREA OF LEAVES											Total	A.	S. D.	C. V.
		3	4	5	6	7	8	9	10	11	12					
		405, Cuban	3	26	58	54	9				
402, Havana	..	1	23	42	41	35	8	150	6.73 ± .063	1.15 ± .045	17.09 ± .684	
(402 x 405)F ₁	..	6	27	46	39	27	5	150	6.46 ± .066	1.19 ± .046	18.42 ± .738	
(402 x 405)-1F ₂	3	10	32	32	45	33	24	8	4	1	..	192	6.95 ± .086	1.76 ± .061	25.29 ± .923	

TABLE XII.

FREQUENCY DISTRIBUTION OF AVERAGE LENGTH OF LEAVES OF CROSS (402 X 405) HAVANA X CUBAN.

No.	CLASS CENTERS FOR AVERAGE LENGTH OF MIDRIB											Total	A.	S. D.	C. V.
	27	30	33	36	39	42	45	48	51	54					
405, Cuban	..	6	33	64	42	5	150	36.1 ± .104	2.67 ± .104	7.40 ± .288
402, Havana	14	31	37	15	150	45.2 ± .183	3.32 ± .129	7.35 ± .286
(402 x 405)F ₁	34	48	42	11	2	150	42.2 ± .191	3.46 ± .135	8.20 ± .319
(402 x 405)-1F ₂	1	2	8	18	28	35	48	34	11	7	..	192	43.2 ± .247	5.28 ± .182	12.22 ± .427

TABLE XIII.

FREQUENCY DISTRIBUTION OF AVERAGE WIDTH OF LEAVES OF CROSS (402 X 405) HAVANA X CUBAN.

No.	CLASS CENTERS FOR AVERAGE WIDTH OF LEAVES								Total	A.	S. D.	C. V.
	12	15	18	21	24	27	30					
	405, Cuban	..	5	46	87	12				
402, Havana	..	2	53	72	23	150	20.3 ± .118	2.14 ± .083	10.54 ± .415	
(405 x 402)F ₁	..	2	38	80	29	1	..	150	20.8 ± .120	2.17 ± .084	10.43 ± .410	
(405 x 402)-1F ₂	1	11	37	62	52	26	3	192	21.8 ± .170	3.49 ± .121	16.01 ± .565	

length of midrib is no greater for F_2 than for the combined parent and F_1 generations.

Table XIII shows an increased variability in F_2 for average leaf width, although the parents have nearly the same Mean and range of variability. This, we believe, is due to correlation between width and length of leaf* and also explains why leaves yielded by F_2 were larger than those of the larger parent. This explanation seems logical in view of the fact that there were no leaves with a smaller average area than that of the smaller parent.

SUMMARY OF RESULTS.

A. Correlation of Characters.

1. In the two types studied and in the first and second generation of crosses between them there was a positive correlation between number of leaves and height of plant although in all but one case this was less than $+0.5$.

2. The number of leaves and average leaf area showed only a slight negative correlation, i. e., a large number of leaves was associated with a slightly smaller average leaf area.

3. There was a distinct *plus* correlation between length and width of leaf, i. e., the longer leaves were on the average also the broader ones.

B. Inheritance of Characters.

1. The characters studied showed very different fluctuating variabilities due to environment. The most uniform character, in this respect, was number of leaves per plant, which was little affected unless the conditions of growth greatly stunted or dwarfed the plant.

2. Reciprocal crosses are equal within the limits of fluctuating variability.

3. The F_1 generation is intermediate in the characters studied, being as a rule somewhat larger than the average of the parents. All characters studied except the number of leaves per plant showed added vigor.

4. The F_1 generation is no more variable than the parents, the variability of F_1 being found slightly greater than the average

* The correlation between length and width of leaf as determined by the correlation coefficient proved to be $+0.814 \pm .016$.

of the parents in six cases and less in five cases. This result agrees with Johannsen's (.07) observation.

5. Different variates in F_1 give similar results in F_2 , showing that the variation in F_1 is fluctuating variation due to environment and is of no germinal value.

6. The F_2 generation is more variable than the parents. When sufficient numbers of variates were studied the F_2 showed a range of variation equal to the combined range of the parents and F_1 .

7. In the two crosses studied there was only a small negative correlation between average leaf area and number of leaves per plant. This indicates that leaf number and average leaf area are inherited independently; therefore we can combine the desirable leaf size characters of one variety with the number of leaves of another form.

8. The results show some variation in the correlation between height of plant and number of leaves. Thus, the correlation coefficients of the two F_2 generations of the cross between (403 x 401) were $+.342 \pm .058$ and $+.408 \pm .036$, while in the F_2 of the cross between (402 x 405) the correlation coefficient was $+.814 \pm .016$.

9. There was found a large positive correlation between length and breadth of leaf, which indicates that the inheritance of these characters depends on the same cause or series of causes.

INTERPRETATION OF RESULTS.

When Mendel's law was rediscovered in 1900 it was generally believed that it applied only to a few isolated cases of inheritance and many apparent exceptions were cited. By a better understanding of the complexity of the facts or by simple extensions of the Mendelian notation, most of these apparent exceptions have, one by one, been shown to follow the law.

The inheritance of morphological characters, i. e., form characters such as size of stalk and leaf, shape of leaf, etc., which show fluctuating variability, has been considered by many to be an exception to the Mendelian rule. By fluctuating variability, as used in this paper, we mean the quantitative fluctuations of characters, which are due solely to environmental conditions, soil, climate, etc. While such fluctuations have

no value in inheritance they make more difficult the correct interpretation of experimental data.

Mendel's principal discovery — the segregation of potential characters in the germ cells of hybrids and their chance recombination in later generations — has given a logical explanation, at any rate, to the facts which we now have. Whether all characters can eventually be shown to be Mendelian is of course not certain.

The results above given are statements of the actual behavior of tobacco plants under careful observation. The interpretation of these results which follows is an expression of opinion.

For the characters studied there is a much greater range of variation in F_2 than in F_1 . In the light of our present knowledge *segregation seems to be the best interpretation of this fact.*

While we have no data regarding the F_2 generations of these crosses, we have no doubt but that some of the F_2 types will breed true. Our reasons for this belief are based upon some unpublished results of the study of the inheritance of number of leaves per plant of a tobacco cross, which show that in generations later than F_2 both intermediates and extremes may breed true. How then may the facts be explained?

The first Mendelian interpretation of variation that is apparently continuous, known to the writer, was made by East (:10). This assumes that the parent plants, for the character in question, differ in more than one separately inherited unit or gene. Each of these independent, interchangeable units, allelomorphic to its own absence, is capable of adding to the character, and the heterozygous condition of any unit is half the homozygous condition.

There are cases of color inheritance which can only be explained by the presence of two or more separately inherited characters in the reproductive cells. Thus, Nilsson-Ehle (:09) found in one case two definite, independently inherited characters for blackness of glumes in oats, although glume blackness in other crosses behaved as a simple Mendelian mono-hybrid.

Many crosses were made between wheat varieties having red and white seeds and in all but one of these the F_2 generation gave the ordinary three-to-one ratio. But a cross between an old red seeded wheat from the north of Sweden and a white variety produced only red seeds in a total progeny of 78 F_2

plants. The expectancy for F_2 if the parents differed in three characters for red would be 63 reds to 1 white. The progeny in F_3 of these 78 F_2 plants gave ratios which proved that he was dealing with three separately inherited characters for red.

East (:10) found that in certain cases there were two indistinguishable independent yellow colors in the endosperm of maize. Some evidence was also received of three independent red colors in the pericarp and two colors in the aleurone cells.

East and Hayes (:11), in a study of inheritance in maize, gave complete results of a number of observed crosses between yellow and white varieties, which behaved as if there were two separately inherited characters for yellow color in the endosperm of maize, either of which could produce the yellow color. Other crosses were mentioned, between yellow and non-yellow (white) families, which behaved as simple mono-hybrids. Data were given of a number of flint-dent crosses, one of which in F_2 gave about one pure ear in every sixteen, while one cross gave an indication of a higher ratio. Crosses between families which showed quantitative differences in morphological characters showed wide ranges of variability in F_2 nearly equal to the combined range of the parents.

Emerson (:10) found that crosses between races of plants which differ in sizes and shapes have increased variability in F_2 as compared with the parent or F_1 forms. His data were on maize, bean and gourd crosses.

Shull (:11), in a study of defective inheritance ratios in *Bursa* hybrids, gave results which indicate the presence of two genes, each of which is independently responsible for the *Bursa-pastoris*-type of capsule. The *Heegeri*-type appeared only when both genes were absent.

The only change which it is necessary to make in the interpretation of Nilsson-Ehle and East for inheritance of color characters, in order to have the hypothesis fit the facts for inheritance of fluctuating plant characters, is to suppose the heterozygous condition for each character to be only half the homozygous condition. Thus the F_1 condition for any character is a blend between the parent types, instead of being like one or the other parent forms as is the case where complete dominance is the rule.

In a discussion of the explanation of results received from crossing certain *Linum* forms, Miss Tammes (:11) uses a similar interpretation and gives an excellent discussion of this hypothesis. The number of individuals studied by Miss Tammes for the different generations is very small.

Table XIV gives the theoretical expectation for the F_2 generation when the above hypothesis is used. The first column of this table shows the number of units or genes in which the P. or parent forms differ. For any case this number may be represented by n .

The second column gives the numerical proportion of the different forms until the parent form is reached. The parent form is represented by P. in the table. These classes are the coefficients in the binominal expansion where the exponent is twice the number of characters; for four characters the condition would be represented by $(a+b)^8$, the coefficients of this expansion giving the numerical results given in the table for four characters.

The third column gives the number of individuals which must be studied in order to have an even chance of receiving some individuals in each class. This number is equal to 4^n where n equals the number of unit characters in which the parents differ.

The fourth column gives the number of homozygous individuals which may be expected in each case. This number equals 2^n . The fifth column gives the per cent. of homozygous individuals which may be expected in each case.

In order to understand this complex class of results we will discuss a specific case. Suppose, for example, we are dealing with number of leaves per plant in tobacco crosses and that both parents of a certain cross are pure for the same basal condition of twenty leaves per plant and that one parent has in addition some inherited properties which result in a production of twenty-six leaves per plant. Let us suppose this condition due to three interchangeable, allelomorphous character pairs, each inherited separately, and that the heterozygous condition is half the homozygous condition. If we follow the usual Mendelian method and represent the presence of our three characters by A, B and C, and their absences by a, b and c, we get a condition in F_1 of AaBbCc, or 23 leaves.

TABLE XIV.

Difference in no. of unit characters of the P _n forms	Numerical Proportions of the Different Forms												No. of individuals 4 ⁿ	No. of homozygous individuals 2 ⁿ	Per cent. of homozygous individuals
1													4	2	50
2													16	4	25
3													64	8	12.5
4													256	16	6.25
5													1024	32	3.125
6													4096	64	1.562

In F_2 we may expect a range of variability shown for three characters in the table. In order to understand the gametic differences in F_2 we must study the gametic formula of these classes so that we may understand their future expectations in breeding. The conditions are as follows:

1	AABBCC	= 26	leaves, will breed true in F_3 .
2	AaBBCC	= 25	"
2	AABbCC	= 25	"
2	AABBcc	= 25	"
4	AaBbCC	= 24	"
4	AaBBcc	= 24	"
4	AABbCc	= 24	"
8	AaBbCc	= 23	"
1	AABBcc	= 24	" will breed true in F_3 .
2	AaBBcc	= 23	"
2	AABbcc	= 23	"
4	AaBbcc	= 22	"
1	AAbbCC	= 24	" will breed true in F_3 .
2	AabbCC	= 23	"
2	AAbbCc	= 23	"
4	AabbCc	= 22	"
1	aaBBCC	= 24	" will breed true in F_3 .
2	aaBbCC	= 23	"
2	aaBBcc	= 23	"
4	aaBbCc	= 22	"
1	AAbbcc	= 22	" will breed true in F_3 .
2	Aabbcc	= 21	"
1	aaBBcc	= 22	" will breed true in F_3 .
2	aaBbcc	= 21	"
1	aabbCC	= 22	" will breed true in F_3 .
2	aabbCc	= 21	"
1	aabbcc	= 20	" will breed true in F_3 .

Thus we see that out of a total of sixty-four individuals we may expect eight to breed true, and of these eight, one will breed true for each parent form, or for twenty and twenty-six leaves, three will breed true for twenty-two leaves, and there for twenty-four leaves.

The remainder will break up again in F_3 although some will show a greater variation than others. Thus, according to our

hypothesis, $AaBbCc$ and $AABbcc$ represents conditions of twenty-three leaves. The form $AaBbCc$ will give a range of variation in F_3 equal to that of F_2 , while the other gametic formula, $AABbcc$, will produce one-half its forms with twenty-three leaves, one-fourth each with twenty-two and twenty-four leaves

The difficulty of correctly interpreting the method of inheritance of such plant characters is greatly increased by fluctuations due to environmental conditions.

In the first cross studied, (405 x 400), Table III, the parents do not probably differ in more than one character pair, for number of leaves per plant, as the range of variability is only increased by two or three classes, due to crossing.

The average difference in the parents of the cross (403 x 401), Table IV, is about ten leaves. According to the hypothesis, each character in a homozygous condition adds two leaves and the heterozygous condition is half the homozygous. On this basis the parents differ in five characters. The numerical proportions given for five characters in Table XIV are very similar to the classes received in F_2 . The number of classes for the cross (403 x 401)-3, B, of which 1,632 plants were counted, is eighteen, while the number of classes for five characters, Table XIV, is eleven. Thus the range of variability in F_2 which is not explained by our hypothesis is seven classes. This is about the same range as is ordinarily received in the parent forms due to fluctuating variability.

Considering now our third family, (402 x 405), we observe that the parent forms each had about the same mode for number of leaves, yet in F_2 there was a large range of variability. This condition is very easily explained by our hypothesis. If we suppose each of the parent forms to be pure for the same basal condition of sixteen leaves, their gametic condition to be $16AABB$ and $16CCDD$, and none of these factors are allelomorphic to each other, we will receive a much greater range in F_2 than in F_1 . In this connection it is interesting to note that in East's original interpretation of the inheritance of variations of this type it was predicted that such a result should occur if the hypothesis was correct. That we are able to give a case which shows such results seems a further proof of the correctness of the interpretation.

In the cross of (403 x 401), Table VI, it seems very probable that we are dealing with a condition of at least five character pairs for difference in average leaf area. This explains why there was so small a range of variability in F_2 , as only 150 plants were studied. According to Table XIV, when the plants differ in a large number of character pairs and only a limited progeny is grown in F_2 , the expectancy is that the greater part of the variates will occupy an intermediate condition.

In the study of leaf area for the cross of (402 x 405), Tables XI, XII and XIII, the difference in leaf size characters for the parent varieties seems chiefly to be one of length. Results indicate that these types did not differ in more than two character pairs.

Conclusions.

Our results are entirely in accord with the Mendelian interpretation of quantitative characters, such as the size of various plant organs, by the hypothesis that a multiplicity of factors exists, each independently inherited and capable of adding to the character, the heterozygous condition being half the homozygous. The difficulty of correctly determining the exact number of factors in any case is greatly increased, however, by the presence of fluctuations which, although of no germinal value, obscure the action of heritable factors. Moreover, some characters seem independently inherited, others closely correlated in inheritance and still others partially correlated. These facts make the analysis of pedigree culture data yet more difficult.

It has been stated by certain critics that by the use of a number of factors or by the juggling of factors that any conditions could be explained. Whether we use the factorial method or not, however, does not change the actual results of experimental work. An examination of the data reported in this paper will convince the reader that the F_2 generation, for each character studied, is more variable than the F_1 and that when a large number of individuals are examined the F_2 generation has a range of variation equal to the combined range of the parents. The results seem most easily explained by segregation, in which a number of factors are concerned.

The characters which have been studied and upon which these conclusions depend are; number of leaves per plant, height of plant, average area of leaf, length and breadth of leaf.

*Suggestions to the Economic Plant Breeder from the Results
Reported in this Paper.*

The value of using inbred tobacco seed for the commercial crop has been previously discussed in our Station reports. By protecting the seed-head from cross pollination, seed from the most desirable plants may be obtained. The results of the different generations of the parent varieties shown in this paper confirm previous conclusions and prove that the progeny of inbred tobacco varieties are very uniform for the characters studied. Thus by selection the grower can obtain the better types and by breeding from these produce uniform crops. Because the tobacco plant is so noticeably affected by conditions of fertility and differences of soil, the selection of a desirable type which will breed true is not so easy as it would seem. It is necessary to make a number of selections from desirable types and test their value the following year by growing them in row selections. Those which breed true to the desired type have proved their ability to reproduce their kind.

The production of new improved forms by crossing is not a simple matter and should not be undertaken by anyone who has not a knowledge of the particular qualities which the trade demands. A good wrapper tobacco must have certain characteristics in order to be of any value; of these, burn, flavor, texture, color when cured, etc., are good examples.

As to the field characters of tobacco, we may give a plan which should be followed when attempting the improvement of tobacco by hybridization.

Crosses should be made between inbred types of known value. This method insures the elimination of unselected strains. When this plan is followed we may rest assured that the F_1 generation will be uniform. Only a few plants need to be grown of this generation, as none will breed true in F_2 . Increased vigor is obtained in F_1 , the cross, as a rule, growing more rapidly than the parents. Observations on the cured leaf of several

F₁ crosses have convinced the writer that the leaves of this generation are of very poor quality.

The F₂ generation should consist of from 5,000 to 6,000 plants, as this is the generation in which there will be a breaking up into different types. Of this generation, seed should be saved from those types which give promise of value and should be grown in row selections the following year. When a type gives promise of commercial value in the row test a larger amount should be grown, and after being harvested, cured and fermented, tested for quality.

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TAMMES, T.

- :11 Das Verhalten fluktuierend variierender Merkmale bei der Bastardierung.

Rec. Trav. Bot. Néerl., Vol. VIII, Livr. 3:201-288.

TABLE XV.

CORRELATION BETWEEN NO. OF LEAVES AND HEIGHT OF PLANT OF
NO. 401, BROADLEAF.

		No. of Leaves.							
		17	18	19	20	21	22		
Height of Plants in Inches.	44	1	1	
	47	..	3	1	4	
	50	..	7	10	3	20	
	53	2	13	17	11	1	..	44	
	56	1	5	21	14	3	1	45	
	59	..	1	10	8	1	1	21	
	62	..	1	6	4	2	1	14	
	65	1	1	
			3	30	65	41	7	4	150

No. of Leaves.	Height of Plants.
A. = 19.2 ±.053	A. = 55.0 ±.212
S. D. = 0.96 ±.037	S. D. = 3.85 ±.150
Coef. Cor. = +.368 ±.048	

TABLE XVI.

CORRELATION BETWEEN NO. OF LEAVES AND HEIGHT OF PLANT
OF NO. 403, SUMATRA.

		No. of Leaves.								
		24	25	26	27	28	29	30		31
Height of Plants in Inches.	62	1	1
	65	1	1	2
	68	..	1	2	4	4	11
	71	6	2	6	2	16
	74	..	1	5	7	17	1	3	..	34
	77	6	11	11	8	1	37
	80	3	5	8	11	5	32
	83	1	2	6	5	2	16
	86	1	1
			2	3	13	23	46	28	27	8

No. of Leaves.	Height of Plants.
A. = 28.3 ±.082	A. = 76.1 ±.251
S. D. = 1.49 ±.058	S. D. = 4.55 ±.177
Coef. Cor. = +.631 ±.033	

INHERITANCE IN NICOTIANA TABACUM.

TABLE XVII.

CORRELATION BETWEEN NO. OF LEAVES AND HEIGHT OF PLANT
OF NO. (403 X 401), SUMATRA X BROADLEAF.

		No. of Leaves.							
		19	21	22	23	24	25	26	
Height of Plants in Inches.	50	1	1
	59	1	1
	62	1	2	1	..	4
	65	1	..	7	2	4	2	1	17
	68	..	1	5	12	8	3	1	30
	71	..	2	5	18	13	5	2	45
	74	3	8	6	11	2	30
	77	6	5	5	2	18
	80	1	2	3
	83	1	..	1
		2	3	21	47	38	29	10	150

No. of Leaves.	Height of Plants.
A. = 23.6 ±.072	A. = 70.8 ±.250
S. D. = 1.30 ±.051	S. D. = 4.54 ±.177
Coef. Cor. = +.406 ±.046	

TABLE XVIII.

CORRELATION BETWEEN NO. OF LEAVES AND HEIGHT OF PLANT
OF (403 X 401)-1, SUMATRA X BROADLEAF, F₂.

		No. of Leaves.										
		19	20	21	22	23	24	25	26	27	28	30
Height of Plants in Inches.	35	1	1
	38	..	2	1	3
	41	1	1	1	3
	44	3	1	1	2	1	8
	47	2	2	4	1	1	1	11
	50	..	3	2	3	3	2	2	2	19
	53	1	1	2	3	3	4	3	2	..	1	20
	56	..	1	..	1	3	1	3	1	..	1	11
	59	..	1	2	3	5	3	1	..	16
	62	3	2	1	1	7
	65	1	2	1	4
68	1	..	2	3	
74	1	..	1	
		1	8	10	11	19	16	18	11	6	6	107

No. of Leaves.	Height of Plants.
A. = 23.8 ±.146	A. = 53.1 ±.471
S. D. = 2.24 ±.103	S. D. = 7.22 ±.333
Coef. Cor. = +.342 ±.058	

TABLE XIX.

CORRELATION BETWEEN NO. OF LEAVES AND HEIGHT OF PLANT OF
(403 x 401)-4, SUMATRA X BROADLEAF, F₂.

		No. of Leaves.												
		18	19	20	21	22	23	24	25	26	27		28	29
Height of Plants in Inches.	38	..	3	2	1	1	2	9
	41	..	5	1	7	5	..	4	..	1	23
	44	..	1	10	11	11	2	2	1	38
	47	2	3	5	5	5	6	1	1	28
	50	2	4	8	12	12	6	3	2	49
	53	2	7	9	5	6	4	1	34
	56	3	7	9	2	4	1	1	27
	59	2	2	1	10	2	1	2	1	22
	62	1	1	1	..	2	2	7
	65	1	2	..	1	4
			5	16	30	50	52	41	22	15	7	1	1	1

No. of Leaves.	Height of Plants.
A. = 22.0 ±.083	A. = 49.9 ±.276
S. D. = 1.91 ±.061	S. D. = 6.36 ±.202
Coef. Cor. = +.408 ±.036	

TABLE XX.

CORRELATION BETWEEN NO. OF LEAVES AND AVERAGE AREA OF
LEAVES OF NO. 401, BROADLEAF.

		No. of Leaves.						
		17	18	19	20	21	22	
Average Area of Leaves in Sq. Dcms.	5	..	1	..	1	1	..	3
	6	4	3	1	..	8
	7	..	7	11	10	3	..	31
	8	2	4	15	5	2	2	30
	9	..	4	18	9	..	2	33
	10	1	8	10	8	27
	11	..	3	2	2	7
	12	..	3	4	2	9
	13	1	1
	14	1	1
		3	30	65	41	7	4	150

No. of Leaves.	Aver. Area of Leaves.
A. = 19.2 ±.053	A. = 8.7 ±.093
S. D. = 0.96 ±.037	S. D. = 1.70 ±.066
Coef. Cor. = -.165 ±.054	

TABLE XXI.

CORRELATION BETWEEN NO. OF LEAVES AND AVERAGE AREA OF
LEAVES OF NO. 403, SUMATRA.

		No. of Leaves.								
		24	25	26	27	28	29	30	31	
Average Area of Leaves in Sq. Dcms.	2			1	2	3	1	2	..	9
	3	2	3	9	15	26	16	22	7	100
	4	3	6	16	10	3	1	39
	5	1	1	2
		2	3	13	23	46	28	27	8	150

No. of Leaves.	Aver. Area of Leaves.
A. = 28.3 ± .082	A. = 3.23 ± .031
S. D. = 1.49 ± .058	S. D. = 0.57 ± .022
Coef. Cor. = -.008 ± .055	

TABLE XXII.

CORRELATION BETWEEN NO. OF LEAVES AND AVERAGE AREA OF
LEAVES OF NO. (403 X 401), SUMATRA X BROADLEAF, F₁.

		No. of Leaves.							
		19	21	22	23	24	25	26	
Average Area of Leaves in Sq. Dcms.	4	1	..	2	2	5
	5	4	13	7	5	3	32
	6	..	1	6	13	13	9	4	46
	7	1	2	4	10	16	11	..	44
	8	1	..	6	8	2	2	..	19
	9	1	2	1	4
	2	3	21	47	38	29	10	150	

No. of Leaves.	Aver. Area of Leaves.
A. = 23.6 ± .072	A. = 6.35 ± .062
S. D. = 1.30 ± .051	S. D. = 1.13 ± .044
Coef. Cor. = -.226 ± .052	

TABLE XXIII.

CORRELATION BETWEEN NO. OF LEAVES AND AVERAGE AREA OF LEAVES OF (403 X 401)-1, SUMATRA X BROADLEAF, F₂.

		No. of Leaves.												
		19	20	21	22	23	24	25	26	27	28	30		
Average Area of Leaves in Sq. Dcms.	3	..	1	1	2
	4	..	1	1	2	6	4	2	4	2	1	1	..	24
	5	1	1	6	2	5	4	4	1	1	4	29
	6	..	2	..	6	4	4	8	4	3	1	32
	7	..	2	2	..	3	2	2	2	13
	8	..	1	1	1	1	2	6
	9	1	1
			1	8	10	11	19	16	18	11	6	6	1	107

No. of Leaves.	Aver. Area of Leaves.
A. = 23.8 ± .146	A. = 5.58 ± .080
S. D. = 2.24 ± .103	S. D. = 1.23 ± .057
Coef. Cor. = -.124 ± .065	

TABLE XXIV.

CORRELATION BETWEEN NO. OF LEAVES AND AVERAGE AREA OF LEAVES OF (403 X 401)-4, SUMATRA X BROADLEAF, F₂.

		No. of Leaves.													
		18	19	20	21	22	23	24	25	26	27	28		29	
Average Area of Leaves in Sq. Dcms.	3	..	1	..	1	2	1	2	..	1	1	9	
	4	..	1	5	6	10	11	6	3	3	..	1	1	47	
	5	1	6	12	18	18	12	8	3	1	79	
	6	1	7	6	17	16	13	5	6	1	72	
	7	2	1	5	6	6	3	1	2	1	27	
	8	1	..	2	2	..	1	..	1	7	
			5	16	30	50	52	41	22	15	7	1	1	1	241

No. of Leaves.	Aver. Area of Leaves.
A. = 22.0 ± .083	A. = 5.34 ± .048
S. D. = 2.24 ± .103	S. D. = 1.11 ± .035
Coef. Cor. = .076 ± .043	

TABLE XXV.

CORRELATION BETWEEN AVERAGE WIDTH OF LEAVES AND AVERAGE
LENGTH OF MIDRIB OF NO. 401, BROADLEAF.

		Aver. Width of Leaves in Cms.						
		18	21	24	27	30	33	
Average Length of Midrib in Cms.	39	4	1	5
	42	4	7	..	1	12
	45	..	27	7	34
	48	..	8	25	5	38
	51	18	14	1	..	33
	54	..	1	6	9	16
	57	3	3	1	7
	60	1	2	1	..	4
	63	1	1
			8	44	57	34	5	2

Aver. Width of Leaves.	Aver. Length of Leaves.
A. = 23.8 ±.164	A. = 48.7 ±.258
S. D. = 2.97 ±.116	S. D. = 4.69 ±.183
Coef. Cor. = +.684 ±.029	

TABLE XXVI.

CORRELATION BETWEEN AVERAGE WIDTH OF LEAVES AND AVERAGE
LENGTH OF MIDRIB OF NO. 403, SUMATRA.

		Aver. Width of Leaves in Cms.				
		12	15	18	21	
Average Length of Leaves in Cms.	24	5	5	10
	27	14	33	7	1	55
	30	2	50	18	2	72
	33	..	2	10	..	12
	36	1	1
			21	90	35	4

Aver. Width of Leaves.	Aver. Length of Leaves.
A. = 15.4 ±.111	A. = 28.8 ±.125
S. D. = 2.03 ±.069	S. D. = 2.27 ±.088
Coef. Cor. = +.497 ±.041	

TABLE XXVII.

CORRELATION BETWEEN AVERAGE WIDTH OF LEAVES AND AVERAGE LENGTH OF MIDRIB OF NO. (403 X 401), SUMATRA X BROADLEAF, F₁.

Aver. Width of Leaves in Cms.

		15	18	21	24	27	
Average Length of Leaves in Cms.	30	1	1
	33	4	2	6
	36	..	22	4	26
	39	..	13	34	3	..	50
	42	26	20	..	46
	45	2	14	1	17
	48	3	1	4
			5	37	66	40	2

Aver. Width of Leaves.

A. = 20.9 ±.138

S. D. = 2.51 ±.098

Aver. Length of Leaves.

A. = 40.0 ±.187

S. D. = 3.39 ±.132

Coef. Cor. = +.818 ±.018

TABLE XXVIII.

CORRELATION BETWEEN AVERAGE WIDTH OF LEAVES AND AVERAGE LENGTH OF MIDRIB OF (403 X 401)-1, SUMATRA X BROADLEAF, F₂.

Aver. Width of Leaves in Cms.

		12	15	18	21	24	27	
Average Length of Leaves in Cms.	30	..	7	7
	33	1	11	5	17
	36	..	4	19	3	26
	39	..	1	11	20	1	..	33
	42	5	5	4	1	15
	45	1	2	2	..	5
	48	2	2	..	4
			1	23	41	32	9	1

Aver. Width of Leaves.

A. = 18.8 ±.186

S. D. = 2.85 ±.131

Aver. Length of Leaves.

A. = 37.4 ±.275

S. D. = 4.22 ±.195

Coef. Cor. = +.737 ±.030

TABLE XXIX.

CORRELATION BETWEEN AVERAGE WIDTH OF LEAVES AND AVERAGE LENGTH OF MIDRIB OF (403 X 401)-4, SUMATRA X BROADLEAF, F₂.

Aver. Width of Leaves in Cms.

		12	15	18	21	24		
Average Length of Leaves in Cms.	27	..	1	1	
	30	2	6	1	9	
	33	..	19	14	33	
	36	..	7	52	3	..	62	
	39	46	36	1	83	
	42	7	25	5	37	
	45	1	8	6	15	
	48	1	..	1	
			2	33	121	73	12	241

Aver. Width of Leaves.

Aver. Length of Leaves.

A. = 18.8 ± .102

A. = 37.9 ± .160

S. D. = 2.34 ± .074

S. D. = 3.69 ± .117

Coef. Cor. = +.761 ± .018

TABLE XXX.

CORRELATION BETWEEN NO. OF LEAVES AND HEIGHT OF PLANT OF (402 X 405)-1, HAVANA X CUBAN, F₂.

No. of Leaves.

		14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33			
Height of Plants in Inches.	41	2	..	1	1	4	
	44	1	1	
	47	..	2	1	..	1	1	5	
	50	..	2	1	..	1	..	1	1	6	
	53	1	..	3	3	6	3	3	1	2	22	
	56	2	3	5	3	3	2	..	1	19	
	59	4	3	5	3	2	1	1	19	
	62	2	4	7	5	3	3	2	1	27	
	65	1	1	1	9	3	8	2	3	28	
	68	2	2	..	4	3	2	1	1	15	
	71	4	2	3	2	..	1	12	
	74	1	5	4	2	1	2	1	1	17	
	77	1	2	2	..	1	1	..	1	8	
	80	2	..	1	1	4	
	83	1	..	1	1	3	
	86	1	1	2	
			3	4	8	8	20	18	30	24	25	17	16	5	4	3	1	1	1	1	2	1	1	192

No. of Leaves.

Height of Plants.

A. = 20.9 ± .161

A. = 62.9 ± .449

S. D. = 3.31 ± .114

S. D. = 9.23 ± .318

Coef. Cor. = +.786 ± .023

TABLE XXXI.

CORRELATION BETWEEN NO. OF LEAVES AND AVERAGE AREA OF LEAVES
OF (402 x 405)-1, HAVANA X CUBAN, F₂.

		No. of Leaves.																					
		14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33		
Average Area of Leaves in Sq. Dcms.	3	1	1	..	1	3		
	4	1	2	2	2	..	1	1	1	..	10		
	5	1	1	1	1	2	3	2	5	3	6	2	2	2	..	1	..	1	32		
	6	1	..	1	..	6	3	3	5	2	2	3	..	1	2	1	..	1	31		
	7	1	1	1	1	2	2	4	9	6	8	2	6	1	1	1	45		
	8	..	1	2	2	4	3	4	4	4	4	2	..	2	1	33		
	9	2	..	4	4	4	2	4	1	2	1	24		
	10	..	1	1	1	2	1	1	1	1	9		
	11	1	1	..	2	4		
	12	1	1		
			3	4	8	8	20	18	30	24	25	17	16	5	4	3	1	1	1	1	2	1	192

	No. of Leaves.	Average Area of Leaves.
A.	= 20.9 ± .161	A. = 6.96 ± .085
S. D.	= 3.31 ± .114	S. D. = 1.76 ± .061
Coef. Cor. = -.092 ± .048		

TABLE XXXII.

CORRELATION BETWEEN AVERAGE WIDTH OF LEAVES AND AVERAGE LENGTH
OF MIDRIB OF (402 x 405)-1, HAVANA X CUBAN, F₂.

		Aver. Width of Leaves in Cms.							
		12	15	18	21	24	27	30	
Average Length of Leaves in Cms.	27	1	1
	30	..	1	1	2
	33	..	5	3	8
	36	..	3	13	2	18
	39	..	2	14	11	1	28
	42	5	22	8	35
	45	1	20	21	6	..	48
	48	7	15	11	1	34
	51	5	6	..	11
	54	2	3	2	7
		1	11	37	62	52	26	3	192

	Aver. Width of Leaves.	Aver. Length of Leaves.
A.	= 21.8 ± .170	A. = 43.2 ± .247
S. D.	= 3.49 ± .121	S. D. = 5.28 ± .182
Coef. Cor. = +.814 ± .016		

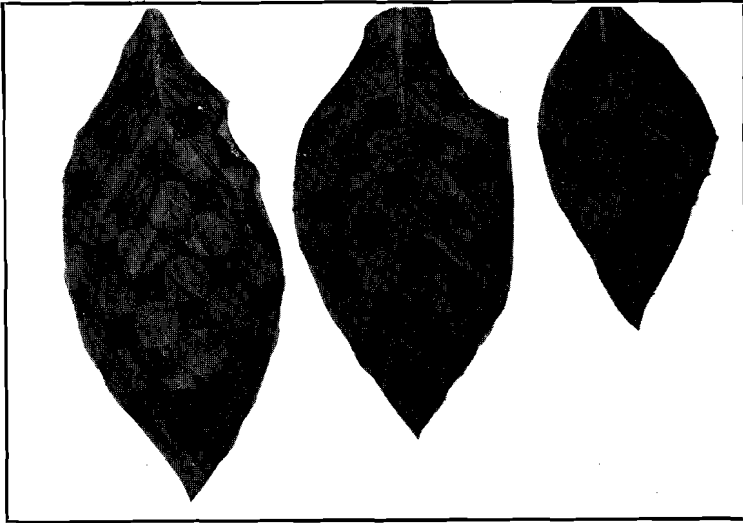
PLATE I.



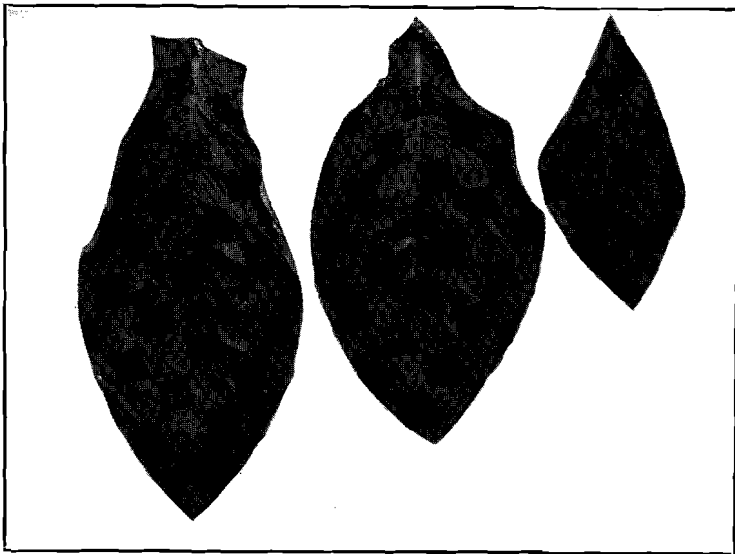
b. No. 402, Havana. Averages about 20 leaves per plant. Grown under shade at Bloomfield, 1911.



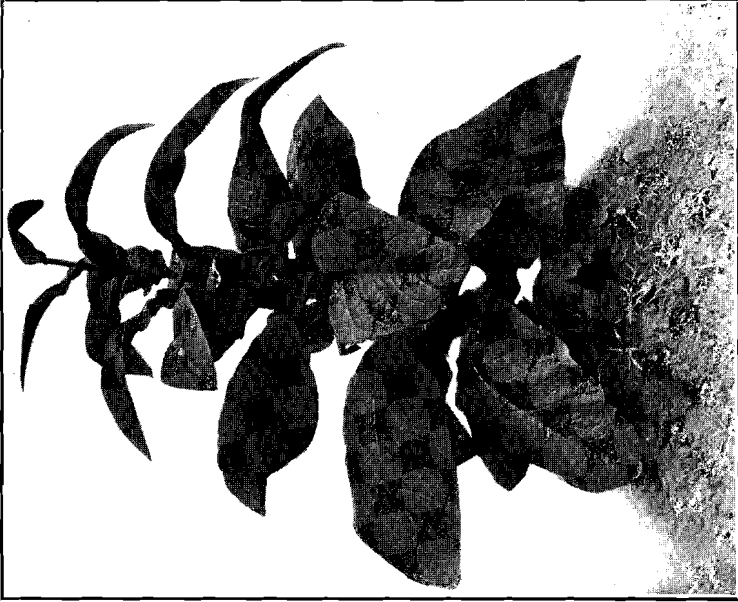
a. No. 405, Cuban. Averages about 20 leaves per plant. Grown under shade at Bloomfield, 1911.



a. Average middle leaf of No. 402, Havana at left, of No. 405, Cuban at right and F_1 in center.



b. Some F_2 middle leaves of cross between No. 402, Havana and No. 405, Cuban.

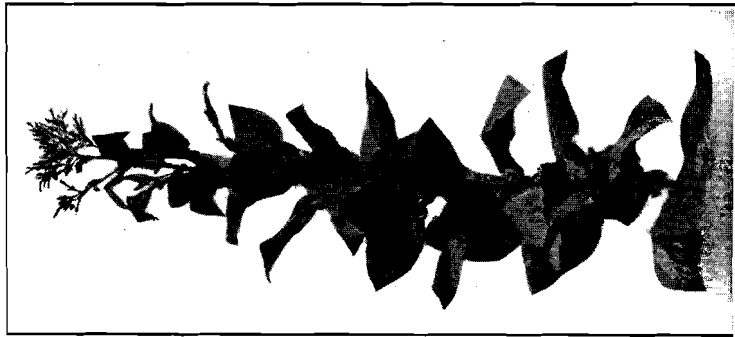


No. 401, Broadleaf. Averages about 19 leaves per plant. Leaves drooping in habit, Centerville, 1911.

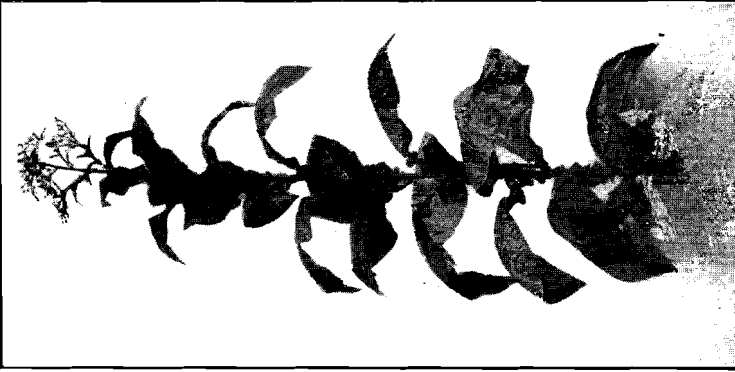


a. (402 x 405) — 1. A 30 leaved plant of the F_2 of a cross between Havana and Cuban. Grown under shade at Bloomfield, 1911.

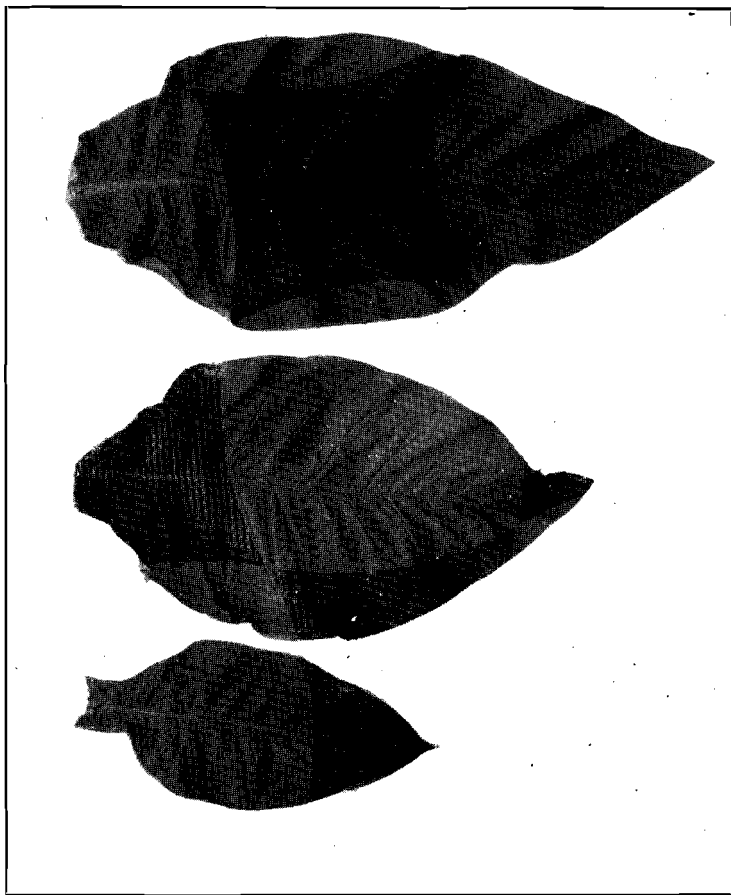
PLATE IV.



a. No. 403, Sumatra. Averages about 28 leaves per plant. Leaves erect, in habit, Centerville, 1911.



b. (403 x 401)—1, F₂ of cross between Sumatra and Broadleaf, with number of leaves and drooping habit of Broadleaf. Size of leaf closely approaches that of the Sumatra parent, Centerville, 1911.



Average middle leaf of No. 403, Sumatra at left, of No. 401, Broadleaf at right and F_1 in center.