The Journal of Agriculture of the University of Puerto Rico

In continuation of The Journal of the Department of Agriculture of Puerto Rico

Published Quarterly: January, April, July and October of each year.

MELVILLE T. COOK, EDITOR

VOL. XVIII OCTOBER 1934 No 4.

INHERITANCE IN NICOTIANA. I. STUDY OF THE GLAUCOUS AND THE YELLOW CHARACTERS IN *N. TABACUM* L.

By J. A. B. NOLLA *

INTRODUCTION

Several years ago the writer became interested in some morphological characters in *Nicotiana tabacum* L. while making preliminary studies with relative resistance of a number of tobacco varieties to tropical diseases. This study is therefore an outgrowth of another investigation. Materials have been accumulated steadily in our collection and although our interest is primarily of a phytopathological nature it has been and will be our purpose to render a genetical interpretation of such morphological characters as come to our attention and which appear not to have been described or analyzed genetically up to this time. We believe that the phytopathologist will make more rapid progress in studies on immunity which may lead to the development of disease-resistant strains of our crop plants when he knows more about the general genetical behavior of his plant materials. This knowledge will eliminate to a considerable extent many of the retarding factors which enter into the picture of the control of plant diseases by the use of resistant varieties, and consequently will simplify the methods, facilitate the planning of the experiments, shorten the period of the investigations and assure more prompt results.

This short paper proposes to constitute the first of what may become a series of studies on the genetics of Nicotiana. These studies were begun at the Insular Agricultural Experiment Station of Puerto Rico in 1928 and continued in Cornell University in 1930–32 and in the University of Wisconsin in 1932–33.

MATERIALS AND METHODS

The *glaucous* character reported herein occurs on a Puerto Rican

* John Simon Guggenheim Memorial Foundation Fellow. Latin American Exchange. July 1932–September 1933.

commercial tobacco which has been known locally under the name of "Ceniza", meaning *ash*. The name refers to the peculiar appearance of the leaves which suggests a bluish or grayish green color. This character can be detected in the seed-bed at an early age but may be difficult to separate when seedlings are very crowded. For this reason, young seedlings should be transplanted to a second plant bed where more space will insure favorable conditions for development thereby minimizing the chances of failure in detecting the *glaucous* plants. Plants of this latter strain grow slower than ordinary tobaccos, the leaves are thick and the veins branch out from the midrib at an acute angle. The *glaucous* character appears not to have been described from any other country.

The *yellow* character as used here applies to a plant color which might more properly be designated as yellowish-green. This color is peculiar to normal plants at all stages of growth and is easily recognized in very young seedlings. The strain used in our studies is a pure line of a wrapper tobacco planted by a local company prior to the year 1927 in the tobacco districts at the higher altitudes of the island and which was believed to have descended from a single yellow plant discovered by a laborer in the back yard of his house. It is undoubtedly a mutation from a Puerto Rican variety. It was given the name of "Consolation" because it was discovered at a time when light wrappers were much in fashion among smokers and the industry here would have suffered tremendously had it not been for this timely discovery. But the advantage which the new tobacco brought to the growers was to dwindle away years later when the Consolation wrapper fell into disrepute. This yellow tobacco should not be confused with the *White Burley* tobacco studied by Henika (1) from which it differs in morphological expression and in being due to a single factor whereas the latter represents a two-factor difference. It seems also to be distinct from a tobacco variety which showed a golden color of leaves just before maturity and which was studied by Kajanus (2), who found an approximation to a genetical ratio of 15:1 for color.

The two characters reported herein were studied in the same crosses, thereby expediting the handling of a larger number of individuals for each character. The normal yellow tobacco is *non-glœucous* while the "Ceniza" or *glaucous*, being green, serves as a contrast to *yellow*. Other crosses which could not be carried beyond the second generation were also made with other *non-glaucous* or *non-yellow* pure lines.

In making counts for the yellow character it was only necessary to sow seed rather thinly in flats, then pricking out the seedlings with forceps when ten to fifteen days old. This method made possible the study of large numbers of seedlings. Another method employed was to transplant large plants from a seed-bed prepared in the usual way and making observations and counts in the field. It was soon found this method was unnecessary. In order to ascertain whether plants classified in the seed-bed as yellow or green were correctly determined, plantings of small seedlings grouped under the two classes were made in the greenhouse in one-and-a half-inch pots. Final counts made at the age of twenty-eight days, showed that the classification had been made accurately.

The separation of the *glaucous* or ashy seedlings was extraordinarily difficult in the seed-bed. It was found, however, that they could be detected in about a month after transplanting into small pots in the greenhouse, or into flats or beds when set at a longitudinal and transversal distance of two and one-half inches. They were transplanted into these when about two weeks old and counts could be made ten to fifteen days later. In doubtful cases the seedlings were further transplanted and kept for an additional period of two weeks when final counts were made on such individuals.

The same procedure was followed for all crosses and selfings.

In the determination of *ashy* or *glaucous* segregates the young seedlings were transplanted into flats of the usual size, transplanting thirty-five plants to each flat. The number of observations made in each progeny varied, depending upon the greenhouse and other facilities available at the time the different progenies were studied. In general, the population was fairly large.

In the season of 1928–1929 the following crosses were made: *glaucous* or "Ceniza" (Ce) $\times$ *yellow* or "*Consolation*" (Kon); green Turkish Sansum (T) $\times$ Kon; Ce $\times$ T; all direct and reciprocal. The first generations of these crosses were all grown at the Insular Experiment Station of Puerto Rico in the year 1928–29 and all selfings and backcrosses were then performed. The second and backcross generations were grown either at the Insular Experiment Station or in the greenhouse at Cornell University in the fall and winter of 1931; while further F_2 and third generations were grown in the spring and summer of 1932 at the latter institution. Third generation progenies were also studied at the Department of Horticulture, University of Wisconsin, in the summer of 1933.

The two characters, *yellow* and *glaucous*, are discussed separately. However, the data are from the same crosses.

In determining the significance of the genetical results given below, the probable error and Chi-square methods were employed. The probable error of numbers was determined in testing the significance of the 3:1 and 15:1 mendelian ratios. The expression Dev./P.E. was used as the measure of significance, taking Dev./P.E. = 3.2, as the lower level of significance, which represents odds of 31.36 to 1 against the occurrence of a deviation as great as or greater than the designated one. Values higher than 3.2 are regarded as giving odds higher than 31.36 that the deviations are not due to random sampling. In the application of the Chi-square method for goodness of fit, values of P were calculated by referring to Elderton's tables. It was considered that values of P equal to 0.05 or lower, indicated odds too high for such deviations to be due to random sampling.

RESULTS

The Yellow Character

The first generation of the crosses for the study of green and yellow was in all cases green, showing that the allelomorph *yellow* is a recessive character.

In the second generation of the direct and reciprocal crosses the seedlings were grouped into the two classes: green and yellow. From the data obtained in the F_2 of the cross *Ce* × *Kon* and *Kon* × *Ce* a hypothesis of a single factor relation between green and yellow was formulated. The figures are given in Table I, under *Kon* × *Ce* — A and *Ce* × *Kon* — A. In either case deviations can be attributed to random sampling.

Evidence from the Second generation.—In order to test the hypothesis, several F_2 progenies of the above cross were studied and in addition the cross *Kon* × *T* was made. Table I contains the distribution of the F_2 phenotypes in six progenies of the cross *Kon* × *Ce;* two progenies of the reciprocal cross and the direct and reciprocal cross *Kon* × *T*.

An examination of the figures shows a fairly close fit of the results to a 3:1 ratio of green to yellow seedlings. In only one progeny *Kon* × *Ce* — D is the deviation high enough to bring the results near the border line of significance. From the above F_2 results it seems evident that the single factor difference between green and yellow is appropriate in this case.

Evidence from the backcross.—Several of the F_1 plants which were selfed for F_2 studies were also backcrossed to the *yellow* parent. The F_1's of the cross *Kon* × *T* were backcrossed to no. 45, a *yellow* segregate from the cross *Ce* × *Kon* — A, which was also recessive for the "Ceniza" character. The latter are included although the crosses had been mainly intended for the study of the *Ce* character. These backcross progenies are given in Table II. Progeny ((*Kon* × *Ce*) × *Kon*) — B shows a deviation in the distribution of green and normal seedlings which appears too high to be attributed to random sampling, the D/P.E. being 3.62. The remaining eight backcross progenies show a fairly close agreement to the expected 1:1 ratio for single-factor differences. It is, therefore, safe to conclude that on the basis of backcross results a single-factor difference exists between green and *yellow*.

Evidence from the F_3 generation.—Further evidence in support of the single-factor pair difference for green and yellow is offered by the F_3 generation. In order to secure that evidence we studied thirty-four F_3 progenies of the cross *Ce* × *Kon* and thirty-four similar progenies of the reciprocal *Kon* × *Ce*. (See Tables III and IV). There should have been justification to regard all *yellow* segregants of the F_2 as pure breeding for that character. However, in the case of the cross *Ce* × *Kon*, *yellow* segregants were carried through the third generation so that in Table III we will find ten progenies of such segregants. This was not done with the similar segregates in the cross *Kon* × *Ce*. According to expectation the F_3 progenies should show a distribution of homozygous green to heterozygous green in the ratio of 1:2. An examination of Table III will reveal that such expectation was very closely realized, the green F_2 plants when carried through the third generation exhibiting a distribution of 8 pure-breeding green to 16 heterozygous individuals. The data in Table IV show a similar agreement with expectation; of 34 F_3 progenies, 23 proved to be heterozygous and 11 homozygous for green; a close approximation to the 2:1 ratio.

The hypothesis of a single-factor difference is further strengthened by the individual behavior in the F_3 of the heterozygous F_2 plants. Of sixteen such progenies in Table III only in family 26 are the results of doubtful significance. There the Dev./P. E. is almost 3.3 and therefore the odds against such a deviation being caused by random sampling are rather high. Whether a 3:1 ratio prevails in that family is not established by those results. All the 23 progenies in Table IV show a fairly good agreement with the expected 3:1 ratio.

From the evidence offered from F_2, B.C. and F_3 generations, a single-factor pair difference is established for *yellow* plant color as contrasted to green. It is proposed that this factor pair be designated *Yy*, green plants to be represented by *YY* and yellow plants by *yy*.

The Ceniza or Glaucous Character

The plants of the first generation crosses were all normal green or *non-glaucous*, indicating dominance of this character over *glaucous* (*Ce*).

In the study of the data on the *Ce* character two phenotypes were easily distinguishable, namely, the *glaucous* and *non-glaucous* and therefore individuals were classified into those two groups. The study of the distribution of the population of the second generation of the direct and reciprocal cross *Ce* × *Kon* and one backcross suggested a ratio of fifteen normal green plants to one "Ceniza" or *glaucous*. Progeny *Ce* × *Kon* — A (Table V) gave 438 normal and 35 *Ce* plants or a ratio of 12.51 to 1. The significance of these results rests on the fact that on the basis of a 15 : 1 ratio, the Dev./P.E. is only 1.53. Progeny *Kon* × *Ce* — A (Table V) showed a distribution of 128 normal to 10 *Ce* plants. These numbers represent a ratio of 12.8 to 1. On the assumption of a 15 : 1 ratio the Dev./P.E. is very low, only 0.72. The backcross progeny (*Kon* × *Ce*) × *Ce* given in Table V is represented by 251 normal to 66 *Ce* individuals, a ratio of 3.8 to 1. On the basis of a 3 : 1 ratio of normal to *Ce* the Dev./P.E. value is 2.55 and therefore such a deviation may be attributed to random sampling. The assumption of a segregation in the ratio of 15 normal to 1 *Ce* in the F_2 seems to be supported by a backcross ratio of 3 normal to 1 *Ce*. Therefore, there are sufficient grounds to assume a *two* factor pair difference between normal and *Ce*, the *Ce* character being exhibited only as the double recessive; and dominance of one or the other, or of both factors, producing normal plants.

Evidence from the second generation.—As proof of the hypothesis of the 15 : 1 relationship several F_2 progenies other than those reported above, were studied. (See Table V). Of 3 progenies of *Ce* × *Kon* only in B do the results appear to invalidate the hypothesis, with a Dev./P.E. reaching 3.37, slightly above the lower level of significance. But with larger numbers in C and D the results were in fairly good agreement with expectations, the Dev./P.E. being as low as 0.33 and 0.45, respectively. Other F_2 progenies which support the assumed 15 : 1 ratio are *Kon* × *Ce* — B, *45* × *T*, and *T* × *45*, A and B, and

$T \times Ce$. All these progenies show a good agreement with the expected ratio.

Evidence from the backcrosses.—Additional evidence in support of the expected backcross ratio of 3 : 1 is furnished by progenies $(45 \times T) \times 45$ and $(T \times 45) \times 45$ which exhibit a D/P.E. of 1.48 and 1.75, respectively, and by $(T \times Ce) \times Ce$ with a D/P.E. = 1.80.

Evidence from the third generation.—If the hypothesis of duplicate genes as an explanation of the results obtained in the F_2 and B.C. generations of crosses involving the study of the *Ce* character holds, it would be expected that in the third generation some progenies should be normal, some should segregate in the ratio of 15 : 1 and some 3 : 1, normal to *Ce*; while one out of sixteen should be *glaucous*. That this expectation was realized is evidenced by the data on 20 progenies of the cross $Ce \times Kon$ (Table VI) and 28 progenies of the reciprocal (Table VII). An examination of Table VI reveals that out of 20 progenies, seven segregated in the ratio of 15 to 1, six in the ratio of 3 : 1, five were pure breeding normal and two were "Ceniza" or *glaucous*. In the segregating families the statistical analysis of the data proves that the results significantly support the assumption of either 15 : 1 or 3 : 1 ratios. A similar behavior is obtained in the F_3 of the reciprocal cross (Table VII). There, seven progenies segregated in a ratio of 15 to 1 and six in the ratio of 3 : 1 normal to *glaucous;* thirteen were pure breeding normal while two were "Ceniza" or *glaucous*. If all the F_3 progenies are considered together the distribution is as follows: 18 progenies pure breeding normal, 14 progenies segregating in the ratio of 15 : 1, 12 others in the ratio of 3 : 1, and four homozygous *glaucous*. If the composition of a normal plant be represented by Ce_1 Ce_1 Ce_2 Ce_2, the *glaucous* by ce_1 ce_1 ce_2 ce_2 and the hybrid in the cross by Ce_1 ce_1 Ce_2 ce_2, the following genotypes and ratios would be expected in F_3 on the basis of the 15 : 1 hypothesis: 1 Ce_1 Ce_1 Ce_2 Ce_2, 2 Ce_1 Ce_1 Ce_2 ce_2, 1 Ce_1 Ce_1 ce_2 ce_2, 2 Ce_1 ce_1 Ce_2 Ce_2, 4 Ce_1 ce_1 Ce_2 ce_2, 2 Ce_1 ce_1 ce_2 ce_2, 1 ce_1 ce_1 Ce_2 Ce_2, 2 ce_1 ce_1 Ce_2 ce_2, and 1 ce_1 ce_1 ce_2 ce_2. Of those with either one or the other factor, or both factors in the dominant condition, Ce_1 ce_1 Ce_2 ce_2 would be expected to segregate in the ratio of 15 : 1, Ce_1 ce_1 ce_2 ce_2 and ce_1 ce_1 Ce_2 ce_2 in the ratio of 3 : 1, ce_1 ce_1 ce_2 ce_2 would be *glaucous* and all the other genotypes would be pure breeding normal. There would then be expected four classes of genotypes in the following ratios: 7 pure breeding normal, 4 segregating 15:1, 4 segregating 3:1 and 1 pure recessive. When the Chi-square test for goodness of fit is applied to the expected results given above, a value of P = 0.78 is obtained.

Class	Expected Ratio	Frequencies		$\frac{O-C^2}{C}$	P
		Observed	Calculated		
Normal	7	18	21		
15:1 ratio	4	14	12		
3:1 ratio	4	12	12		
Pure Recessive	1	4	3		
Total	16	48	48	1.09523	0.78046

The deviations from the expected ratio of the distribution of the F_3 families are such as might be expected by chance alone eleven times in twenty trials and it may be concluded, therefore, that the results obtained support the suggested hypothesis of duplicate genes.

On the basis of F_2, B.C. and F_3 results it is concluded that the assumption of a 2–factor difference for the *Ce* character is justified. These factors are designated as Ce_1 and Ce_2 with their corresponding allelomorphs ce_1 and ce_2. The presence of either factor in the dominant condition produces normal plants while both factors must be recessive to produce the "Ceniza" character. The constitution of a "Ceniza" plant will be represented by $ce_1\ ce_1\ ce_2\ ce_2$.

Independent Inheritance

It was of interest to determine from the data whether there existed any linkage relations between the factor pair Yy and $Ce_1\ ce_1$ or $Ce_2\ ce_2$. The fact that *N. tabacum* has twenty-four pairs of chromosomes would make the detection of linkage between those factors of unique interest especially since the occurrence of the mutants has been reported from Puerto Rico simultaneously. From the analysis of the distribution of the phenotypes in three F_2 progenies, twelve F_3's and one backcross progeny it appears that no linkage exists between the factor pairs $Ce_1\ ce_1$ and $Ce_2\ ce_2$ and yellow (Yy). The reader is referred to Table VIII. The F_2 progenies *Ce* × *Kon* — C and — D and *Kon* × *Ce* —A, on the basis of independent inheritance of the characters should yield four classes in the following ratios: 45 normal green, 15 normal yellow, 3 *Ce* green and 1 *Ce* yellow. The Chi-square method of testing the goodness of fit showed that for *Ce* × *Kon* — *C*, P = 0.53; for *Ce* × *Kon* — D, P = 0.80 and *Kon* × *Ce* — A, P = 0.52. These values of P all show that the deviations from the expected are not significant.

In the F_3 of the direct and reciprocal crosses of *Ce* × *Kon*, progenies 6, 7, 52, 67, 68 and 76, segregating in the ratio of 3 normal to 1 *Ce* and 3 green to 1 yellow, should show a distribution of phenotypes as follows: nine normal green, 3 normal yellow, 3 *Ce* green and 1 *Ce* yellow. These expectations are realized in all these progenies (see Table VIII). In all these progenies the values of P are high, the lowest being 0.13 for family no. 68. This value, however, indicates that the deviations might be expected to be due to chance alone, once in eight times.

Progenies 30, 55, 62, 66, 71 and 85 which segregated in the ratio of 15 normal to 1 *Ce* and 3 green to 1 yellow, would be expected to show the phenotypes in the same ratios as the F_2 progenies, namely 45 : 15 : 3 : 1. Such expectation is fully accomplished in all the progenies except no. 55. An examination of the distribution of the phenotypes in that progeny, however, shows that the deficiencies may not be attributed to linkage.

The distribution of the genotypes in the F_3 generation is given in Table IX. The normal expectation of genotypes on the basis of a 15 : 1 ratio for the *Ce* character and 3 : 1 segregation for green and yellow is as follows. Green genotypes to give only, 7 normal; 4 segregating in the ratio of 15 normal to 1 *Ce*; 4 in the ratio of 3 normal to 1 *Ce;* and 1 pure breeding "Ceniza". Those green individuals of the composition *Yy* should show the following distribution: 14 normal, 8 segregating 15 normal to 1 *Ce*, 8 segregating into 3 normal and 1 *Ce*, and 2 pure breeding *Ce*. The yellow genotypes are not analyzed in the above table, but the expectation would be the same as for pure breeding greens.

A consideration of the results given in Table IX shows that the deviations from the expected ratio are such as can well be attributed to conditions of the experiment.

The results of F_2 and F_3 progenies given in support of the hypothesis of the independent inheritance of the Yy and Ce_1 ce_1 Ce_2 ce_2 are further complemented by the backcross results.

So, from the above results it may safely be concluded that no linkage exists between the factor for *yellow* plant color and those factors responsible for the "Ceniza" or *glaucous* character.

ACKNOWLEDGMENTS

The writer gratefully acknowledges his indebtedness to Hon. C. E. Chardon, Commissioner of Agriculture of Puerto Rico at the time this work was begun, for his cooperation and interest; to Prof. R.

APPENDIX

TABLE I

SEGREGATION OF THE GREEN (Y) AND *YELLOW* (y) CHARACTERS IN THE F_2 OF CROSSES BETWEEN VARIOUS PURE LINES OF TOBACCO

Progeny	Color	n	Frequencies		Dev.	P. E.	D/P. E
			Observed	Calculated (3:1)			
Kon x Ce—A..........	Green	461	359	345.75	13.25	6.27	2.11
	Yellow....		102	115.25			
Kon x Ce—B..........	Green.....	1995	1489	1496.25	7.25	13.08	0.55
	Yellow....		506	498.75			
Kon x Ce—C..........	Green.....	400	297	300.00	3.00	5.84	0.51
	Yellow....		103	100.00			
Kon x Ce—D..........	Green.....	912	656	684.00	28.00	8.82	3.17
	Yellow....		256	228.00			
Kon x Ce—E..........	Green.....	824	638	618.00	20.00	8.38	2.39
	Yellow....		186	206.00			
Kon x Ce—F..........	Green.....	713	536	534.75	1.25	7.80	0.16
	Yellow....		177	178.25			
Ce x Kon—A..........	Green.....	1150	856	862.50	6.50	9.90	0.66
	Yellow....		294	287.50			
Ce x Kon—B..........	Green.....	358	279	268.50	10.50	5.53	1.89
	Yellow....		79	89.50			
Kon x T—A..........	Green.....	4642	3522	3481.50	40.50	19.90	2.04
	Yellow....		1120	1160.50			
T x Kon—B....	Green.....	5156	3844	3867.00	23.00	20.97	1.10
	Yellow....		1312	1289.00			

TABLE II

SEGREGATION OF THE GREEN (Y) AND *YELLOW* (y) CHARACTERS IN THE BACK-CROSS GENERATION OF CROSSES BETWEEN VARIOUS PURE LINES OF TOBACCO

Progeny	Color	n	Frequencies		Dev.	P. E.	D/P. E.
			Observed	Calculated (1:1)			
(Kon x Ce) x Kon—A.	Green..... Yellow....	1797	869 928	898.50 898.50	29.50	14.29	2.06
(Kon x Ce) x Kon—B.	Green..... Yellow....	730	398 332	365.00 365.00	33.00	9.11	3.62
(Kon x Ce) x Kon—C.	Green..... Yellow....	974	490 484	487.00 487.00	3.00	10.53	0.28
(Kon x Ce) x Kon—D.	Green..... Yellow....	141	64 77	70.50 70.50	6.50	4.00	1.62
(Kon x Ce) x Kon—E.	Green..... Yellow....	367	184 183	183.50 183.50	0.50	6.46	0.08
(Ce x Kon) x Kon—A.	Green..... Yellow....	154	80 74	77.00 77.00	3.00	4.19	0.72
(Ce x Kon) x Kon—B.	Green..... Yellow....	362	191 171	181 00 181.00	10.00	6.42	1.56
(Kon x T) x 43........	Green..... Yellow....	911	460 451	455.50 455.50	4.50	10.18	0.44
(T x Kon) x 43........	Green..... Yellow....	1187	589 598	593.50 593.50	4.50	11.62	0.36

A. Emerson, Head of the Department of Plant Breeding at Cornell University, Prof. James G. Moore, Chairman of the Department of Horticulture at the University of Wisconsin, and Prof. James Johnson, Tobacco Pathologist at Wisconsin, for generously placing at the writer's disposal the equipment in their laboratories and helping in the field operations. To Professors Emerson and Johnson as well as to Prof. John H. Parker of Kansas State College, and Prof. A. C. Fraser of Cornell, he is also indebted for valuable criticisms and encouragement. Finally, his acknowledgments are due to The John Simon Guggenheim Memorial Foundation of New York for the fellowship which made the conclusion of these studies possible.

SUMMARY

1. Two previously undescribed characters of *N. tabacum* are described and studied genetically. The *yellow* plant color appears to be distinct from similar deficiencies heretofore reported. It is not to be confused with the *Burley* character in White Burley tobacco.

2. Green color is dominant to *yellow* color.

3. Normal green is dominant to *glaucous* or "Ceniza".

4. Green and *yellow* are differentiated by a single factor pair which is designated *Yy*.

5. Normal green and *Ce* or *glaucous* plants are differentiated by two factor pairs; therefore segregation occurs in the proportion of 15 normal green to 1 *glaucous* (*Ce*). These are designated by Ce_1 ce_1 Ce_2 ce_2.

6. The factors for *glaucous* and for *yellow* are inherited independently of each other.

DEPARTMENT OF AGRICULTURE AND COMMERCE, SAN JUAN, PUERTO RICO.

LITERATURE CITED

(1) **Henika, F. S.** The inheritance of the White Burley character in tobacco. Jour. Agr. Res. **44**: 477–493, fig. 1. 1932.

(2) **Kajanus, B.** Über eine Kreuzung zwischen grunblättrigem und gelbblättrigem Tabak. Hereditas **5**: 84–86. 1924.

TABLE III

RESULTS OF THE F_3 GENERATION OF THE CROSS *Ce* × *Kon* IN THE STUDY OF THE *YELLOW* CHARACTER

Progeny	Color	n	Frequencies Observed	Frequencies Calculated (3:1)	Dev.	P. E.	D/P. E.
2	Green Yellow	996	776 220	747.00 249.00	29.00	9.22	3.15
4	Green Yellow	920	708 212	690.00 230.00	18.00	8.86	2.03
6	Green Yellow	1135	876 259	851.25 283.75	24.75	9.84	2.52
7	Green Yellow	470	359 111	352.50 117.50	6.50	6.33	1.03
8	Green Yellow	483	373 110	362 25 120.75	10.75	6.42	1.67
10	Green Yellow	144	115 29	108.00 36.00	7.00	3.50	2 00
13	Green Yellow	517	393 124	387.75 129.25	5.25	6.64	0.79
21	Green Yellow	1353	1033 320	1014.75 338.25	18.25	10.71	1.70
25	Green Yellow	158	120 38	118.50 39.50	1.50	3.67	0.41
26	Green Yellow	689	542 147	516.75 172.25	25.25	7.67	3.29
31	Green Yellow	459	363 96	344.25 114.75	18.75	6.26	2.99
32	Green Yellow	333	241 92	249.75 83.25	8.75	5.33	1.64
33	Green Yellow	1250	966 284	937.50 312.50	28.50	10.30	2.77
34	Green Yellow	202	150 52	151.50 50.50	1.50	4.15	0.36
44	Green Yellow	406	315 91	304.50 101.50	10.50	5.88	1.79
46	Green Yellow	751	560 191	563.25 187.75	3.25	8.00	0.41

Families breeding true to green: 1, 5, 9, 14, 20, 23, 45 and 47.

Families breeding true to yellow: 15, 16, 17 18, 19, 39, 40, 41, 42 and 43

TABLE IV

BEHAVIOR OF THE F_3 GENERATION OF THE CROSS *Kon* × *Ce* IN THE STUDY OF THE *YELLOW* CHARACTER

Progeny	Color	n	Frequencies		Dev.	P. E.	D/P. E.
			Observed	Calculated (3:1)			
52	Green Yellow	585	445 140	438.75 146.25	6.25	7.06	0.89
54	Green Yellow	376	291 85	282.00 94.00	9.00	5.66	1.59
55	Green Yellow	1016	772 244	762.00 254.00	10.00	9.31	1.07
56	Green Yellow	492	373 119	369.00 123.00	4.00	6.48	0.62
61	Green Yellow	761	566 195	570.75 190.25	4 75	8.06	0.59
62	Green Yellow	759	570 189	569.25 189.75	0.75	8.05	0.09
63	Green Yellow	439	335 104	329.25 109.75	5.75	6.12	0.94
66	Green Yellow	452	339 113	339.00 113.00	0	6.21	0
67	Green Yellow	405	302 103	303.75 101.25	1.75	5.88	0.30
68	Green Yellow	416	318 98	312.00 104.00	6.00	5.96	1.01
69	Green Yellow	497	375 122	372.75 124.25	2.75	6.51	0.42
70	Green Yellow	435	332 103	326.25 108.75	5.75	6.09	0.94
71	Green Yellow	325	253 72	243.75 81.25	9.25	5.27	1.76
72	Green Yellow	213	153 60	159.75 53.25	6.75	4.26	1.58
76	Green Yellow	208	154 54	156.00 52.00	2.00	4.21	0.48
77	Green Yellow	208	155 53	156.00 52.00	1.00	4.21	0.24
79	Green Yellow	260	202 58	195.00 65.00	7.00	4.71	1.49
85	Green Yellow	360	270 90	270 00 90.00	0	5.54	0
87	Green Yellow	359	284 75	269.25 89.75	14.75	5.53	2.67
88	Green Yellow	248	191 57	186.00 62.00	5.00	4.60	1.09
89	Green Yellow	266	210 56	199.50 66.50	10.50	4.76	2.20
90	Green Yellow	549	428 121	411.75 137.25	16.25	6.84	2.38
91	Green Yellow	196	149 47	147.00 49.00	2.00	4.09	0.49

Families breeding true to green: 53, 57, 58, 59, 60, 64, 65, 74, 78, 81 and 83.

TABLE V

SEGREGATION OF THE CENIZA (ce) OR *GLAUCOUS* CHARACTER AND THE NORMAL CHARACTER (Ce) IN THE SECOND AND BACKCROSS GENERATIONS OF CROSSES

Progeny	Color	n	Frequencies			Dev.	P. E.	D/P. E.
			Observed	Calculated				
				n	ratio			
Ce x Kon—A.......	Normal... Ceniza....	473	438 35	443.44 29.56	15:1	5.44	3.55	1.53
Ce x Kon—B.......	Normal... Ceniza....	451	411 40	422.71 28.29	15:1	11.71	3.47	3.37
Ce x Kon—C.......	Normal... Ceniza....	997	933 64	934.69 62.31	15:1	1.69	5.16	0.33
Ce x Kon—D.......	Normal... Ceniza....	981	922 59	919.69 61.31	15:1	2.31	5.11	0.45
Kon x Ce—A.......	Normal... Ceniza....	138	128 10	129.38 8.62	15:1	1.38	1.92	0.72
Kon x Ce—B.......	Normal... Ceniza....	181	167 14	169.69 11.31	15:1	2.69	2.20	1.22
45 x T..............	Normal... Ceniza....	85	81 4	79.69 5.31	15:1	1.31	1.51	0.87
T x 45—A..........	Normal... Ceniza....	246	229 17	230.62 15.38	15:1	1.62	2.56	0.63
T x 45—B..........	Normal.. Ceniza....	210	199 11	196.87 13.12	15:1	2.12	2.37	0 90
T x Ce.............	Normal... Ceniza....	292	266 26	273.75 18.25	15:1	7.75	2.69	2.88
(T x Ce) x Ce.....	Normal... Ceniza....	379	274 105	284.25 94.75	3:1	10.25	5.69	1.80
(Kon x Ce) x Ce..	Normal... Ceniza....	317	251 66	237.75 79.25	3:1	13.25	5.20	2.55
(45 x T) x 45......	Normal... Ceniza....	66	53 13	49.50 16.50	3:1	3.50	2.37	1.48
(T x 45) x 45......	Normal... Ceniza....	175	138 37	131.25 43.75	3:1	6.75	3.86	1.75

TABLE VI

BEHAVIOR OF THE F_3 PROGENIES OF THE CROSS *Ce* × *Kon* IN THE STUDY OF THE *CENIZA* OR *GLAUCOUS* CHARACTER

Progeny	Color	n	Frequencies			Dev.	P. E.	D/P. E.
			Observed	Calculated				
				n	ratio			
17	Normal... Ceniza....	137	133 4	128.440 8.560	15:1	4.560	1.91	2.39
18	Normal... Ceniza....	34	31 3	31.880 2.120	15:1	0.880	0.95	0.93
19	Normal... Ceniza....	55	51 4	51.560 3.440	15:1	0.560	1.21	0.46
23	Normal... Ceniza....	130	122 8	121.875 8.125	15:1	0.125	1.86	0.07
30	Normal... Ceniza....	120	114 6	112.500 7.500	15:1	1.500	1.79	0.84
40	Normal... Ceniza....	128	122 6	120.000 8.000	15:1	2.000	1.85	1.08
42	Normal... Ceniza....	128	123 5	120.000 8.000	15:1	3.000	1.85	1.62
5	Normal... Ceniza....	246	181 65	184.500 61.500	3:1	3.500	4.58	0.76
6	Normal... Ceniza....	175	138 37	131.250 43.750	3:1	6.750	3.86	1.75
7	Normal... Ceniza....	153	111 42	114.750 38.250	3:1	3.750	3.61	1.04
16	Normal... Ceniza....	153	141 12	143.440 9.560	3:1	2.440	3.61	0.68
25	Normal... Ceniza....	120	94 26	90.000 30.000	3:1	4.000	3.20	1.25
32	Normal... Ceniza....	120	96 24	90.000 30.000	3:1	6.000	3.20	1.87

Families breeding true to normal: 4, 9, 15, 26 and 33.

Families breeding true to "Ceniza" or *glaucous*: 39 and 43.

TABLE VII

BEHAVIOR OF THE F_3 PROGENIES OF THE CROSS *KON* x *CE* IN THE STUDY OF THE CENIZA OR *GLAUCOUS* CHARACTER

Progeny	Color	n	Frequencies			Dev.	P. E.	D/P. E.
			Observed	Calculated				
				n	ratio			
55	Normal... Ceniza....	365	334 31	342.19 22.81	15:1	8.19	3.12	2.62
62	Normal... Ceniza....	282	264 18	264.32 17.62	15:1	0.37	2.74	0.14
65	Normal... Ceniza....	311	299 12	291.56 19.44	15:1	7.44	2.88	2.58
66	Normal... Ceniza....	448	421 27	420.00 28.00	15:1	1.00	3.46	0.29
71	Normal... Ceniza....	308	281 27	288.75 19.25	15:1	7.75	2.87	2.70
85	Normal... Ceniza....	286	268 18	268.13 17.87	15:1	0.13	2.76	0.05
91	Normal... Ceniza....	149	142 7	139.69 9.31	15:1	2.31	1.99	1.16
52	Normal... Ceniza....	401	319 82	300.75 100.25	3:1	18.25	5.85	3.12
58	Normal... Ceniza....	327	258 69	245.25 81.75	3:1	12.75	5.28	2.41
67	Normal... Ceniza....	380	287 93	285.00 95.00	3:1	2.00	5.69	0.35
68	Normal... Ceniza....	406	313 93	304.50 101.50	3:1	8.50	5.88	1.45
76	Normal... Ceniza....	198	155 43	148.50 49.50	3:1	6.50	4.11	1.58
83	Normal... Ceniza....	252	201 51	189 00 63.00	3:1	12.00	4.64	2.59

Families breeding true to normal: 53, 57, 60, 63, 64, 69, 70, 72, 77, 78, 79, 89 and 90.

Families breeding true to "Ceniza": 59 and 61.

TABLE VIII

SHOWING PHENOTYPIC DISTRIBUTION IN F_2, F_3 AND B. C. PROGENIES OF CROSSES IN THE STUDY OF THE *YELLOW* AND CENIZA CHARACTERS

Progeny	Class *	Frequencies			Chi Square	P
		Observed	Calculated			
			ratio	n		
Ce x Kon—C	NY	703	45	701.0160		
	Ny	230	15	233.6720		
	nY	43	3	46.7340		
	ny	21	1	15.5780		
	Total	997	....	997.0000	=2.24376	0.53
Ce x Kon—D	NY	693	45	689.7660		
	Ny	229	15	229.9220		
	nY	41	3	45.9840		
	ny	18	1	15.3280		
	Total	981	....	981.0000	=1.02484	0.80
Kon x Ce—A	NY	100	45	97.0310		
	Ny	28	15	32.3440		
	nY	9	3	6.4688		
	ny	1	1	2.1562		
	Total	138	....	138.0000	=2.28431	0.52
Ce x Kon—6	NY	94	9	98.4375		
	Ny	44	3	32.8125		
	nY	29	3	32.8125		
	ny	8	1	10.9375		
	Total	175	....	175.0000	=5.24636	0.16
Ce x Kon—7	NY	81	9	86.0625		
	Ny	30	3	28.6875		
	nY	35	3	28.6875		
	ny	7	1	9.5625		
	Total	153	....	153.0000	=2.43355	0.49
Ce x Kon—30	NY	49	45	42.1875		
	Ny	8	15	14.0625		
	nY	2	3	2.8125		
	ny	1	1	0.9375		
	Total	60	....	60.0000	=3.95250	0.27
Kon x Ce—55	NY	226	45	256.6410		
	Ny	119	15	85.5470		
	nY	12	3	17.1090		
	ny	8	1	5.7030		
	Total	365	....	365.0000	=19.19081	0.0003
Kon x Ce—62	NY	196	45	198.2810		
	Ny	68	15	66.0940		
	nY	12	3	13.2190		
	ny	6	1	4.4060		
	Total	282	....	282.0000	=1.26496	0.74
Kon x Ce—66	NY	322	45	315.0000		
	Ny	99	15	105.0000		
	nY	22	3	21.0000		
	ny	5	1	7.0000		
	Total	448	....	448.0000	=1.11746	0.77

*The class *NY* stands for normal green, *Ny* is normal yellow, *nY* is ce, or *glaucous* green, and *ny* represents ce yellow.

TABLE VIII—(Cont.)

SHOWING PHENOTYPIC DISTRIBUTION IN F_2, F_3 AND B. C. PROGENIES OF CROSSES IN THE STUDY OF THE *YELLOW* AND CENIZA CHARACTERS

Progeny	Class *	Frequencies			Chi Square	P
		Observed	Calculated			
			ratio	n		
Kon x Ce—71	NY	217	45	216.5620		
	Ny	64	15	72.1870		
	nY	22	3	14.4380		
	ny	5	1	4.8130		
	Total	308	....	308.0000	=4.89732	0.18
Kon x Ce—85	NY	186	45	201.0940		
	Ny	82	15	67.0310		
	nY	13	3	13.4060		
	ny	5	1	4.4690		
	Total	286	....	286.0000	=4.55113	0.21
Kon x Ce—52	NY	223	9	225.5620		
	Ny	96	3	75.1870		
	nY	59	3	75.1880		
	ny	23	1	25.0630		
	Total	401	....	401.0000	=9.44557	0.24
Kon x Ce—67	NY	207	9	213.7500		
	Ny	80	3	71.2500		
	nY	72	3	71.2500		
	ny	21	1	23.7500		
	Total	380	....	380.0000	=1.61403	0.66
Kon x Ce—68	NY	239	9	228.3750		
	Ny	74	3	76.1250		
	nY	79	3	76.1250		
	ny	14	1	25.3750		
	Total	406	....	406.0000	=5.76136	0.13
Kon x Ce—76	NY	123	9	111.3750		
	Ny	32	3	37.1250		
	nY	31	3	37.1250		
	ny	12	1	12.3750		
	Total	198	....	198.0000	=2.94275	0.40

TABLE IX

BEHAVIOR OF GENOTYPES IN RELATION TO THE *CE* CHARACTER OR ITS ALLELOMORPH IN F_3 FAMILIES WHICH ARE PURE BREEDING FOR GREEN OR SEGREGATING FOR GREEN AND YELLOW

Class		Calculated ratio	n		Chi Square	P
			Observed	Calculated		
Green	Normal...	7	6	5.250		
	15:1.......	4	2	3.000		
	3:1........	4	3	3.000		
	ce.........	1	1	0.750		
	Total.....	16	12	12.000	=0.52380	Over 0.80
Segregating Green & Yellow	Normal...	14	11	11.375		
	15:1.......	8	6	6.500		
	3:1........	8	8	6.500		
	ce.........	2	1	1.625		
	Total.....	32	26	26.000	=0.63734	Over 0.80