INHERITANCE OF BRANCHING HABIT IN TOBACCO¹

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INTRODUCTION

In recent years a considerable number of papers have appeared on the inheritance of various quantitative characters in tobacco. Such characters are usually of the greatest economic interest although they do not lend themselves as readily to strict genetic interpretation as do qualitative characters, owing to the more pronounced influence of environmental conditions upon quantitative results. The general consensus of opinion among plant breeders now is, however, that quantitative characters behave according to Mendelian principles, even though the determination of the exact ratios may be impossible because of the multiplicity of factors concerned. Whatever the correct theory may be, the accumulation of facts from various sources and for various characters will no doubt strengthen the foundation for future theory and practice. Although a considerable number of characters in tobacco crosses have been studied by the writer since 1908, it is proposed to discuss here particularly the inheritance of branching or "suckering" habit, for the reason

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that this conspicuous character in tobacco seems to have received practically no attention by other investigators. It is, moreover, a character which possesses very considerable practical as well as scientific interest. The lateral branches or suckers which develop usually from the axils of the leaves grow to a considerable size and in most forms of tobacco culture must be broken off before harvest. This involves much labor, very often of a slow and tedious sort, as well as frequent mechanical injury to the leaves and possibly also a lowered yield since it is probable that the branches are partly instrumental in diverting foodstuffs from the commercial leaves to themselves. One and sometimes two or more removals of these lateral shoots or suckers are therefore necessary. It is safe to say that the ideal tobacco plant of the growers would possess no suckers. The removal of the terminal inflorescence together with the leaves immediately below (topping) is widely practised, and this naturally tends to stimulate to a considerable degree the rate of growth of the lateral shoots or suckers. These suckers are usually largest at the uppermost remaining node and gradually decrease in size to practically none below the fourth to sixth node. Varieties and also strains differ very much in this respect, however. The suckers may be present and of a considerable size not only at the node of every leaf, but they may also spring from the oldest nodes at the base of the stem where the leaves have long since perished in the normal physiology of the plant. We may therefore possess types with more suckers than remaining leaves.

The possibility that types of tobacco of limited- or non-suckering habit might be produced by simple selection or by crossing followed by selection, has occurred to many observers of tobacco culture. In the absence of any data on this character it would be quite unsafe even to venture a guess as to the practical results to be obtained in undertaking such a problem. As a result of the study of a cross between a small- and a large-suckering type of tobacco, it is believed that the evidence presented will be sufficient to place its behavior in inheritance in line with that of leaf number, size, and shape of leaves, as worked out by EAST and HAYES in particular.

It is admitted that the branching habit is not well adapted for study of inheritance as such, but if we are to understand various plant characters they must be dealt with as best we can. The branching habit is quite as readily modified by environmental conditions as yield of crop. The time of removal of the terminal bud, or the lodging of the plant are marked influencing factors, as well as the time of maturity of the

plants (itself not a definite character), in relation to time of suckering. These factors are to be considered as largely eliminated in the comparative data given, although some discrepancy may be due to time of maturity since the counts and weights were all taken at approximately the same time. The point is of commercial rather than biological significance, however.

REVIEW OF LITERATURE

It is not deemed necessary to consider in detail the literature upon inheritance in tobacco or of the inheritance of quantitative characters, in general. Mention will be made of only a few investigations bearing most closely on the problem.

SHAMEL and COBEY (1907) under the general subject of tobacco breeding, consider briefly "the production of non-suckering types." They attach considerable importance to the variation in amount of suckering of different individuals in the same field but without adequate consideration of the part played by fluctuating variation in this regard in even the purest strains of seed. Judging, however, from the statement that strains were produced by two years' selection which were "almost free from suckers" in comparison with the ordinary seed which produced "many large suckers," the authors were apparently dealing with a strain of seed heterozygous for suckering habit. There are other conditions, however, which may account for their results, such as relative differences in actual time of maturity due either to germinal differences in this character or due indirectly to a variation in resistance to the Thielavia root-rot disease which in the writer's earlier experience in tobacco breeding was found to have almost completely vitiated results. The authors, in any case, lean towards the belief that environment, as such, produces permanent variations, permitting the fixing of type by selection, a theory which now has few followers.

The authors further add that a correlation exists between the number, shape, and character of the leaves borne by individual plants and the number and size of suckers produced by these plants. Many large suckers are said to be correlated with few, heavy, dark, and usually narrow, pointed leaves. This correlation is explained as being due to the large sucker branches taking from the plants the elements of plant food which would otherwise be utilized in the development of many broad, round leaves. No data for these conclusions are presented however.

The work of HAYES (1913) and of HAYES, EAST, and BEINHART

(1913) in Connecticut and Massachusetts, as presented in several papers, has carefully developed the facts of the inheritance of several characters in tobacco as far as they were obtainable, and with these data, laid the foundation of the generally accepted modern theory of the inheritance of quantitative characters according to Mendelian interpretation. The primary facts are the intermediate and uniform nature of the first filial generation in respect to the characters of the parents used in the cross, followed by distinct segregation giving a wide range of variability in the second generation; this range is usually as great or greater than the combined range of variability of the parents. The individuals selected in the F_2 generation may breed true to type, or may continue to show germinal variation. This has been shown to be true for various characters in tobacco, including leaf number, leaf area, length and breadth of leaves, and height of plants (excluding heterosis). This principle has also been shown to hold for various characters in several other plants by a considerable number of recent investigations.

The branching habit has received some attention from breeders of other plants, and although it may be that these habits are not in all cases similar to that in tobacco, they should perhaps be at least mentioned in this connection. Some of the cases are, however, merely brief statements of observations or based on limited data and cannot be satisfactorily correlated with the results presented in this paper.

SHULL (1908) concluded that in the case of the sunflower (*Helianthus annuus* var.) the branching habit followed Mendelian principles and that the branched habit was dominant to the unbranched.

SAUNDERS (1911) working with Stocks believes that the unbranched habit is recessive to the branched. The F_1 of branched with unbranched is branched and the pure unbranched reappears in the F_2 in what seems to be a proportion of 1 to 4, although this was apparently not satisfactorily determined. WEBBER (1912) reports on inheritance of branching habit in peppers. He finds the F_1 intermediate and gets marked variation in F_2 with the production of so-called giants and dwarfs, as a result of transferring fine and coarse branches. In connection with other studies, EMERSON and EAST (1913) report on the inheritance of number of stalks per plant in maize. "Stooling" in corn is probably quite different from branching, but on the other hand it does resemble it in many ways. This character was found to segregate upon crossing, in a manner similar to other quantitative characters.

NORTON (1915) has reported upon the inheritance of habit in the

common bean in which the branching habit is at least characteristic for certain varieties. Nothing of a definite nature is stated in regard to this character unless it be considered that all bush beans are branched. He makes the statement, however, that in a cross between Refugee Wax and Blue Pod some lots homozygous for axial branching were isolated, many individuals of which showed signs of climbing.

METHODS USED

Studies on suckering habit are based particularly on reciprocal crosses of two types which in my cultures have gone under the names of Little Dutch and Cuban. The former is undoubtedly the same as that which has in the past been grown commercially in Ohio as filler tobacco. The leaves are relatively narrow and are distinctly erect (plate 3, P_1). The number of branches ranges from four to six and these are small in comparison with most varieties of tobacco. The number of suckers is much more constant than that of most varieties, which normally have a stronger tendency to sucker toward the base of the stalk. The Cuban type (plate 3, P_2) used is not the same strain as that now grown commercially under shade in the Connecticut valley, although it probably is one of the strains or types from which the shade-grown Cuban has been developed. It differs from the latter especially in that it does not grow quite as large and also in the fact that it branches much more profusely. The number of suckers is usually the same as the number of leaves, plus two to four additional large basal suckers which often grow to the height of the parent plant, beginning to develop soon after the plant is well established in the soil. That this type has bred true in its general conformation since it was first grown in connection with these studies (1908), has been repeatedly shown. The longevity of tobacco seed permits the growing of a considerable number of generations at any one time. In 1915 and again in 1916, succeeding generations of seed from the most vigorous plant in the cultures of the preceding years were grown side by side and certain measurements made of height, leaf number, and leaf size. The averages for these on twenty-five plants for the year 1915 are given in table 1, and show that no improvement or permanent change has occurred. This is in accord with the conclusions of HASSELBRING (1912) and of HAYES (1914) that modification through effects of environment of a southern type of tobacco grown in the north do not occur. Although the Little Dutch parent has not been subjected to a similar test in any one season, the data for the years 1908 to 1918 in-

TABLE I
Measurements of height, number, and size of leaves of inbred Cuban seed of different generations grown the same year. Averages of 25 plants.

Designation	Generation	Stalk Height in inches	Leaves (inches)								Average breadth-index	
			Number	Top		Middle		Bottom		Average		
				Length	Width	Length	Width	Length	Width	Length		Width
14	1	30.6	13.3	11.9	5.6	14.0	7.9	11.6	7.1	12.5	6.8	54.4
140I	2	29.8	13.2	11.4	5.3	13.7	7.2	11.3	6.7	12.1	6.4	52.4
140II	3	30.2	13.3	11.3	5.1	13.4	7.2	11.6	6.8	12.1	6.4	52.9
140III	4	30.7	13.3	11.9	5.5	14.6	7.5	11.6	7.2	12.7	6.7	52.7
140IIII	5	30.6	13.3	11.9	5.6	14.3	7.6	11.0	6.7	12.4	6.6	53.2

Progeny rows of strains isolated from the F_2 generation of the Little Dutch and Cuban cross showing the variation in suckering habit and other characteristics. (A) 42M, (B) 42G21, (C) 42F21, (D) 42B11, (E) 42A11.

dicating that this variety is one of the most uniform strains of tobacco grown at the Experiment Station under all sorts of environmental conditions.

The usual precautions to prevent experimental error have been taken. Selfed seed has been obtained by covering the flower heads with manila paper bags. The seeds of individual plants were used in all cases, and these were sown in sterilized soils and the seedlings transplanted to separate rows in the field. The early experiments were complicated due to the stunting of the plants by the root-rot disease, but in recent years special care has been taken to avoid infested soils.

The parent types have been given numbers under which they were grown in the field, and later generations were merely designated by adding one digit to this number. The original Cuban seed was given the number 14, the next generation of seed plants 141, 142, up to 149 if desired. The following generation from 141 would then be 1411 or 1412, and so on. The cross of Little Dutch with Cuban, for the sake of convenience, was also given a number (42). The F_1 individuals selected for seed were then 421, 422, up to 429. The selection of individuals for growing the F_3 generations, however, were designated by letters, as 42A, 42B, 42C, and the F_3 selections became 42A1, 42B1, and so on.

The plants were topped as nearly as possible at the same relative point, which was just below the "bald sucker." The "bald sucker" is usually regarded as belonging to the terminal inflorescence. It is not believed that the results are altered by the fact that an arbitrary standard is chosen. This same objection has been used against the counts of leaf number of tobacco as a genetic measurement when the plants have been previously topped. As a check on this, a count was made of all nodes of the plants before topping and of leaf numbers after topping (tables 2 and 3). The last column in table 3 shows the ratio of leaf number to node number. This ratio, though showing some range, is believed to be sufficiently close to indicate a high correlation between the number of nodes per plant and number of leaves after topping. Since we have been dealing with plants apparently normal in growth, it is not believed that the facts brought out by ALLARD (1916) respecting the variable location of the "bald sucker" in stunted plants have played a part in these results.

In counting the number of suckers, only those which were large enough to warrant breaking off in commercial practice were included, that is, very small suckers which might later develop to a considerable size were

TABLE 2
Frequency distribution of number of leaves of *Little Dutch* and *Cuban* cross after topping.

Designation	Gen.	Classes for number of leaves per plant																				No.	Mean
		6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
<i>Little Dutch</i> (15)											2	8	7	7	1							25	17.8
<i>Cuban</i> (14)										8	11	4	2									25	15.0
15 X 14	F ₁								1	1	9	8	5	1								25	15.6
14 X 15	F ₁							1	2	7	11	1	3									25	15.6
428	F ₂				3	2	11	18	14	14	13	9	11	4				1				100	15.8
424	F ₂				2	3	13	22	15	10	9	9	4	9	2	1	1					100	15.6
42V	F ₃						1	5	2	5	6	4	1	1								25	16.2
42M	F ₃									1	1	1	2	2	4	7	2	2	1	2		25	21.5
42N1	F ₄				2	1	6	4	6	4		1					1					25	14.4
42O1	F ₄				1	1	4	7	4	3	1	1	1	1			1	1				25	14.0
42X1	F ₄					1	3	5	8	2	4	1				1						25	12.2
42Y1	F ₄					1	2	3	5	1	3	3	2	3	2							25	15.6
42A11	F ₅											2	5	3	8	3	3					24	19.5
42B11	F ₅				2	2	3	11	3	4												25	11.9
42F21	F ₅										7	8	6	3	1							25	16.3
42G21	F ₅		6	3	1	2	4	2	3	2	1	1										25	9.4
42J11	F ₅				4	7	11	2														25	11.6

not included in the counts. Since every leaf axil or every node on the plant has the potential power of developing a lateral shoot, the line in any case would have to be drawn at some arbitrarily chosen point. The weights of the suckers in grams were taken immediately after their removal, on a torsion balance set conveniently in the field for this purpose. Linear measurements of plant height, and length and breadth of leaves were made with a steam-fitter's rule, which is especially convenient for this purpose.

EXPERIMENTAL RESULTS

In 1909 a very considerable number of varieties and strains of tobacco were crossed for the purpose of studying the inheritance of various characters as well as with the hope of developing new types suitable for commercial culture in Wisconsin. It is expected that the practical phase of the work will be discussed elsewhere. It may be mentioned, however, that a new type of tobacco has been produced by crossing two "strains" (believed to be mutations from the normal) of the Connecticut Havana variety. This new type (Connecticut Havana No. 38) has become quite popular in Wisconsin, considering the length of time it has been introduced.

Many of the types crossed in 1909 were quite similar in general habit and could not be relied upon for results of genetic interest, but where distinct varieties were crossed, "blending" in the F_1 generation was practically always observed. A large number of the F_1 generations from seemingly markedly different types when grown for the F_2 gave apparently no good indication of segregation. Whether this was due to lack of sufficient numbers of individuals or to various obscuring environmental factors is not clear, but the writer is tentatively, at least, inclined to agree with LOCK (1909) that the intermediate form of certain crosses in tobacco may persist in the second generation. This matter must, however, be left for further study and in the light of more recent investigations may be subject to analysis.

In 1913, however, it was noted especially that considerable variation was occurring in the F_2 of a cross of Little Dutch with Cuban and several of the more distinctive types were saved for seed to be grown as F_3 families the following year. The F_1 generation of this cross appeared strikingly intermediate in most respects (plate 3, F_1), especially as regards size, shape, and position of the leaf, and in number and size of suckers produced, although the latter habit was usually regarded as domi-

TABLE 3
Frequency distribution of number of nodes of Little Dutch and Cuban cross, 1917.

Designation	Gen.	Classes for number of nodes																																										No.	Mean	Mean leaf number	Ratio of leaf number after topping to total node number																									
		7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42																																			
Little Dutch (15)	P ₁																6										14	17	8	7	1	1														54	30.0	17.8	1: 1.69																							
Cuban (14)	P ₁																1										2	5	15	10	16	3	2																		54	27.8	15.0	1: 1.85																		
15 × 14	F ₁																2										9	15	19	5	2																						52	28.5	15.6	1: 1.82																
14 × 15	F ₁																1										11	20	14	4	3																		53	28.3	15.6	1: 1.81																				
428	F ₂																3	4	9	9	14	7	22	20	28	16	15	12	10	5	5	3	3	2	4													201	27.5	15.8	1: 1.74																					
424	F ₂	1															4	6	11	16	20	25	28	25	18	18	14	10	7	3	5																		211	28.4	15.6	1: 1.82																				
42V	F ₃																1										2	6	8	9	6	7	7	1	2	2	2																		53	27.9	16.2	1: 1.72														
42M	F ₃																										1										3	10	4	11	5	2	6	3	1	1													47	3.62	21.5	1: 1.68										
42N1	F ₄																2										1	3	4	5	7	6	7	5	2	4	3	1										1													51	28.6	14.4	1: 1.98								
42O1	F ₄																2										1	8	15	7	6	4	7	1	2	1	1																		55	24.3	14.0	1: 1.74														
42X1	F ₄																3										6	3	8	6	6	6	7	4	3	1																						53	21.6	12.2	1: 1.77											
42Y1	F ₄																1										1										2	2	9	8	10	4	5	8	3	1																						54	28.9	15.6	1: 1.85	
42A11	F ₅																										1										3	5	7	12	8	3	2	4	5	1										1													52	31.9	19.5	1: 1.64
42B11	F ₅																1										1										2	3	6	13	12	6	4	3	1																		52	22.4	11.9	1: 1.88						
42F21	F ₅																										7										13	15	13	3	3	1																		55	29.0	16.3	1: 1.77									
42G21	F ₅	1	2	2	2	2	1	1					2	2					7	6	3	1	4	2	2	4	2										1	2	1													50	19.5	9.4	1: 2.07																	
42J11	F ₅																4										7	18	10	7	1	2	1																		50	21.5	11.6	1: 1.85																		

nant to small suckers. It was also found that in crosses of Cuban with several other small-suckering types, as Connecticut Havana and Connecticut Broadleaf, the Cuban suckering habit apparently predominated. The Little Dutch and Cuban cross, however, was chosen as the best for a more detailed study of this character in tobacco. Twenty-four families from the F_2 generation as well as several from the F_3 have been grown; some were carried as far as the sixth generation. Marked segregation of leaf characters as well as of branching habit occurred (see plate 2).

Inheritance of number of suckers

The frequency distribution for number of suckers for 1917 in the Little Dutch and Cuban cross, together with the usual biometric terms, are given in table 4. It will be seen that the mean for number of suckers in the Little Dutch variety is $4.55 \pm .07$ as compared with $18.32 \pm .16$ for the Cuban type, a difference of about 13.7 suckers in the two types. The average number of suckers of the two parents for 1917 is 11.4, agreeing very closely with the mean found for the F_1 generation which is seen to be $11.28 \pm .22$ in one case, and $11.6 \pm .24$ in the reciprocal. The truly intermediate nature of the F_1 for number of suckers is therefore surprisingly close in this case. The standard deviation and coefficient of variability show, however, that the F_1 is somewhat more variable than the parents. It seems probable that this result may be due to other factors than that of germinal variation, namely, to heterosis. Turning to the F_2 generations (reciprocals) for this year, it may be seen by the frequency tables that the range of variation is practically equal to that of both parents combined. The mean for the reciprocals will be noted to be very close to that of the F_1 , a fact which seems to be of some significance in indicating the dominating feature of the suckering character in the second generation. The standard deviation shows that the F_2 varies considerably more from the mean than does either of the parents or the first generation. The standard deviation for the Little Dutch is only $.75 \pm .05$, and of the Cuban $1.64 \pm .11$, while that of the F_1 is $2.26 \pm .15$ as compared with $4.07 \pm .14$ for the F_2 .

The F_3 and succeeding generations, show in a more striking manner the marked segregation which has occurred in this cross. Families have been produced which range in means from $4.11 \pm .09$ suckers (42J11) to a family with a mean of $15.40 \pm .33$ suckers (42V). Furthermore, the standard deviations show that families like 42J11 and 42A11 are

LEGEND FOR PLATE 2

Illustrating the variation in leaf size and leaf shape produced in the F_2 of the Little Dutch and Cuban cross. All leaves selected from the same relative position on the plant. P_1 , Cuban parent; P_2 , Little Dutch parent. F_1 , first generation. A, B, F, G, G2, O, S, and X are from strains isolated from F_2 and represent typical leaves of families 42A, 42B, etc., respectively.

breeding relatively true, having deviations of only $.98 \pm .065$ and $1.22 \pm .08$, respectively. Other families, however, as 42G2I and 42M show a standard deviation as large or larger than the F_2 generation, being $4.03 \pm .27$ and $4.81 \pm .23$ respectively (plates 6, 7 and 8).

It may be objected that these figures do not represent in an entirely correct way the true state of affairs, in that they do not take into consideration the relative time of maturity of the two families. If we let the time of the opening of the first flower of the plant represent the relative time of maturity (table 5), we find that 42G2I (heterozygous for this as well as for other factors) is a relatively early type, consequently, the production of numerous suckers is favored, and that 42M is a relatively late type, consequently not so much disposed to the production of numerous suckers within the given time. The means, therefore, would be lower for the one and higher for the other. These cases are extremes, however, and serve only to show that the problem may be complicated

TABLE 5
Frequency distribution of time of flowering of Little Dutch and Cuban cross, 1917.

Designation	Gen.	Class centers in days for time of flowering														No.	Mean	
		2	5	8	11	14	17	20	23	26	29	32	35	38	41			44
Little Dutch (15)	P ₁								17	9	15	7	5				53	27.5
Cuban (14)	P ₁						1	11	24	13	1	2	2				54	23.8
15 × 14	F ₁						11	24	9	6	2						52	20.9
14 × 15	F ₁						15	20	11	6	2						54	20.7
428	F ₂					2	17	31	25	30	31	27	27	7	4	1	202	27.0
424	F ₂						17	18	46	43	35	18	23	6	3	1	210	26.7
42V	F ₃								12	9	17	6	5	3			52	28.5
42M	F ₃									4	11	4	12	8	2		41	33.1
42N1	F ₄						16	9	15	5	2	1	2				50	21.7
42O1	F ₄						6	18	11	10	1	1	2				49	22.5
42X1	F ₄				9	7	24	4	3	2	1	2					52	17.2
42Y1	F ₄						3	4	12	12	8	5	4	4	2		54	27.3
42A11	F ₅						1		3	6	11	12	14	4	1		52	31.2
42B11	F ₅				1	5	26	13	5	2	1						53	18.4
42F21	F ₅							2	13	23	12	4	1				55	26.3
42G21	F ₅	5	7		17	5	12	2	1	2		1					52	12.5
42J11	F ₅					2	24	18	2	4	1		1				52	19.4
Actual dates of flowering		July																
		14	17	20	23	26	29	1	4	7	10	13	16	19	22	25		
		16	19	22	25	28	31	3	6	9	12	15	18	21	24	27		

TABLE 4
Frequency distribution of number of suckers per plant in Little Dutch and Cuban cross, 1917.

Designation	Generation	Classes for number of suckers per plant																					No.	Mean	Standard deviation	Coefficient of variation
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22				
Little Dutch (15) Cuban (14)	P ₁																						44	4.55 ± .07	.75 ± .05	16.43 ± 1.21
	P ₁	3	18	19	4																		49	18.32 ± .16	1.64 ± .11	8.95 ± .61
15 × 14 14 × 15	F ₁																						49	11.28 ± .22	2.26 ± .15	20.08 ± 1.41
	F ₁			1		2	5		7	9	11	8	3	1	2								50	11.60 ± .24	2.49 ± .17	21.52 ± 1.51
428 424	F ₂		4	5	6	10	13	16	14	10	17	20	10	20	10	10	8	14	1	1			189	11.33 ± .20	4.07 ± .14	35.90 ± 1.38
	F ₂	2	1	6	19	13	18	8	15	21	17	14	14	9	9	12	9	4	3			1	195	10.27 ± .20	4.11 ± .12	40.00 ± 1.56
42V 42M	F ₂																						52	15.40 ± .33	3.49 ± .23	22.68 ± 1.50
	F ₂		1					1	6	1		4	3	5	6	11	7	4		3			40	13.90 ± .51	4.81 ± .36	34.64 ± 2.89
42OI 42NI 42XI 42YI	F ₄		1			1	1	2	8	8	4	9	1	1								36	11.08 ± .23	2.07 ± .16	18.68 ± 1.35	
	F ₄		1		2	1	1	3	7	7	5	8	3	3	3	2							46	11.69 ± .29	2.87 ± .20	24.57 ± 1.82
	F ₄		1	2	3	5	7	6	6	7	4	5	2	1		1							50	9.74 ± .26	2.76 ± .18	28.42 ± 2.06
	F ₄		3	2	11	6	3	5	7	5	1	2	2										47	8.29 ± .26	2.64 ± .183	31.81 ± 2.42
42AII 42BII 42F2I 42G2I 42JII	F ₅	3	10	18	6	9	1																47	5.23 ± .12	1.22 ± .08	23.30 ± 1.69
	F ₅		2	6	1	9	11	7	6	3	4	2		1								52	8.46 ± .23	2.44 ± .16	28.80 ± 2.05	
	F ₅	1	2	2	5	6	4	8	5	3	5	6	2	1								50	9.22 ± .37	2.94 ± .20	31.88 ± 2.35	
	F ₅	1		4	3	4	6	3	6	3	4	4	5	1	1	2		1	2			50	10.62 ± .38	4.03 ± .27	38.02 ± 2.90	
	F ₅	1	13	21	12	3	1																51	4.11 ± .09	.98 ± .06	23.80 ± 2.06

Typical plants of Little Dutch parent (P_1) first generation of cross between Little Dutch and Cuban (F_1) and of Cuban parent (P_2). "Topping" stage illustrating general growth habit.

Second generation individuals of cross between Little Dutch and Cuban. (A) 42M, (B) 42G, (C) 42F. "Topping" stage of growth.

Second generation individuals of cross between Little Dutch and Cuban. (D) 42E, (E) 42H, (F) 42L. "Topping" stage of growth.

by the factor of maturity. In the majority of cases of the families studied, this factor cannot be said to have played a part.

The strain 42G the original plant of which is shown in plate 4, B, has been in many respects, the most interesting of all the families studied. It appeared first in 1914 and was at once recognized as a dwarf form. This plant was only 17 inches high and possessed twelve small leaves and fifteen suckers. Although the strain has now run to the sixth generation, it shows no sign of giving off any homozygous forms, although several distinct types of plants have occurred in greater or less numbers. In 1917 a number of deformed plants or monstrosities appeared. Certain of the top leaves appeared to make no growth on one side, hence resulting in a curling to one side. The first flowers appeared very early and were malformed, various degrees of catacorolla and fasciation appearing which terminated the inflorescence, though the plants soon produced branches which flowered normally, but whose flowers were much smaller than those on the normal plants.

Family 42F (plate 4, C) on the other hand seemingly bred true in all characteristics from the start. This plant was selected in the F_2 on account of its desirable habit of growth and because it appeared to possess commercial possibilities. No variation which could be taken as germinal has been observed up through the F_5 generation.

The results in 1918 for number of suckers (table 6) are quite in accord with the results of 1917. The mean number of suckers for the Cuban type is 19.14 ± 1.70 , while that of the Little Dutch is $4.14 \pm .05$. The mean of the F_1 is $15.69 \pm .02$, considerably above the average of the two parents, which is 11.63. The explanation of this fact in view of the results in 1917, where the average of the parents and the obtained mean for F_1 were very close, probably lies in a more favorable condition for heterosis (the stimulus of heterozygosis) to occur. The F_1 generation is again somewhat more variable than the parents, as shown by the standard deviation, but only slightly more so than the Cuban. The standard deviation for the F_1 is $2.09 \pm .01$ as compared with $1.86 \pm .12$ for the Cuban parent and only $.57 \pm .07$ for the Little Dutch parent.

The F_2 , however, shows a standard deviation of $4.54 \pm .08$ and a mean of $11.98 \pm .11$, which again shows the strong tendency on the part of the majority of the F_2 population toward the suckering habit of the Cuban parent.

In 1918 the succeeding generations of some of the F_3 families were grown side by side up to the F_4 , together with the parents, F_1 and F_2 ,

TABLE 6
Frequency distribution for number of suckers per plant in Little Dutch and Cuban cross, 1918.

Designation	Gen.	Classes for number of suckers per plant																											No.	Mean	Standard deviation	Coefficient of variation
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27					
Little Dutch (15)	P ₁		6	38	14																							58	4.14 ± .05	.57 ± .07	13.79 ± .88	
Cuban (14)	P ₁													1		3	6	9	14	6	9	5	1					54	19.14 ± 1.70	1.86 ± .12	9.71 ± .63	
14 × 15	F ₁								1		1	2	2	6	16	7	8	8	3	1								55	15.69 ± .02	2.09 ± .01	13.35 ± .87	
424	F ₂	2	3	22	43	38	32	45	36	45	51	46	50	74	54	55	54	33	17	14	2	1				1		718	11.98 ± .11	4.54 ± .08	37.90 ± .76	
42A	F ₂		1	2	6	2	9	7	4	4	3	1	1	2			1	1										44	8.61 ± .32	3.13 ± .24	36.38 ± 2.92	
42A1	F ₂				1			3	4	5	3	5	7	6	3	4		1	1									43	12.30 ± .29	2.88 ± .21	23.48 ± 1.79	
42A11	F ₂		1	9	27	14	3	2																				56	5.26 ± .09	.97 ± .06	18.45 ± 1.48	
42A111	F ₂			8	17	9	8	2	6	2	1	1			1													55	6.45 ± .20	2.26 ± .14	35.05 ± 2.51	
42J	F ₂			3	19	12	7	5	4	5	1	2	1															59	6.81 ± .19	2.18 ± .13	32.05 ± 2.18	
42J1	F ₂		1	15	24	7	2	3	3		2																	57	5.47 ± .15	1.71 ± .11	31.37 ± 3.41	
42J11	F ₂		2	19	21	9	4	1	1																			57	5.01 ± .10	1.16 ± .07	23.14 ± 1.68	
42J111	F ₂		7	20	17	8	3	1	1																			57	4.77 ± .11	1.25 ± .08	26.25 ± 1.76	
42G	F ₂						1			1	1		3	4	3	5	10	13	4	6	4	1	1					57	17.14 ± .03	2.93 ± .18	17.14 ± 1.75	
42G2	F ₂						1	1	3	1	2	6	3	3	2	3	5	3	7	8	4	4	3	1				60	16.70 ± .36	4.19 ± .26	25.13 ± 1.64	
42G21	F ₂					1	2	2		2	5	7	1	5	9	3	2	3	5	6	3	1						57	14.85 ± .04	4.04 ± .25	27.21 ± 1.83	
42M	F ₂										4	6	4	4	6	4	4	4	2	1	3	1					1	44	15.63 ± .35	3.48 ± .25	22.28 ± 1.67	
42M1	F ₂					1	2	2	1	1	2	4	2	5	4	3	2	6	4	3	2	1			1	1		47	15.74 ± .44	4.49 ± .31	28.56 ± 2.14	
42V	F ₂								1	2	3	4	5	5	4	5	7	6	4	2	1							49	15.28 ± .28	2.95 ± .20	19.32 ± 1.36	
42V1	F ₂						1	1	2	1	8	7	7	13	5	3	2	1	1									52	13.12 ± .23	2.37 ± .16	18.07 ± 1.24	
42P	F ₂				1	2	2	3	2	3	2	3	7	5	4	1	5	1	1	2							1	45	13.04 ± .43	4.33 ± .31	33.18 ± 2.60	
42R	F ₂		5	12	14	4	5	5	2	1																		48	5.41 ± .17	1.76 ± .12	32.56 ± 2.47	
42T	F ₂					1	4	2	4	3	1		3	3	14	9	5	7	1			1			1			59	14.22 ± .34	3.92 ± .24	27.54 ± 1.82	

this being possible owing to the long period of viability of tobacco seed. The conditions were consequently good for the comparison of the different generations. In family 42A it may be noted that the mean has shifted upward and downward. This is better shown by the standard deviation which gradually shifted downward to a point approaching the homozygous condition but which rises again in the F_6 generation. In family 42J, however, the mean has been gradually shifted downward as has also the variability as shown by the standard deviation. Whether this could be still further lowered is in doubt. The results in the F_4 , F_5 , and F_6 are, however, too close to warrant much significance being attached to them in this respect, and it seems quite probable that this family has been practically homozygous for number of suckers since the F_4 generation. Other families, as 42G, as indicated by the standard deviation, have shown no tendency to decrease in variability thus far, and are almost as variable as the F_2 .

The coefficients of variability are not regarded as a good measure of the conditions in these studies and the comparison of the different generations can be much better supplied by growing them in the same season and comparing the standard deviations, than by comparing the coefficient of variability under dissimilar conditions.

Inheritance of weight of suckers

It will be shown that considerable correlation exists between weight of suckers and number of suckers. In a study of suckering habit, however, it is just as necessary to consider size of the suckers as their number and it is not to be expected that those families which show the greatest number of suckers will necessarily show the greatest weight. A plant may form many small suckers or relatively few large suckers within a given period (plate 7, A and C).

The first data on weight of suckers were taken in 1914. The data for 1915 and 1917 only, will be presented, however, though the results of the five years bear out the conclusions drawn. Table 7 for sucker weight in 1915 shows the mean weight of the Little Dutch variety to be 22.2 ± 1.08 decigrams as compared with 49.63 ± 1.14 for the Cuban. Owing to the fact that the weights were taken relatively late, the Little Dutch suckers show a weight greater than normal as compared with Cuban, i.e., the Cuban suckers had reached their maximum weight some time before the weights were recorded, permitting the Little Dutch to make a proportionate increase. The mean weight of the F_1 closely approaches that

TABLE 7
Frequency distribution of weight of suckers per plant in cross between Little Dutch and Cuban, 1915.

Designation	Gen.	Class centers in decigrams for weight of suckers															No.	Mean	Standard deviation	Coefficient of variation	
		5	15	25	35	45	55	65	75	85	95	105	115								
Little Cuban (15)	P ₁	6	20	9	12	3												50	22.20 ± 1.08	11.32 ± .76	50.99 ± 3.43
Cuban (14)	P ₁			4	10	16	12	7	4									54	49.62 ± 1.14	12.42 ± .80	25.09 ± 1.55
15 × 14	F ₁	4	4	24	28	18	8	7	6	1								100	49.00 ± 1.15	17.15 ± .81	35.00 ± 1.66
423	F ₂	52	145	157	148	67	56	15	10	5	5	2	1					666	31.20 ± .47	18.12 ± .33	58.10 ± 1.07
42A	F ₃	7	5	15	14	5	1	2	2	3	1		1					50	37.80 ± 1.86	19.55 ± 1.31	51.71 ± 3.48
42B	F ₃	2	5	10	12	7	2	2	2	3	1							44	46.81 ± 1.89	18.62 ± 1.33	39.76 ± 2.85
42C	F ₃	8	14	10	5	3	2	2	1									45	25.02 ± 3.51	17.51 ± 1.24	70.06 ± 4.98
42D	F ₃	1	5	7	11	10	7	4	1	1	1							48	41.45 ± 1.81	18.65 ± 1.28	44.99 ± 3.09
42E	F ₃			15	13	9	7	2	2	2	1							49	40.71 ± 1.46	15.17 ± 1.03	37.25 ± 2.53
42F	F ₃	15	17	9	6	3												50	18.00 ± 1.13	11.87 ± .80	65.96 ± 4.38
42G	F ₃	4	7	13	10	11		4	1									50	32.60 ± 1.57	16.56 ± 1.11	50.76 ± 3.42
42H	F ₃	1	3	11	13	8	8	4	2	1								51	40.68 ± 1.61	17.06 ± 1.13	41.95 ± 2.80
42I	F ₃	8	15	15	4	6	1											49	22.55 ± 1.23	12.86 ± .87	57.03 ± 3.88
42J	F ₃	1	4	11	19	10	2	2		1								50	35.60 ± 1.32	13.91 ± .93	39.08 ± 2.02
42K	F ₃		1	5	15	12	5	6	3	1	2							50	47.40 ± 2.10	22.09 ± 1.49	46.61 ± 2.94
42L	F ₃	3	19	16	6	4	2											50	24.00 ± 1.13	11.87 ± .80	49.41 ± 3.33

Typical plants of Little Dutch parent (P_1), first generation of cross between Little Dutch and Cuban (F_1), and of Cuban parent (P_2) illustrating "suckering" habit.

Second generation individuals of cross between Little Dutch and Cuban, illustrating segregation in "suckering" habit. (A) $42V$, (B) $42G$, (C) $42M$.

Second generation individuals of cross between Little Dutch and Cuban, illustrating segregation in "suckering" habit. (D) 42F, (E) 42J, (F) 42B.

of the Cuban parent, a fact which is again believed to be due to the stimulus of heterozygosis. The most significant feature in the results for 1915 are that, although a range of variation greater than that of the parents combined occurred in the F_2 , the F_3 generations show a distinct segregation into families some of which, as 42F, show a smaller-suckering habit than the Little Dutch parent, while others like 42K closely approach the Cuban parent in mean weight of suckers.

Passing to the results of 1917 (table 8), which illustrate in a more satisfactory way the important points, we find that the mean weight of the Little Dutch suckers is $9.4 \pm .62$ as compared with 46.4 ± 1.41 for the Cuban. The mean of the F_1 and its reciprocal are very close and compare quite favorably with the average of the two parents, showing, however, some heterosis. The mean weight for the F_2 and its reciprocal is on the average about midway between that of the two parents, and the F_3 families show means approaching that of the small-suckering parent to above that of the large-suckering parent. Considering the standard deviation of the weights of suckers for 1917, it should be first noted that the Little Dutch is not nearly as variable as the Cuban variety, and if we consider the average of the two as a measure of the standard deviation of the parents, we find the F_1 is only slightly more variable than the average of the parents as regards suckering habit and not as variable as the Cuban parent considered alone. The F_2 shows some increase in variability, but not as much as expected, although the range is equal to that of both parents combined.

Strain 42AII has a comparatively low standard deviation ($8.35 \pm .58$) but is probably not homozygous since results in 1918 for number of suckers apparently showed increased variation in the F_6 . Strain 42BII, 42V and 42M have greater deviation from the mean than the F_2 and the two former are apparently considerably more heterozygous for weight than for number of suckers. It is worthy of note that whereas 42JII showed the least deviation from the mean in number of suckers 42AII showed the lowest deviation in weight of suckers, but the 42M, which showed the greatest deviation as regards number of suckers, also gave the greatest variation in weight of suckers. The question therefore arises as to the relation existing between the number and weight of suckers per plant. It will be shown that a significant correlation exists between these characters. The inheritance of weights of suckers in the cross of Little Dutch and Cuban is therefore similar to that of number of suckers. The marked variation in size of suckers as well as in number of suckers in this cross is illustrated in plates 6, 7 and 8.

TABLE 8
Frequency distribution of weight of suckers of Little Dutch and Cuban cross, 1917.

Designation	Generation	Class centers in decigrams for weight of suckers																No.	Mean	Standard deviation	Coefficient of variation
		5	15	25	35	45	55	65	75	85	95										
Little Dutch (15) Cuban (14)	P ₁	28	14	3															9.4 ± .62	6.19 ± .44	65.85 ± 4.68
	P ₁		1	4	13	13	10	4	3	1									46.4 ± 1.41	14.66 ± .99	31.60 ± 2.15
15 × 14 14 × 15	F ₁	1	7	17	15	7	1	1											30.5 ± 1.09	11.40 ± .77	37.38 ± 2.54
	F ₁	3	8	14	16	8	1	0	1										30.1 ± 1.25	13.26 ± .88	44.07 ± 2.94
428	F ₂	41	46	32	31	24	10	3	1	1									25.2 ± .82	16.82 ± .63	66.75 ± 2.31
	F ₂	31	46	52	33	22	3	6	0	1									30.9 ± .67	14.00 ± .48	45.30 ± 1.55
42V	F ₃	5	6	13	9	8	8	1	2										34.0 ± 1.65	17.66 ± 1.17	51.95 ± 3.43
	F ₃	11	10	9	1	6	3	0	1										23.7 ± 1.87	17.80 ± 1.32	75.12 ± 5.59
42Ni 42Oi 42Xi 42Yi	F ₄	3	10	21	11	1	0	1											27.3 ± 1.02	10.34 ± .71	37.90 ± 2.63
	F ₄	2	4	17	12	5	3	2											31.8 ± 1.35	13.45 ± .95	42.30 ± 3.00
	F ₄	3	3	12	19	7	4	2											33.8 ± 1.28	13.49 ± .91	39.91 ± 2.69
	F ₄	11	13	17	2	2	1	0	1										20.6 ± 1.33	13.56 ± .94	65.84 ± 4.57
42Ai1 42Bi1 42Fi2i 42Gi2i 42Ji1	F ₅	16	20	9	2														14.3 ± .82	8.35 ± .58	58.16 ± 4.40
	F ₅	1	6	11	15	5	6	6	1	1									38.4 ± 1.65	17.64 ± 1.16	45.85 ± 3.03
	F ₅	4	15	21	7	3													23.0 ± .93	9.79 ± .66	41.73 ± 2.81
	F ₅	3	3	3	5	18	12	5	1	1	2								48.8 ± 1.61	16.94 ± 1.14	34.71 ± 2.34
	F ₅	1	12	17	9	10	1	1											39.3 ± 1.18	12.53 ± .83	31.88 ± 2.09

Correlations

As already stated, a marked correlation appears to exist between the number and weight of suckers per plant in tobacco. Table 9 shows the distribution and correlation of these characters in 374 plants of the F_2

TABLE 9
*Correlation between number of suckers and weight
of suckers in Little Dutch $\times$ Cuban F_2 .*

		Class centers of No. of suckers							Totals
		3	6	9	12	15	18	21	
Class centers of weight of suckers	50	13	26	16	7	3			65
	150	3	18	31	20	16	7		95
	250		15	16	20	15	10		76
	350		10	11	18	16	12	1	68
	450		6	6	16	10	6	1	45
	550			1	4	6	1		12
	650			1	3	4	2		10
	750						1		1
	850			1	1				2
Totals		16	75	83	89	70	39	2	374

Coefficient of correlation, $.423 \pm .028$

generation of Little Dutch and Cuban grown in 1917. The number and weight of the suckers of each plant were recorded as they were broken off. The coefficient of correlation is found to be $.423 \pm .028$ indicating a relatively good correlation between number and weight of suckers. It is quite likely that a greater correlation would have been obtained if a pure strain of seed had been used. This would not have brought out the point which it is desired to emphasize since the variability in such a case would be merely due to fluctuating variation.

In the same manner, it is shown (table 10) that no correlation between number of leaves and number of suckers per plant can be said to exist, the coefficient obtained being $-.012 \pm .05$. According to SHAMEL and COBEY (1907) a significant negative correlation should be obtained, i.e., a large number of leaves should result in fewer suckers, since such leaves make it physiologically more difficult for suckers to grow. While admitting that such a physiological relationship may exist, the results presented here indicate that there is little or no genetical relationship between these characters.

With respect to the relation of the shape and size of the leaf and size of suckers, it is to be expected that some negative correlation may exist,

TABLE II

Comparison of certain plant and leaf characters with number and weight of suckers in Little Dutch and Cuban cross.

Designation	Gener- ation	Number of plants measured	Stalk height (inches)	Leaves										Suckers	
				No.	Top		Middle		Bottom		Average		Breadth- index	Mean number	Mean weight (grams)
					Length	Width	Length	Width	Length	Width	Length	Width			
14 Cuban	P	25	39.9	15.0	11.5	6.1	14.5	8.7	10.9	6.5	12.3	7.1	57.7	18.3	464
15 Little Dutch	P	25	32.4	17.8	17.8	6.5	25.7	9.9	15.5	7.4	19.7	7.9	40.1	4.5	94
14 × 15	F ₁	25	38.2	15.7	15.6	6.3	21.1	10.1	13.7	7.3	16.8	7.9	47.0	11.6	307
15 × 14	F ₁	25	37.4	15.7	16.5	6.7	21.3	10.3	13.8	7.2	17.2	8.0	46.5	11.3	305
424	F ₂	100	39.1	15.8	14.7	6.1	20.4	9.9	13.7	5.8	16.3	7.2	44.1	10.3	309
428	F ₂	100	37.1	15.8	14.5	6.4	20.2	9.7	13.2	7.2	15.9	7.8	49.0	11.3	252
42A11	F ₃	25	40.9	19.8	11.7	7.6	18.1	11.8	12.6	8.1	14.1	9.2	65.2	5.2	143
42B11	F ₃	25	26.6	11.8	14.5	5.0	18.1	7.9	12.1	5.8	14.9	6.2	41.6	8.5	385
42F21	F ₃	25	36.7	16.3	15.7	8.7	20.8	11.6	14.9	9.1	17.1	9.8	57.3	9.2	230
42G21	F ₃	25	18.8	9.4	10.5	3.3	12.1	4.0	8.9	2.9	10.5	3.4	32.3	10.6	485
42J11	F ₃	25	24.2	11.6	14.7	9.4	18.0	11.5	12.9	7.9	15.2	9.6	63.1	4.1	393
42N1	F ₃	25	36.0	14.4	16.2	6.1	21.4	9.7	17.7	6.9	18.4	7.5	40.7	11.7	273
42O1	F ₃	25	29.0	14.0	18.9	6.2	23.8	9.8	14.9	7.0	19.2	7.7	40.1	11.0	318
42X1	F ₃	25	23.6	12.2	14.1	3.5	19.2	6.2	12.2	4.0	15.1	4.6	30.4	9.7	338
42Y1	F ₃	25	40.6	15.6	13.6	9.0	19.2	12.9	14.0	9.4	15.6	10.4	66.6	8.3	206
42M	F ₃	25	57.0	21.5	13.0	6.3	20.9	10.5	13.2	7.8	15.7	8.2	52.2	13.9	237
42V	F ₃	25	40.0	16.2	13.8	9.5	18.5	13.5	13.5	9.7	15.3	10.9	71.2	15.4	340

TABLE 10

Correlation between number of leaves and number of suckers per plant of Little Dutch $\times$ Cuban F_2 .

Number of leaves per plant	Number of suckers per plant																	Totals
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
11		1		1						1	1							4
12							1	1		1		1						4
13			4			1			2	4	1	7	1			1		21
14				3	3	3	1	3	2	1	2	4	2	3	3	1		31
15	1		1	2	3	3	1	1		2		3	3	2	2	1		25
16				3	2		1	1		5	1	1		2		3		19
17			1	1		3	2	2	3	2			1	2		2		19
18	1	1	1					2	1	2		1	1			1		11
19					3	1	2						1		2	2	2	13
20		1	1		2	1	1						2	2				10
			1															1
																		0
						1												1
Totals	2	3	9	10	14	12	9	10	8	18	5	17	11	11	7	11	2	159

Coefficient of correlation, $-.012 \pm .05$

since a large-leaved plant may tend to shade the suckers in some degree, hence reducing their rate of growth. It is not expected that this point can be cleared up definitely with the data at hand, but it has been thought best to present all the data for the various families in 1917 in the shape of a table of averages (table 11) of leaf measurements rather than to construct a correlation table. The breadth-index is given as a measure of leaf shape. It is obtained by dividing the breadth by the length and expressing the result in percent. No measurements have been made on leaf area, but a good idea of leaf size may be obtained by consulting the average length and breadth of the top, middle, and bottom leaves. The relative size and shape of leaves in this cross are illustrated in plate 2, showing that material for such a study was at hand. Without going into a comparison of these data in detail, suffice it to say that the family with the lowest breadth-index (42X1) does not possess the greatest average number of suckers. In the same way the family with the largest breadth-index (42V) does not possess the lowest average number of suckers (in fact it has the greatest number) nor the smallest average weight of suckers. Again the family with the largest-sized leaves does not possess the smallest number or weight of suckers. There seems to be no indication in these data, therefore, that shape and size of leaves are consistently associated in any way with number or weight of suckers.

DISCUSSION OF RESULTS

The Little Dutch and Cuban cross in tobacco offers a striking case of combination of parental characteristics and uniformity of type in the F_1 generation, and of segregation in F_2 into a great variety of forms in regard to various morphological characters. Furthermore, some of these F_2 types may breed true from the start with respect to certain characters; other types become fixed in the fourth or succeeding generations; and still others apparently continue in a heterozygous condition through the sixth generation.

Although ratios in these various characters have been sought for, nothing satisfactory has been obtained which could be in any way made to conform to typical Mendelian ratios with any number of genes considered. This is not believed, however, to signify that the characters are not conforming to Mendelian principles. The assumption of "multiple" factors and continuous variation as propounded by NILSSON-EHLE (1908, 1909) and EAST (1910) and later by a considerable number of investigators for various characters, can be made to explain the facts as they occur. This theory assumes that the parent plants differ in two or more separate genes for the character in question. These independent genes, allelomorphic to their own absence, are capable of adding to the character and the heterozygous condition of any unit is half of the homozygous condition. Little can be gained at present by passing into a discussion of the number of probable genes involved in the inheritance of the suckering habit. There are undoubtedly a great number of such factors concerned, especially in weight. In any case the same mathematical scheme as applied by HAYES (1913) for number of leaves in tobacco or by various other writers for quantitative characters might be developed to fit the situation at hand. On the other hand, as assumed by SHULL (1914), it is probable that some of the variability in the F_2 and succeeding generations may be due to heterosis.

If we can assume that the small-suckering habit of the Little Dutch is an expression of an unbranched condition and the large-suckering habit of the Cuban is the branched condition, the question arises as to which is the recessive condition. There seems to be little doubt that if we can justifiably use this term in this case, the unbranched or small-suckering habit tends to be recessive to the large-suckering habit. This conclusion is based largely on the predominance of large-and-numerous-suckering types in the F_2 and on the fact that several small-suckering F_2 individuals have shown a tendency to breed true, whereas the large-suck-

ering types have been more difficult to obtain in a homozygous condition. This is in accord with Miss SAUNDERS's observations on the inheritance of branching habit in stocks. Miss SAUNDERS (1911) was apparently dealing with a true unbranched parent, rendering her results perhaps more easy of interpretation.

Our results with tobacco are more similar possibly to the data of EMERSON and EAST (1913) on number of stalks per plant in corn. The results are at least closely comparable, as are also those of WEBBER (1912) in a study of branching habit in peppers.

The origin and behavior of family 42G in this cross has been very interesting. The original plant and a certain proportion of its offspring are truly "dwarfs" (figure 1, B), if such a word can be used with any degree of definiteness. Since the dwarf has not yet been obtained in the homozygous condition, considerable variation in height occurs, as may be seen by referring to family 42G21 in table 12. The true dwarfs, however, lie considerably below the mean given.

The behavior of 42G has been in many respects similar to that described by STOUT (1915) for dwarf plants in *Hibiscus oculiroseus*. Its origin, however, is clearly that of a variate due to crossing two distinct varieties of tobacco belonging to the same species. No one would recognize this plant as related in any way to its grandparents. Furthermore, no plant in any way resembling it has appeared in several thousand F_2 plants grown. The similarity of its behavior to mutating forms and

FIGURE 1.—Strains 42M and 42G growing side by side showing the characteristic of a "giant" (A) and the "dwarf" (B) forms produced in the Little Dutch and Cuban cross.

TABLE 12
Frequency distribution of height in Little Dutch and Cuban cross, 1917.

Designation	Gen.	Class centers for height of plants in inches													No.	Mean
		5.5	11.5	17.5	23.5	29.5	35.5	41.5	47.5	53.5	59.5	65.5	71.5	77.5	83.5	
Little Dutch (15)	P ₁						17	30	3						50	45.8
Cuban (14)	P ₁							1	22	24	3				50	56.9
15 × 14	F ₁							3	20	26					49	56.3
14 × 15	F ₁							3	33	15					51	54.9
428	F ₂						18	50	60	44	16	3			191	53.9
424	F ₂				1	9	40	65	60	19	1				195	54.7
42V	F ₂					3	9	21	14	2					49	53.8
42M	F ₂							4	17	14	6	1			42	69.0
42N1	F ₄					2	7	20	19						38	53.1
42O1	F ₄				3	22	18	5							48	50.6
42X1	F ₄			2	20	11									53	39.8
42G1	F ₄				2	5	16	20	2						45	56.7
42A11	F ₆				2	15	18	6							41	51.5
42B11	F ₆				3	21	26	2							52	44.6
42F21	F ₆					17	29	9							55	52.6
42G21	F ₆	4	7	3	11	9	5	2							52	26.1
42J11	F ₆				12	34	5								51	40.6

especially to mutating dwarfs is sufficiently striking to warrant mention. The author is inclined to believe, however, that it is a case of "true" segregation.

Another abnormality which has arisen in this cross, which has not occurred in either the Little Dutch or Cuban parent or in any other known type of tobacco, was first noted in 1917. This abnormality has evidenced itself as a peculiar "physiological weakness" of the plants occurring late in the season. The veins of the leaves starting from below first show signs of browning and deterioration (not decay) (figure

FIGURE 2.—Small portion of area of leaf of 42A showing the characteristic pattern on leaves of plants exhibiting "physiological weakness".

2). This results in an intermediate stage in a peculiar netting of the leaves, which finally dry up from the bottom. In 1918 it was noted that the suckers coming from the base of plants cut off a few weeks previously began to die from this trouble indicating strongly that the difficulty arises at the roots of the plants, which apparently lose their power to function properly, although close examination showed no striking abnormality of these organs. In the F_2 these plants occurred in a ratio of about 1 to 25. Two F_3 strains, 42A and 42M, were uniformly affected in 1917 and were again affected in 1918 in a similar manner. This characteristic was therefore behaving as a recessive. The appearance of this variation, entirely new and different from anything observed in a large number of cultures grown under a wide variety of

conditions for a number of years, is sufficiently significant to warrant mention, since it indicates the production of an entirely new character in tobacco so far as my observations have gone.

SUMMARY

The inheritance of the branching or suckering habit of tobacco has been studied in a cross between a Cuban type possessing many large suckers and a Little Dutch strain possessing few and small suckers. The conclusions are based largely on counts and weights of suckers of the parental types and the succeeding generations of the cross made over a period of several years under widely varying environmental conditions. The conclusions are more specifically drawn, however, upon the data here presented in which the parents and several succeeding generations of the cross were grown in the same year under identical conditions. Some data are also given on correlations between number of leaves and number and weight of suckers and on the inheritance of height of plants, number of nodes and leaves, flowering, and leaf size and shape. The results seem to justify the following conclusions:

1. The branching or suckering habit of tobacco is a distinct characteristic and its behavior in inheritance is similar to that of other inheritable characters, although it is subject to very considerable fluctuating variation due to environmental conditions and to certain physiological factors.

2. The F_1 generation of the cross between the variety with large and numerous suckers and the one with small and few suckers is intermediate between the two parents for number of suckers, although it is somewhat above the intermediate condition for weight of suckers, due no doubt to the stimulus of heterozygosis.

3. The reciprocal F_1 generations behave in an almost identical manner and the variation in this generation is on the whole no more than that of the most variable parent as shown by the standard deviation.

4. The F_2 generation possesses a range of variation as great or greater than that of the combined range of the two parents. The standard deviation from the mean as regards suckering habit is practically twice that of the average of the parents or of the F_1 . The large majority of the F_2 plants seem to approach more nearly the numerous-and-heavy-suckering type than they do the parent with few and small suckers, although this cannot be said with certainty as the means more nearly resemble the intermediate condition found in the F_1 .

5. Segregation in regard to suckering habit is definitely shown in the F_3 and succeeding generations. Strains have been isolated which sucker even less profusely than the Little Dutch parent, while others have been almost as prolific in this respect as the Cuban type. The large majority of the strains, however, range between the two extremes. The standard deviations show that certain of these strains are no more variable than the parents and are probably breeding true for suckering habit. Other strains, however, carried as far as F_6 , have failed to show any signs of the homozygous condition. The production of few and small suckers is seemingly the recessive condition.

6. The inheritance of suckering habit is purely quantitative and not separable into satisfactory classes or ratios. The results are comparable with those obtained by EAST, HAYES, and EMERSON for various quantitative characters in tobacco, maize, and other plants. It is believed the data should be interpreted in a similar way on the multiple factor hypothesis.

7. A considerable number of random observations and some systematically recorded data tend to show that no particular correlation exists between number, size, or shape of leaves, and the number or size of suckers in the second generation of a cross between a large-suckering and a small-suckering type. The production of a non-suckering type of tobacco combined with the commercial practice of "topping" is probably impossible for purely physiological reasons. It is believed, however, that by crossing and selection, the production of relatively-few-and-small-suckering strains of a certain type of leaf may be obtained which may be of some commercial importance; although it is probable that, on account of the number of factors involved, the combination of this characteristic with the proper leaf shape and quality will be extremely difficult to obtain.

8. Combination and segregation of characters has also been shown in this cross for such characters as height of plant, number of nodes and leaves, size and shape of leaves, and time of flowering.

9. The occurrence of two abnormalities entirely foreign to the parents, one a morphological monstrosity and the other a "physiological weakness," are recorded merely as illustrating the occurrence of "new" characters in a variety cross under controlled conditions.

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