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THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION

NEW HAVEN, CONN.

BULLETIN 176, MAY, 1913.

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TOBACCO BREEDING IN CONNECTICUT.

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INTRODUCTION.

The investigations, with which this paper deals, were commenced in the year 1908, and since that time have been carried on in co-operative agreement between the Office of Tobacco Investigations of the Bureau of Plant Industry, United States Department of Agriculture, Laboratory of Genetics of Harvard University, and The Connecticut Agricultural Experiment Station.

The primary object of the work has been to study some of the fundamental principles involved in tobacco breeding, with the belief that a knowledge of these principles is absolutely necessary if one is to build up a system of both practical and scientific breeding.

It is self evident that the complex nature of the problems involved makes it impossible to reach anything like a final solution at present; this paper, therefore, is to be considered in the nature of a report of progress. In it are described the results obtained during the past four years.

EFFECTS OF INBREEDING IN A CLOSE-FERTILIZED SPECIES.

Tobacco is a naturally close pollinated plant, although intercrossing through the agency of insects is probably somewhat frequent. Observations on the earlier blossoms of the flower head have convinced the writers that in many cases, at least, fertilization of the pistil has taken place before the blossom opens. In the later flowers the chances of intercrossing are much greater, as the blossom often opens before fertilization has been accomplished. It is evident that, as tobacco is a naturally close-fertilized plant, it must be vigorous under self fertilization, but some data on actual controlled inbreeding are given to further substantiate this belief.

Darwin, in his classical experiments on inbreeding and cross-breeding, found some types which were very vigorous when continually self-fertilized.

Garner (1912) reports that a number of types have been inbred under bags for six or eight years by the United States Department of Agriculture without any observable change in vigor or growth habit. A certain strain of our present Connecticut Cuban shade type, now grown on one of our large plantations, was inbred for a period of five years (1903-1908) by saving seed from individual plants under a paper bag. Since that time seed has been saved from desirable plants under cloth tent, the chances, however, seeming very small that seed so produced will be cross-fertilized. Instead of showing a loss of vigor due to self-fertilization, this type seems more vigorous than in the early years of its introduction.

The Sumatra type, which has been used as one of our parent varieties, has been inbred for a period of seven years, without giving any evidence of accumulated evil effects of inbreeding.

In a large series of generic crosses of *Nicotiana* the writers

have observed a wide range of variation as to increased vigor due to crossing. In some cases the first hybrid generation was very vigorous while other species crosses were non-vigorous.

In a previous paper (Hayes, 1912) on variety crosses within the species, five characters were measured in F_1 and were compared with the average of their parents for three sets of crosses. These characters were height of plant, length, breadth and size of leaf, and number of leaves per plant. All showed an increase over the average of the parents, except in the number of leaves per plant, which was almost exactly intermediate.

To quote from a previous paper (East and Hayes, 1912):

"We believe it to be established that:

"1. The decrease in vigor due to inbreeding naturally cross-fertilized species, and the increase in vigor due to crossing naturally self-fertilized species, are manifestations of the same phenomenon. This phenomenon is heterozygosis.* Crossing produces heterozygosis in all characters by which the parent plants differ. Inbreeding tends to produce homozygosis automatically.

"2. Inbreeding is not injurious in itself, but weak types, kept in existence in a cross-fertilized species through heterozygosis, may be isolated by its means. Weak types appear in self-fertilized species, but they must stand or fall by their own merits."

The matter has been mentioned here because of its bearing on the subject in hand. Houser (1911) has advocated the system of growing first generation hybrid tobacco as a commercial proposition. This was suggested for the heavy filler types

*Owing to the rediscovery of Mendel's law of inheritance, we now know that many characters are separately inherited, and by the use of descriptive factorial formulas the breeding facts are made clear. If a certain character breeds true it is in a homozygous condition and each male or female reproductive cell is supposed to bear some substance or factor for the development of the character. If a cross is made between two races which differ in a certain character we know that of the two uniting reproductive cells, the one contains the factor for the contrasted character and the other does not. The resulting plants of this cross will not breed true in the next generation and they are said to be in a heterozygous condition for the character involved. The amount of heterozygosis produced by any cross depends on the number of gametic factorial differences of the parent plants.

of tobacco which are grown in Ohio. While it is doubtless true that by this method the yield could be somewhat increased, the yield factor, for cigar wrapper types at least, is only of secondary importance compared with quality. Because of the great importance of quality it seems much more reasonable to suppose that further advance can be made by the production of fixed types which in themselves contain desirable growth factors, such as size, shape, position, uniformity, venation, and number of leaves, together with that complex of conditions which goes to make up quality, than by any other method.

PREVIOUS WORK ON EFFECTS OF SELECTION.

It is a well-recognized fact that among both plants and animals no two individuals are exactly alike. This diversity is due to two main kinds of variation:

1. Fluctuating Variations, such as size, shape, and number of various plant organs, which are due to different conditions of fertility, or to better positions for development. Such variations are not inherited.

2. Inherited Variations, which may be either large or small, but are caused by some differences in the factors of inheritance and are entirely independent of their surrounding conditions for their transmission, although favorable environment is often needed for their full development.

The real basis of the Mendelian conception of heredity is a recognition of the fact that the appearance of a plant is not a correct criterion of that particular plant's possibilities of transmitting any particular quality, but that the breeding test is the only real means of determining the plant's hereditary value.

By the universal adoption of Vilmorin's "isolation principle," in which the average condition of a plant's progeny is used as the index of that particular plant's breeding capacity, breeders have recognized these classes of variation.

A practical example demonstrating the truth of this classification is the work of Dr. H. Nilsson and his associates at Svalöf, Sweden. In 1891 a large number of heads from autumn wheat varieties were collected and were separated into their respective botanical and morphological groups, about 200

groups in all being thus selected. In several cases certain forms were found which had no duplicates, and in these cases the individual form represented a group in itself. The following season each group was given a separate plot and careful records were made of the number of heads and plants which were the ancestors of each plot.

A careful study of the resulting harvest showed that, of all the cultures under observation, only those which originally came from a single plant produced a uniform progeny (Newman, 1912).

The theoretical interpretation of this class of results was given by Johannsen (1909) through his work with beans and barley. This investigator found that a commercial variety was in reality composed of different and distinct types which could be separated from each other by self-pollinating the individual plants and studying their progeny. For example, he investigated the character weight as applied to individual beans and found that progress could be made when larger beans were selected from the mixed commercial crop for several seasons. On the other hand, after types comparatively homozygous had been isolated by inbreeding, the same results were obtained in each isolated line when large beans were planted as when the smaller ones were used for seed — although fluctuation due to external conditions still continued. This he explained as due to the fact that environmental influences were not inherited but that a plant simply transmits its inherent germinal qualities.

Certain corroborative results which show that fluctuating variations are not inherited and that characters in a homozygous condition are reproduced in practically the same degree generation after generation have been obtained by Barber (1907) with yeasts; Pearl and Surface (1909) and Pearl (1912) with poultry; East (1910) with potatoes; Hanel (1907) with *Hydra*; Jennings (1908, 1910) with *Paramaecium*; Love (1910) with peas, and Shull (1911a) with maize.

It is true that Castle (1911, 1912 a. b.) reports experiments with a variable black and white coat color of the rat, in which he shows that selection progressively modifies a character which, in crossing with other types, behaves as a simple Mendelian unit. These results can be interpreted and, we believe, interpreted in a manner more helpful to practical breeding by assum-

ing that although the coat pattern is transmitted as a single unit, its development is affected by several other unit characters independent of the general color pattern in their transmission. It may be that a few characters are so unstable that they may be modified by selection after reaching a homozygous condition, but so many thousand characters have been shown to Mendelize and to breed true in successive generations when in the homozygous state that for all practical purposes these laws may be assumed to be universal in sexual reproduction. Further reasons for this conclusion are given in the next few pages.

PREVIOUS WORK ON INHERITANCE OF SIZE CHARACTERS.

Since different degrees of expression of quantitative characters are inherited, as has been shown by Johannsen, and since within an inbred line homozygous for a character, change can seldom if ever be effected by selection, there seems good reason — as stated before — for believing that size characters are inherited in the same manner as qualitative or color characters.

The discovery of Nilsson-Ehle (1909) that certain hybrids are heterozygous for several inherited factors, either of which alone is capable of producing the character, laid the foundation for the proof of the generality of the Mendelian interpretation of inheritance in sexual reproduction.

It was from similar facts that East (1910a) made the first Mendelian interpretation of the inheritance of quantitative characters by assuming absence of dominance and a multiplicity of factors each inherited independently and capable of adding to the character, the heterozygous condition of any character being half the homozygous.

In the last few years a number of investigations have been made which show that linear or quantitative characters show segregation. Some of the investigations which show segregation in quantitative characters are as follows: Emerson (1910) for shapes and sizes in maize, beans and gourds; Shull (1910, 1911b) for row classes of maize and for *Bursa* characters; East (1911) and East and Hayes (1911) for height of plants, length of ears, weight of seeds, and row classes in maize; Tammes (1911) for certain characters of *Linum* forms; Tschermak

(1911, 1912) for time of flowering in peas and for weight of seeds; Hayes (1912) for height of plants, area of leaves, and leaf number of tobacco; Davis (1912) for *Oenothera* characters; Webber (1912) for plant characters of peppers; Belling (1912) for plant characters of beans; McLendon (1912) for cotton characters; Gilbert (1912) for characters of tomatoes; Heribert-Nilsson (1912) for *Oenothera* characters; Phillips (1912) for body size in ducks; Pearl (1912) for fecundity in fowls; and Emerson and East (1913) for other characters of maize.

A few investigations which also comprise the F_2 generation show that in some cases forms breed true giving no greater variability than the parent types. These results are of value in any system of breeding which, in a large measure, deals with size characters. Thus, by crossing two types which differ in quantitative characters we may expect to obtain a segregation in F_2 and in F_3 , some forms breeding true for some characters and others again recombining the characters in which they are heterozygous.

The possibilities of obtaining pure forms in F_3 will, then, largely depend on the number of character differences of the parental types. A complete exposition of both theory and practice when dealing with quantitative characters is given in Research Bulletin No. 2 of the Nebraska Agricultural Experiment Station entitled "The Inheritance of Quantitative Characters in Maize" by collaboration of Emerson and East (1913).

PREVIOUS WORK ON TOBACCO BREEDING.

There are two factors which must be reckoned with in any system of breeding. These are heredity and environment.

Previous tobacco investigations have shown the great importance of environmental conditions for both quality and productivity. For example, Jenkins (1896) shows that on similar land there are large variations in quality and yield due to different systems of fertilization.

Selby and Houser (1912) have shown that the time of harvesting, after topping, has a great effect on both quality and yield.

It has been stated by Frear and Hibsham (1910) that the

climate of Pennsylvania has a much greater effect on the character of tobacco produced than either hereditary varietal differences or soil.

It is a well-known fact that tobacco harvested by the priming method (picking individual leaves) has a different character than when harvested by cutting the whole stalk. These few illustrations, while in no way complete, indicate the great importance of the environmental factor in tobacco breeding.

One of the earliest experiments on inheritance of tobacco characters ever recorded was made by Naudin (Focke, 1881). This careful experimenter crossed one variety which had lanceolate leaves with a type which produced broadly oval leaves. The plants, resulting from this cross were alike in all essential features. In the second generation the differences were more marked and many individuals were found which resembled the parent types. Godron received two types of these hybrid forms from Naudin, the one with small leaves and the other with broad leaves. Both forms bred true in later generations.

Since the year 1900 many attempts have been made to improve the present types of tobacco by selection and crossbreeding. Shamel and his co-workers have done an important work by pointing out the value of selecting good type individuals for seed plants, and the production of inbred seed by bagging the seed head. Such methods have accomplished much by tending to produce uniform and better races.

In regard to the benefits which may be obtained from hybridization and subsequent selection, our knowledge is very meagre. On this subject Shamel and Cobey (1906) say:

“The best plan which can be followed in the case of crosses is to grow 100 plants of each cross and carefully note the characteristics of the hybrid plants. It will be found that there will be considerable variation in the plants the first season. Seed should be saved from those plants which are the most desirable and which show the greatest improvement over the native varieties. The next season a larger area can be planted from this seed; and if the crop is uniformly of the type desired, enough seed can then be selected the second season, to plant the entire crop the third year.”

This quotation certainly shows a lack of belief in the uniformity of the first hybrid generation, and on the other hand, no conception of segregation in F_2 .

Shamel (1910) also says:

“The writer believes that the two efficient means of inducing variability as a source of new types are change of environment and crossing. So far as the writer is concerned, the change of environment — usually the growing of southern grown seed in the north — is the most effective means of inducing variability.”

Hasselbring (1912), however, gives experimental evidence from a number of pure lines of tobacco which he grew both in Cuba and in Michigan, and comes to the conclusion that there is no breaking up in type due to changes of environment, and that whatever changes take place affect all individuals of a strain in a similar manner.

Some observations of the writers on the appearance of several types grown in the Connecticut Valley from foreign seed serve to corroborate Hasselbring's conclusions.

These few citations from previous investigators show that there is no very definite knowledge of the manner of inheritance of tobacco characters, and the writers hope that the present paper may clear up some of the more important phases of this subject.

THE MATERIAL USED.

Four different types of commercial tobaccos furnished the starting point for these investigations. They consisted of two imported varieties tested for shade purposes, which prior to 1908, had been grown for a number of years in row selections from selfed seed, and the two standard Connecticut types — Broadleaf and Havana — which have been grown in Connecticut since the early history of the tobacco industry. The following descriptions give some of the more important features of these types.

No. 401 Broadleaf.

The Broadleaf variety produces long, pointed, drooping leaves, averaging in length a little over twice the breadth, with an average leaf area of about 9 sq. dcms. The number of leaves per plant ranges from 16 to 23 and averages from 19 to 20. The average height of plant is about 56 inches. This variety sells for slightly more per pound than the Havana, and when

used as a wrapper or binder is generally considered to give a little better flavor to a cigar than the Havana type.

No. 402 Havana.

Havana produces medium length leaves, standing nearly erect though drooping slightly at the tip. The average length of the leaves is a little over twice the breadth. The number of leaves per plant ranges from 16 to 25 and averages from 19 to 20. The average height of the plant is about the same as the Broadleaf. This variety is well known as a wrapper and binder tobacco.

No. 403 Sumatra.

This variety produces short, round pointed, erect leaves, a little over half as broad as long, with an average leaf area of about 3 sq. dcms. The upper leaves of this type are generally narrow and pointed. The number of leaves ranges from 21 to 32 and averages from 26 to 28. The average height, when grown under shade, is about 6½ feet. This variety produces a larger percentage of wrappers than the Cuban type but the quality is very inferior, being of a light, papery texture.

No. 405 Cuban.

The leaf of this variety averages about the same width as the Havana, but is shorter and rounder. The position of the leaves is nearly erect. The leaf number ranges from 16 to 25 and averages about 20 per plant. The leaves are somewhat larger than those of Sumatra. This type is grown widely in the Connecticut Valley under shade covering, and produces wrapper tobacco of high quality.

THE METHODS USED.

As far as possible every precaution was taken to prevent experimental errors. With the exception of a very few cases the parental varieties have been grown from inbred seed, and if, for various reasons, other seed has been used, the fact is noted. Selfed seed has been obtained by covering the seed head with a Manila paper bag, and crosses have been made in the manner explained in previous papers (Hayes, 1912).

Much efficient aid has been given by Mr. C. D. Hubbell of The Connecticut Agricultural Experiment Station, who has materially helped in taking data, shelling and filing seed, and in the calculations. In the summer of 1912 Mr. A. F. Schulze, of the Connecticut Agricultural College, assisted in the field work.

We also wish to express our thanks to the Windsor Tobacco Growers' Corporation and its manager, Mr. J. B. Stewart, for so faithfully carrying out their part of the agreement by which means we were enabled to obtain the accurate data reported here.

As in previous work, each parental type has been given a number. A cross between No. 402 Havana and 403 Sumatra has been written (402×403), the female parent appearing first. Later generations have been designated (402×403)-1, (402×403)-1-1, and 403-1-2, which denote respectively the second and third generations of a cross between Havana and Sumatra, and the third parental generation of Sumatra.

The seedlings have been grown in sterilized soil. The sterilization of the beds has been accomplished by the use of steam at a pressure of at least 70 pounds, as explained by Hinson and Jenkins (1910). The actual sowing of the seed has always been done by one of the authors.

The different families and selections have been marked in the field by heavy stakes, to which wired tree labels were attached, and a planting plan has always been kept on file showing the exact location of the different selections. With this brief description of methods used, we will take up the consideration of the results obtained, and for convenience each family will be discussed separately.

FAMILY (402×403) HAVANA×SUMATRA.

A large number of crosses between tobacco varieties were made by Shamel in 1903, and among these was one between Havana as female and a small-leaved Sumatra type as male. Shamel (1905) states that the male parent, which was descended from Florida Sumatra seed, had been grown in Connecticut for two seasons and was partially acclimated. The Havana parent was a type which had been grown for a number of

years by Mr. D. P. Cooley of Granby, Conn. The cross was grown at the Cooley farm in 1904 and 1905.

According to Shamel the first hybrid generation grew somewhat more vigorously than the parent types and was rather uniform in its habit of development. The second generation was thought to be no more variable than the first. Selected plants of this generation were grown at the farm of Edmund Halladay in Suffield in 1906.

It was the custom of the tobacco experts of The United States Department of Agriculture, who at this time conducted the work of tobacco breeding in Connecticut, to select desirable field types, harvest the leaves from each seed plant separately, and to base their judgment on the combined data from the growing plants and the cured leaves.

After examining the data on the F_3 generation collected in this manner, Mr. Halladay and Mr. J. B. Stewart concluded that one particular plant, bearing 26 short, round, pointed leaves with short internodes between them, gave great promise of becoming a desirable commercial type. Accordingly, Mr. Halladay added one row of plants from inbred seed of this individual to the two acres of experimental tobacco grown by him in pursuance of a co-operative agreement with the Department of Agriculture.

The plants in this row, numbered 2h-29 in accordance with the Department nomenclature, grew comparatively uniformly and several were inbred. In Mr. Halladay's absence, however, Mr. Shamel and an employee of Mr. Halladay's, in reducing the number of seed plants saved, topped all the plants except a late one, which was afterwards inbred.

In view of Mr. Halladay's high opinion of this type, the seed of this plant and that remaining from its parent were used for planting in 1908, each generation being given a separate number.

The field in 1908 presented a fairly uniform appearance and gave promise of producing a valuable wrapper tobacco. The new type was named "Halladay Havana," in honor of Mr. Halladay, who, in a large measure, was responsible for its production. It averaged about twenty-six leaves per plant and grew to about the height of Havana. The leaves were of medium length, averaging slightly shorter than Havana; they were fairly uniform in shape, with somewhat rounded tips.

The crop, when cured, lacked uniformity. Some leaves of exceptionally fine quality were produced, but the general fault of the crop was a lack of grain and too large a proportion of the heavy leaves known to the trade as "tops."

From this 1908 crop one hundred seed plants were saved, the leaves of each being carefully harvested, cured and fermented. Mr. J. B. Stewart and one of the writers made careful notes on the quality of these individuals, especial attention being paid to the feature known as "grain." The plants showed great variability; some of them had produced a fairly high grade of wrapper tobacco, others exhibited rather poor quality.

In 1909, seed from twelve of the best of these plants was used to continue our own experiments, but small amounts were also distributed to a number of Connecticut farmers. In addition, three acres were grown in Massachusetts. Some of these results were very promising. At the Arnold farm in Southwick, Mass., for example, a measured acre produced 3,000 pounds and brought the grower over \$700. Other results were less favorable, but on the whole the experiment seemed worth repeating on a larger scale.

Accordingly, about 125 acres of Halladay Havana were grown in the Valley the following year and, while some men sold their crops at a good price, the results, in the main, were not encouraging. The chief faults mentioned by the buyers were lack of grain, too large proportion of dark and heavy leaves, and poor burn, although, in some cases, the burn was satisfactory.

This was the status of the work on the Havana×Sumatra cross when the data collected previously were turned over to the writers in 1908. Shamel, who had been in charge of the work up to this time, had come to the conclusion that the Halladay type was the result of a mutation. Apparently, he did not lend his approval to certain biological beliefs current at this time which indicated an alternative theory as an interpretation of its origin. For example, he believed that in general there was no greater variation in the second generation of a cross than in the first, and that considerable progress could be made by selecting good F_1 plants, some of which would breed true and give uniform progeny in F_2 .

The writers did not take this view of the problem. It was

contrary to all modern ideas of breeding to expect a cross between two self-fertilized varieties to be variable in F_1 . High variability should occur in F_2 , due to the recombination of Mendelian factors. New types should be produced in F_2 which could be reduced to an homozygous condition by selection and thereby fixed.

It was not impossible that the many-leaved type could have originated by mutation, but it appeared much more probable that it had been produced by recombination of parental characters. The type had the number of leaves and leaf shape of the Sumatra parent, combined with the habit of growth of Havana, and a close approach to the Havana leaf size. Other characters were in a somewhat intermediate condition; for example, the crinkling of the leaf was apparently a blend of the smooth Havana leaf with the much crumpled Sumatra leaf.

Family (403 × 402) Sumatra × Havana.

To test the hypothesis that the Halladay is a result of the recombination of parental characters and can be reproduced whenever desired, a cross was made in 1910 between Sumatra female and Havana male. The Sumatra was a direct descendant of the type used by Shamel in 1903 and had been grown from inbred seed for a number of generations. The Havana was the commercial variety grown at the Windsor Tobacco Growers' Corporation in Bloomfield. Although this variety of Havana was not exactly the same as that used by Shamel, it was the same in all essential features, the probability being very large that both types originally came from the same source.

The data on number of leaves per plant in this cross are given in Table I. The Sumatra and F_1 generation were grown at New Haven in 1911; the Havana was grown at Bloomfield from commercial seed of the same type as that used for the male parent of the cross. The F_1 generation was intermediate for leaf number and leaf size and was as uniform as the parental types. The variability of the F_2 generation for leaf number, size, shape and height of plants was very large. Some types were produced which could not be distinguished from pure Sumatra; others had Sumatra leaf characters and Havana leaf number; others resembled Havana in all features; and

TABLE I.
FREQUENCY DISTRIBUTION OF NUMBER OF LEAVES PER PLANT IN CROSS BETWEEN SUMATRA AND HAVANA.

| No. | Leaf Classes. | | | | | | | | | | | | | | | Total. | A. | C. V. |
|----------------------------------|---------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--------|------------|-------------|
| | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | |
| Havana | 3 | 22 | 44 | 42 | 22 | 10 | 6 | 1 | .. | .. | .. | .. | .. | .. | .. | 150 | 19.8 ± .08 | 6.98 ± .27 |
| Sumatra | .. | .. | .. | .. | .. | .. | 3 | 13 | 27 | 25 | 21 | 16 | 15 | 4 | 1 | 125 | 26.5 ± .11 | 6.64 ± .28 |
| Sumatra × Havana, F ₁ | .. | .. | .. | 2 | 4 | 9 | 14 | 15 | 5 | 2 | 1 | .. | .. | .. | .. | 52 | 23.3 ± .14 | 6.24 ± .41 |
| Sumatra × Havana, F ₂ | .. | 1 | 9 | 21 | 33 | 48 | 66 | 71 | 71 | 59 | 49 | 25 | 18 | 7 | 2 | 480 | 24.4 ± .08 | 10.29 ± .23 |

still others had the leaf size and growth habit of the Havana, combined with the leaf number of the Sumatra. These results, illustrated in Plates I-IV, give conclusive evidence that the Halladay type can be reproduced whenever desired.

Effects of Selection on the "Havana × Sumatra" Cross.

Let us now consider the effects of three years of selection on the Halladay strains of Shamel's cross. The purely genetic results of selecting for high and low leaf number are described in another paper. The work is considered briefly at this point, however, as the results have an important bearing on practical tobacco breeding. They show why the type lacked uniformity in 1908 and 1909, and hence the reason for its failure as a commercial proposition. Further, they go far toward indicating the proper procedure in obtaining results of economic value after hybridization.

In brief, the method pursued in this selection experiment was as follows:

Of the nine families with which the experiment was started (Table II), eight were grown at the Krohn Tobacco Company, in Bloomfield, in 1909, and the other (No. K) at a farm nearby. These nine families were selected from the 100 seed plants of Shamel's cross which were grown at the farm of Edmund Halladay, in Suffield, in 1908. From each of these families an inbred plant was saved which bore a high leaf number, and another with a low leaf number. These were made the basis of *plus* and *minus* selections, which were grown the following year, and from this time on seed plants with a high leaf number have been saved from the high or *plus* selection, and seed plants bearing a low leaf number from the low or *minus* selection.

These results, given in Table II, include the selection number, year grown, generation, number of leaves of parent, range of variation for leaf number, total plants, and biometrical constants, consisting of the mean for leaf number (A), and coefficient of variability (C. V.).

A consideration of these data shows that in one family, No. 27, no appreciable shift of the mean has been obtained, the mean of the low selection for 1912 being $25.9 \pm .07$, and that of the high selection being $25.0 \pm .06$.

TABLE II.
RESULTS OF SELECTION FOR HIGH AND LOW LEAF NUMBER IN CROSS BETWEEN HAVANA X SUMATRA.

| No. | Year Grown. | Generation. | Leaves of Parent. | Range of Variation. | Total. | A. | C. V. |
|-----------|-------------|----------------|-------------------|---------------------|--------|------------|-------------|
| (5-1)-1 | 1911 | F ₈ | 24 | 23-32 | 239 | 26.5 ± .06 | 5.13 ± .16 |
| (5-1) | 1910 | F ₇ | 25 | 21-33 | 211 | 26.6 ± .09 | 7.18 ± .24 |
| 5 | 1909 | F ₆ | 28 | 23-33 | 294 | 28.1 ± .06 | 5.34 ± .15 |
| (5-2) | 1910 | F ₇ | 31 | 25-34 | 226 | 29.2 ± .08 | 5.75 ± .18 |
| (5-2)-1 | 1911 | F ₈ | 32 | 24-34 | 243 | 28.6 ± .08 | 6.05 ± .19 |
| (5-2)-1-3 | 1912 | F ₉ | 33 | 23-34 | 282 | 29.0 ± .07 | 6.34 ± .18 |
| (6-1)-2 | 1911 | F ₈ | 23 | 21-32 | 285 | 25.1 ± .07 | 6.05 ± .19 |
| (6-1) | 1910 | F ₇ | 25 | 21-33 | 181 | 25.2 ± .08 | 6.07 ± .22 |
| 6 | 1909 | F ₆ | 28 | 22-31 | 307 | 25.8 ± .06 | 6.16 ± .17 |
| (6-2) | 1910 | F ₇ | 30 | 25-36 | 205 | 30.7 ± .09 | 6.18 ± .21 |
| (6-2)-1 | 1911 | F ₈ | 32 | 26-34 | 239 | 29.1 ± .05 | 4.17 ± .13 |
| (6-2)-1-4 | 1912 | F ₉ | 32 | 18-36 | 243 | 30.5 ± .13 | 9.93 ± .30 |
| (12-1)-1 | 1912 | F ₈ | 29 | 24-35 | 296 | 29.1 ± .08 | 6.67 ± .19 |
| (12-1)-1 | 1911 | F ₈ | 29 | 24-34 | 210 | 28.7 ± .09 | 6.72 ± .22 |
| (12-1) | 1910 | F ₇ | 23 | 29-31 | 6 | | |
| 12 | 1909 | F ₆ | 24 | 21-28 | 113 | 24.5 ± .10 | 6.53 ± .29 |
| (12-2) | 1910 | F ₇ | 28 | 21-32 | 215 | 26.1 ± .10 | 8.12 ± .26 |
| (12-2)-1 | 1911 | F ₈ | 30 | 23-32 | 188 | 26.8 ± .07 | 5.61 ± .20* |
| (12-2)-1 | 1912 | F ₉ | 30 | 23-36 | 231 | 29.0 ± .08 | 6.52 ± .21 |
| (27-1)-1 | 1912 | F ₈ | 22 | 20-31 | 316 | 25.9 ± .07 | 6.76 ± .18 |
| (27-1)-1 | 1911 | F ₈ | 22 | 22-31 | 214 | 26.3 ± .06 | 5.01 ± .16 |
| (27-1) | 1910 | F ₇ | 25 | 21-31 | 254 | 26.5 ± .08 | 7.32 ± .22 |
| 27 | 1909 | F ₆ | 29 | 22-31 | 300 | 27.8 ± .06 | 5.04 ± .14 |
| (27-2) | 1910 | F ₇ | 28 | 21-29 | 222 | 25.2 ± .07 | 6.47 ± .21 |
| (27-2)-1 | 1911 | F ₈ | 28 | 21-29 | 222 | 26.0 ± .07 | 5.78 ± .19 |
| (27-2)-1 | 1912 | F ₈ | 28 | 21-32 | 305 | 25.0 ± .06 | 6.68 ± .18 |

TABLE II — CONTINUED.

| No. | Year Grown. | Generation. | Leaves of Parent. | Range of Variation. | Total. | A. | C. V. |
|------------|-------------|----------------|-------------------|---------------------|--------|------------|-------------|
| (41-1)-2 | 1912 | F ₈ | 25 | 22-32 | 288 | 27.4 ± .07 | 6.42 ± .18 |
| (41-1)-2 | 1911 | F ₈ | 25 | 24-32 | 225 | 28.1 ± .07 | 5.85 ± .19 |
| (41-1) | 1910 | F ₇ | 24 | 21-30 | 224 | 26.3 ± .08 | 6.65 ± .21 |
| 41 | 1909 | F ₆ | 26 | 19-29 | 296 | 23.9 ± .07 | 7.25 ± .20 |
| *(41-2) | 1910 | F ₇ | 28 | 12-30 | 234 | 25.7 ± .09 | 7.47 ± .23 |
| †(41-2)-1 | 1911 | F ₈ | 30 | 18-32 | 142 | 25.6 ± .14 | 9.71 ± .39 |
| (41-2)-3 | 1911 | F ₈ | 12 | 8-30 | 126 | 19.8 ± .28 | 23.50 ± .11 |
| (41-2)-1 | 1912 | F ₈ | 30 | 20-33 | 310 | 26.9 ± .08 | 7.70 ± .21 |
| (41-2)-3-2 | 1912 | F ₉ | 10 | 11-27 | 278 | 17.8 ± .08 | 11.24 ± .33 |
| (73-1)-2-1 | 1912 | F ₈ | 24 | 21-30 | 221 | 25.7 ± .08 | 7.12 ± .23 |
| (73-1)-2 | 1911 | F ₇ | 23 | 21-30 | 217 | 25.6 ± .07 | 5.71 ± .19 |
| (73-1) | 1910 | F ₆ | 25 | 20-33 | 216 | 26.3 ± .09 | 7.64 ± .25 |
| 73 | 1909 | F ₅ | 28 | 23-32 | 300 | 26.9 ± .06 | 5.39 ± .15 |
| (73-2) | 1910 | F ₆ | 29 | 19-30 | 201 | 26.3 ± .08 | 6.58 ± .22 |
| (73-2)-3 | 1911 | F ₇ | 31 | 24-34 | 195 | 28.2 ± .09 | 6.37 ± .22 |
| (73-2)-3-3 | 1912 | F ₈ | 32 | 22-30 | 76 | 26.7 ± .13 | 6.18 ± .34 |
| (76-1)-1 | 1911 | F ₇ | 23 | 20-28 | 310 | 23.9 ± .05 | 5.28 ± .14 |
| (76-1) | 1910 | F ₆ | 22 | 20-27 | 31 | 25.2 ± .19 | 6.07 ± .52 |
| 76 | 1909 | F ₆ | 23 | 20-28 | 89 | 24.1 ± .11 | 6.64 ± .34 |
| (76-2) | 1910 | F ₆ | 27 | 21-30 | 209 | 24.4 ± .07 | 6.27 ± .21 |
| (76-2)-1 | 1911 | F ₇ | 28 | 22-32 | 230 | 26.1 ± .08 | 6.88 ± .22 |
| (76-2)-1-1 | 1912 | F ₈ | 29 | 22-32 | 275 | 26.9 ± .07 | 6.28 ± .18 |
| (77-1)-1-2 | 1912 | F ₈ | 20 | 14-25 | 236 | 18.4 ± .07 | 8.37 ± .26 |
| (77-1)-1 | 1911 | F ₇ | 20 | 18-26 | 306 | 21.3 ± .05 | 6.60 ± .18 |
| (77-1) | 1910 | F ₆ | 20 | 17-28 | 266 | 21.9 ± .08 | 9.27 ± .27 |

* One 12-leaved plant appeared not used in computations.

† End row poorly fertilized.

TABLE II — CONTINUED.

| No. | Year Grown. | Generation. | Leaves of Parent. | Range of Variation. | Total. | A. | C. V. |
|-----------|-------------|----------------|-------------------|---------------------|--------|------------|------------|
| 77 | 1909 | F ₅ | 23 | 20-27 | 85 | 22.4 ± .11 | 6.38 ± .33 |
| (77-2) | 1910 | F ₆ | 27 | 20-32 | 224 | 24.9 ± .11 | 9.32 ± .30 |
| (77-2)-1 | 1911 | F ₇ | 30 | 22-33 | 281 | 26.6 ± .07 | 6.92 ± .20 |
| (77-2)-1 | 1912 | F ₇ | 30 | 21-33 | 280 | 25.8 ± .08 | 7.48 ± .21 |
| (K-1)-1-2 | 1912 | F ₈ | 24 | 17-28 | 209 | 21.5 ± .08 | 7.77 ± .26 |
| (K-1)-1 | 1911 | F ₇ | 22 | 20-29 | 202 | 23.5 ± .07 | 6.52 ± .22 |
| (K-1) | 1910 | F ₆ | .. | 21-29 | 148 | 24.4 ± .09 | 6.93 ± .27 |
| K | 1909 | F ₅ | 26 | 20-24 | 31 | 22.3 ± .13 | 4.62 ± .40 |
| (K-2) | 1910 | F ₆ | .. | 19-29 | 130 | 22.8 ± .11 | 7.98 ± .33 |
| (K-2)-1 | 1911 | F ₇ | 26 | 17-29 | 204 | 24.0 ± .07 | 6.03 ± .20 |
| (K-2)-1-6 | 1912 | F ₈ | 26 | 18-30 | 223 | 22.8 ± .07 | 7.15 ± .23 |

All other *plus* selections except (73-2)-3-3 and (K-2)-1-6 have given a change toward the high leaf condition. These selections gave about the same average leaf number as in 1909. In some strains the mean has been gradually shifted, as in the *plus* selection of family 76, which gave progressive changes from a mean leaf value in F_5 of $24.1 \pm .11$ to $24.4 \pm .07$ in F_6 , then to $26.1 \pm .08$ in F_7 , and finally in F_8 to $26.9 \pm .07$. Other families, as Nos. 5 and 6, gave a large change in mean due to the first year of selection but in later generations have given no further changes due to continued selection. In general, the results have been what one would expect if selection simply isolated homozygous types from a heterozygous population.

Selection for low leaf number has caused decreases in (5-1)-1, (K-1)-1-2 and (77-1)-1-2, and slight decreases in (6-1)-2, (73-1)-2-1 and (76-1)-1, but of such a small nature that little dependence can be placed upon them. A negative effect is shown in case (41-1)-2.

In previous papers we have shown that the number of leaves per plant is a very stable character and, as such, little affected by environment. That selection has made various degrees of change in the mean of some types and no change in others, we believe to be due to the fact that some selections, as for example No. 27, were in a pure or nearly homozygous condition in 1909, while others were heterozygous for different numbers of factors for leaf number.

General field notes on the Halladay types, which were grown in 1912, are given in Table III. Three different observations on these types were made: general vigor, shape of leaf, and leaf character, whether smooth or crinkled. Of the fourteen selections given in this table, three were classed as very vigorous, seven as having good vigor, three as of fair vigor, and one as non-vigorous. As to shape, eleven have broad round tipped leaves, one has broad leaves with a pointed tip, and two from family No. 77 have leaves which resemble the Havana in shape. Considering fullness between the veins, one selection has very crinkled leaves, eight have crinkled leaves, two have slightly crinkled leaves, and three are classed as smooth-leaved types.

It is of interest to know that the leaf character and also the length of internodes of No. 77 closely approach the type of the Havana parent.

TABLE III.

GENERAL CHARACTERISTICS OF SELECTED HALLADAY STRAINS
GROWN AT BLOOMFIELD IN 1912.

| No. | General Vigor | Shape of Leaf | Type of Leaf |
|----------|---------------|---------------------------|-------------------|
| 5-2-1-3 | Very good | Broad, round tip | Slightly crinkled |
| 6-2-1-4 | Good | " pointed " | " " |
| 12-1-1 | Very good | " round " | Smooth |
| 12-2-1 | " " | " " " | Very crinkled |
| 27-1-1 | Good | " " " | Crinkled |
| 27-2-1 | " | " " " | " |
| 41-1-2 | Fair | " " " | " |
| 41-2-1 | " | " " " | " |
| 73-2-3-3 | Good | " " " | " |
| 76-2-1-1 | " | " " " | " |
| 77-1-1-2 | Fair | Fairly broad, pointed tip | Smooth |
| 77-2-1 | Good | " " " | " |
| K-1-1-2 | Poor | Broad, round tip | Crinkled |
| K-2-1-6 | Good | " " " | " |

Some data obtained on comparative leaf length of these Halladay types are given in Table IV. This table gives the average number of leaves per plant, by actual count, the total yield of cured tobacco on an acre basis, and the number of pounds of tobacco in each leaf length class. This, of course, does not give the number of leaves of each length, as it naturally takes more 12-inch leaves than 20-inch leaves to weigh a pound. However, a general idea of the average length of leaves of a selection can be obtained by this means.

This table shows that leaf length is not very closely correlated with number of leaves per plant. For example, selection (73-2)-3-3, which averaged 26.7 leaves per plant, produced only 256 pounds of 18-inch tobacco, while selection (12-1)-1, which averaged 29.1 leaves per plant, produced 1,162 pounds of 18-inch tobacco. (K-1)-1-2, which averaged 21.5 leaves, produced only 113 pounds of 20-inch length, while (K-2)-1-6, which originally, in 1908, came from the same plant as (K-1)-1-2, and which averaged 22.8 leaves per plant, gave a production of 944 pounds of 20-inch length.

TABLE IV.

COMPARATIVE LENGTH OF LEAVES OF THE HALLADAY STRAINS IN 1912.

| No. | Average No. of Leaves per Plant | Yield per Acre | Yield in Pounds for Leaf Length Classes in Inches | | | | | | | |
|----------|--|----------------------|--|-----|-----|-----|-----|-----|------|-----|
| | | | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 |
| 5-2-1-3 | 29.0 | 2813 | 87 | 126 | 199 | 349 | 538 | 709 | 730 | 75 |
| 6-2-1-4 | 30.5 | 2822 | 82 | 109 | 181 | 245 | 402 | 588 | 872 | 343 |
| 12-1-1 | 29.1 | 3370 | 38 | 131 | 142 | 254 | 363 | 812 | 1162 | 467 |
| 12-2-1 | 29.0 | 3085 | 143 | 152 | 253 | 423 | 629 | 755 | 677 | 52 |
| 27-1-1 | 25.9 | 2766 | 86 | 138 | 146 | 300 | 483 | 628 | 833 | 150 |
| 27-2-1 | 25.0 | 2736 | 95 | 65 | 93 | 180 | 356 | 495 | 909 | 543 |
| 41-1-2 | 27.4 | 2196 | 72 | 93 | 125 | 175 | 271 | 430 | 800 | 234 |
| 41-2-1 | 26.9 | 2694 | 101 | 112 | 160 | 220 | 351 | 523 | 971 | 257 |
| 41-2-3-2 | 17.8 | 1936 | 115 | 122 | 199 | 263 | 323 | 355 | 462 | 97 |
| 73-2-3-3 | 26.7 | 2645 | 229 | 229 | 379 | 512 | 617 | 423 | 256 | ... |
| 76-2-1-1 | 26.9 | 2721 | 126 | 119 | 204 | 356 | 566 | 672 | 634 | 44 |
| 77-1-1-2 | 18.4 | 2271 | 35 | 40 | 97 | 137 | 185 | 316 | 638 | 823 |
| 77-2-1 | 25.8 | 2341 | 64 | 47 | 88 | 138 | 219 | 359 | 942 | 483 |
| K-1-1-2 | 21.5 | 2332 | 84 | 65 | 142 | 239 | 343 | 524 | 822 | 113 |
| K-2-1-6 | 22.8 | 2740 | 62 | 49 | 86 | 216 | 210 | 392 | 781 | 944 |
| Havana | *20.0 | 2119 | 56 | 57 | 86 | 128 | 191 | 284 | 570 | 747 |

*Estimated.

The largest amount of tobacco by weight was produced in the 18-inch class by ten of the selections, in the 17-inch class by two, in the 16-inch class by one, and in the 20-inch class by two selections. The Havana grown for comparison also produced the greatest amount of tobacco in the 20-inch class.

Quality of Cured Leaves.

The data already submitted have shown that by 1912 several types markedly different in leaf number have been produced. Though it is less easy to demonstrate by concrete figures, these types also differ in vigor, shape of leaf, plant height, etc. This fact is of practical importance and gives conclusive evidence for believing that the Halladay type, as grown commercially in 1908-1910, was not the uniform type which it was, in general, considered to be. May not these facts explain the reason for the commercial failure of the Halladay by showing that the

type, as a whole, was in a heterozygous condition and, therefore, could not give tobacco uniform in quality. That some growers were favorably impressed and others less so may then be entirely due to the fact that some grew favorable types, and others types which, from a commercial standpoint, were very inferior. It was for this reason, justifiable from the commercial point of view, that the culture of the Halladay was dropped.

From 1909 to 1911 inclusive, no data were taken on the cured leaf of the Halladay, as our sole aim was to study the effects of selection on the field habit. In 1912, however, the tobacco was harvested, cured, fermented, and assorted, to determine if certain selections had come to be better than the others and if any gave promise of commercial value. Because the season of 1912 was a dry one and not very favorable for tobacco, the crop, as a whole, was of inferior quality. A small plot of commercial Havana of the same type as that grown by the Windsor Tobacco Growers' Corporation was grown on the same field, however, and was cured, fermented, and assorted in the same manner as the experimental tobacco. By this method we were able to obtain some idea of the comparative value of our selections, using Havana as the standard.

However, it should be noted that on account of practical difficulties the time of harvesting the various pickings was not always at the proper degree of ripeness. For example, the first and third pickings should probably have been made a few days earlier, but for unavoidable reasons this was impossible. Further, some selections were a few days earlier in maturity than others, and as all selections were harvested on the same day, some may have received more favorable treatment. This was partly corrected by making a larger picking, that is, by taking more leaves from the very mature types at an early picking than were taken from the later maturing types at the same picking.

The method of harvesting tobacco by the "priming" method is well known (see Stewart, 1908) and will be mentioned only briefly here. Four pickings were made of our experimental tobacco, as follows: About 5 leaves were harvested at the first picking, 5 to 8 at the second picking, 7 to 12 at the third picking, and all remaining leaves of commercial size at the last picking. The leaves of each picking were then tagged with the

selection number and carried to the barn, where they were strung and hung on laths, from 36 to 40 leaves to the lath, with a tag containing the selection number attached to each lath.

The curing season was somewhat wet and at two different times it was necessary to dry out the tobacco by firing, which was accomplished by building charcoal fires in small stoves.

After the tobacco was cured it was taken down when in "kase," that is, when just damp enough to be pressed in the hands without breaking the leaves. The leaves from each lath, with tag attached, were tied into hands, and the tobacco then placed in a "bulk" to go through a period of fermentation. The experimental tobacco was not fermented sufficiently for commercial use, but the fermentation tended to even up the colors so that the tobacco could be assorted with better judgment.

After the tobacco had remained in the bulk for about four weeks it was removed and all of each selection placed together, the different pickings being kept separate. Four hands of the first three pickings of the different selections were drawn at random and were examined for quality by three tobacco judges. The same hands were carefully examined by the writers for "grain" and "texture."

The total crop of tobacco was then sized by the usual method. This consists in separating the leaves into different lengths, from 12 to 20-inch classes being made. This work was done by girls under our supervision.

After the tobacco was sized it was assorted into grades as in commercial practice. The actual work of assorting was done by experienced sorters, and the different lengths and grades were weighed in pounds and ounces.

"Grain" in Tobacco Leaves.

The presence of small pimple-like projections scattered over the cured leaf of tobacco is called "grain." It is a well-known fact that all tobacco does not exhibit this tendency in the same degree. In some cases the grain is large and easily seen, and in other cases small and scarcely visible to the naked eye.

One of the tobacco experts who kindly examined our Halladay selections made the criticism that the "grain" was over-devel-

oped, and another expert expressed the opinion that the selections, as a whole, were lacking in grain. This fact is mentioned to show that the ideals of some of the best growers differ on this matter. Both men desired grain in the leaves, but one preferred large pimplly grains, easily seen, and the other a fine grain, scarcely distinguishable.

Sturgis (1899) found by microscopical examination that the grain of tobacco leaves was due to a crystalline deposit of some material, the compound being, in his opinion, calcium oxalate. Contrary to expectations, he found no increased deposit due to heavy liming of the soil but he did find that the thinner leaves which were produced under shade apparently contained it in smaller amounts.

If grain is calcium oxalate and as such of no value for burning qualities, it is very probable that it does not deserve the importance that it generally receives, although, as Connecticut growers generally consider the presence of grain to be an indication of quality and as tobacco buyers as a rule make it a factor in their judgment of the crop, it becomes necessary to consider its production. From the writers' standpoint a fine-grained wrapper leaf presents a more handsome appearance than leaf with larger grains, although the final test of any quality depends upon the demand of the consumer.

As has already been mentioned, some of the parent plants of our 1909 selections were examined for grain because it was believed that the Halladay Havana, as a whole, lacked in this particular. We have therefore considered this character in our experimental work in 1912.

Before the tobacco was sized and after fermentation had taken place, four hands containing approximately forty leaves each were drawn at random from the first three pickings of each selection and were examined for grain. The method followed was an arbitrary one. Seven general classes were made; those leaves which had a maximum amount of grain were placed in Class 1, and those in which no grain could be distinguished were placed in Class 7. Obviously the remaining classes ranged in value from maximum to minimum grain production. The results are given in Table V.

TABLE V.
 VARIATION IN GRAIN OF HALLADAY STRAINS IN 1912.

| No. | Leaves per Plant | Picking | Grain Classes | | | | | | | Mean Class |
|---|------------------------|---------|---------------|----|-----|-----|-----|----|----|---------------|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| 5-2-1-3 From good grained plant in 1908 | 30.5 | 1 | 15 | 20 | 45 | 46 | 19 | .. | .. | 3.23 |
| | | 2 | 2 | 7 | 27 | 49 | 22 | 4 | .. | 3.85 |
| | | 3 | 1 | 4 | 15 | 26 | 67 | 37 | .. | 4.77 |
| | | Total | 18 | 31 | 87 | 121 | 108 | 41 | .. | 3.97 |
| 6-2-1-4 From fair grained plant in 1908 | 29.1 | 1 | 16 | 28 | 52 | 27 | 23 | .. | .. | 3.09 |
| | | 2 | 6 | 25 | 27 | 68 | 22 | .. | .. | 3.50 |
| | | 3 | 2 | 6 | 21 | 46 | 54 | 21 | .. | 4.38 |
| | | Total | 24 | 59 | 100 | 141 | 99 | 21 | .. | 3.66 |
| 12-1-1 | 29.1 | 1 | 2 | 5 | 24 | 59 | 40 | 16 | .. | 4.21 |
| | | 2 | 5 | 18 | 31 | 54 | 37 | 10 | .. | 3.84 |
| | | 3 | .. | 2 | 7 | 30 | 63 | 52 | 2 | 5.04 |
| | | Total | 7 | 25 | 62 | 143 | 140 | 78 | 2 | 4.37 |
| 12-2-1 | 29.0 | 1 | 13 | 24 | 41 | 33 | 18 | 2 | .. | 3.19 |
| | | 2 | 7 | 22 | 46 | 56 | 16 | .. | .. | 3.35 |
| | | 3 | 1 | 11 | 25 | 13 | 63 | 27 | .. | 4.48 |
| | | Total | 21 | 57 | 112 | 102 | 97 | 29 | .. | 3.68 |
| 27-1-1 From fair grained plant in 1908 | 25.9 | 1 | 4 | 18 | 23 | 49 | 39 | 9 | 1 | 3.92 |
| | | 2 | .. | 5 | 20 | 52 | 47 | 23 | .. | 4.43 |
| | | 3 | .. | .. | 10 | 40 | 64 | 41 | .. | 4.88 |
| | | Total | 4 | 23 | 53 | 141 | 150 | 73 | 1 | 4.42 |
| 27-2-1 as 27-1-1 | 25.0 | 1 | 10 | 18 | 48 | 47 | 25 | .. | .. | 3.40 |
| | | 2 | 5 | 13 | 53 | 61 | 16 | .. | .. | 3.47 |
| | | 3 | 1 | 8 | 28 | 68 | 36 | 18 | .. | 4.16 |
| | | Total | 16 | 39 | 129 | 176 | 77 | 18 | .. | 3.69 |
| 41-1-2 From good grained plant in 1908 | 27.4 | 1 | .. | 18 | 27 | 47 | 34 | 19 | 1 | 4.08 |
| | | 2 | 3 | 15 | 30 | 52 | 38 | 9 | .. | 3.91 |
| | | 3 | .. | .. | .. | .. | .. | .. | .. | |
| | | Total | .. | .. | .. | .. | .. | .. | .. | |
| 41-2-1 as 41-1-2 | 26.9 | 1 | 8 | 17 | 31 | 55 | 27 | 4 | .. | 3.62 |
| | | 2 | 8 | 19 | 33 | 57 | 30 | 4 | .. | 3.54 |
| | | 3 | .. | .. | 4 | 41 | 92 | 15 | .. | 4.78 |
| | | Total | 16 | 36 | 68 | 153 | 149 | 23 | .. | 4.02 |
| 73-2-3-3 From good grained plant in 1908 | 26.7 | 1 | 4 | 11 | 22 | 28 | 21 | 6 | .. | 3.75 |
| | | 2 | 8 | 15 | 36 | 49 | 18 | 9 | .. | 3.60 |
| | | 3 | .. | 2 | 16 | 45 | 60 | 31 | .. | 4.66 |
| | | Total | 12 | 28 | 74 | 122 | 99 | 46 | .. | 4.07 |
| 76-2-1-1 | 26.9 | 1 | 6 | 26 | 43 | 44 | 54 | 20 | .. | 3.90 |
| | | 2 | 5 | 15 | 31 | 46 | 42 | 10 | .. | 3.91 |
| | | 3 | .. | 1 | 25 | 60 | 46 | 20 | .. | 4.39 |
| | | Total | 11 | 42 | 99 | 150 | 142 | 50 | .. | 4.05 |

TABLE V—CONTINUED.

| No. | Leaves per Plant | Picking | Grain Classes | | | | | | | Mean Class |
|---|------------------------|---------|---------------|-----|-----|-----|-----|-----|----|---------------|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| 77-1-1-2 | 18.4 | 1 | 8 | 28 | 52 | 51 | 13 | .. | .. | 3.22 |
| | | 2 | 13 | 34 | 41 | 43 | 4 | .. | .. | 2.93 |
| | | 3 | .. | 6 | 40 | 74 | 23 | .. | .. | 3.87 |
| | | Total | 21 | 68 | 133 | 168 | 40 | .. | .. | 3.32 |
| 77-2-1 | 25.8 | 1 | 25 | 36 | 37 | 40 | 4 | .. | .. | 3.44 |
| | | 2 | 5 | 20 | 52 | 57 | 19 | .. | .. | 3.42 |
| | | 3 | .. | .. | 4 | 37 | 64 | 10 | .. | 4.70 |
| | | Total | 30 | 56 | 93 | 134 | 87 | 10 | .. | 3.54 |
| K-1-1-2 | 21.5 | 1 | 13 | 31 | 42 | 42 | 16 | .. | .. | 3.12 |
| | | 2 | 9 | 15 | 35 | 54 | 23 | 9 | .. | 3.65 |
| | | 3 | .. | .. | .. | 26 | 65 | 59 | 2 | 5.24 |
| | | Total | 22 | 46 | 77 | 122 | 104 | 68 | 2 | 4.02 |
| K-2-1-6 | 22.8 | 1 | 4 | 17 | 38 | 45 | 33 | 3 | .. | 3.68 |
| | | 2 | 5 | 12 | 44 | 35 | 15 | 3 | .. | 3.46 |
| | | 3 | 1 | 11 | 35 | 69 | 36 | 7 | .. | 3.94 |
| | | Total | 10 | 40 | 117 | 149 | 84 | 13 | .. | 3.72 |
| Havana | 20.0 | 1 | 36 | 37 | 37 | 24 | 10 | 1 | .. | 2.57 |
| | | 2 | 36 | 53 | 37 | 17 | 2 | .. | .. | 2.28 |
| | | 3 | 8 | 29 | 29 | 37 | 28 | 12 | 4 | 3.68 |
| | | Total | 80 | 119 | 103 | 78 | 40 | 23 | 4 | 2.92 |
| 82-2-1 From poor grained plant in 1908 | 26.7 | 1 | .. | 6 | 19 | 55 | 52 | 15 | .. | 4.35 |
| | | 2 | .. | 3 | 20 | 41 | 51 | 32 | 1 | 4.62 |
| | | 3 | .. | .. | 2 | 21 | 70 | 58 | 5 | 5.28 |
| | | Total | .. | 9 | 41 | 117 | 173 | 105 | 6 | 4.76 |

A consideration of this table brings some interesting facts to light. It will be seen that in general there is less grain in the upper leaves—that is, the later pickings—than in the lower leaves. On comparing the results obtained from the experimental selections with the Havana selection grown on the same field, we observe that although the Havana was variable in this character it had a larger amount of grain than the other selections. This, however, we know is due to the fact that each individual “grain” of the Havana was larger than in the other selections, our classes representing total grain production and not closeness of grain.

In the first column of the table, under the selection numbers, the “grain” condition of the 1908 ancestral parent plant is given when known. Of the sixteen selections given in the table only eight can be considered under this head, and in one of the eight no third picking was examined, so only seven cases remain for discussion. Of these seven, three descended from plants

classed as having good grain, three from fair-grained plants, and one from a poor-grained plant. Those descending from good-grained plants have means of 4.02, 4.07 and 3.97; those from fair-grained plants have means of 3.66, 4.42 and 3.69; and the selection descending from the poor-grained plant has a mean of 4.76.

Of course it would not be fair to lay very much stress on these results, it being probable that all tobacco has the ability to produce some grain. Our results simply indicate that some types, under favorable conditions, produce more grain than others. As such is the case, it seems only fair to conclude that different degrees of grain production are inherited.

Texture Observations.

The same leaves which were examined for grain were also classed as to texture. In this work grain received no weight, and the following brief descriptions give an idea of the characteristics of each class.

CLASS I — Included those leaves having a dry nature, lacking in oils and gums, with a body so thick as to render it too heavy for the best wrapper leaf.

CLASS II — Included those leaves of a semi-dry nature, apparently having no more oil than those of Class I, but more gum. The body stiff but sufficiently elastic as to allow its use for wrapper purposes.

CLASS III — Included those leaves most desirable for wrapper purposes, the oils and gums being present in sufficient quantity and accompanying a medium body, resulting in a leaf of good elasticity, soft but firm handling qualities.

CLASS IV — Included those leaves of medium body and the gum content, but with excessive amount of oils, giving the leaf a coarse appearance with a tendency to a "rubbery" nature.

CLASS V — Included those leaves of excessive oil and gum content with a medium to heavy body, resulting in a texture of a decided "rubbery" nature.

Of the classes here given Class III is most desirable from a wrapper standpoint and Classes I and V least desirable.

The results given in Table VI show that many of the selections have a much greater percentage of leaves in Class III than Havana, while other selections have a smaller percentage of leaves of good texture than Havana.

TABLE VI.
 VARIATIONS IN TEXTURE OF HALLADAY STRAINS IN 1912.

| No. | Texture Classes | | | | | | | | | | | |
|----------|-----------------|-----------|------------|-----------|------------|-----------|------------|-----------|------------|-----------|--|--|
| | I | | II | | III | | IV | | V | | | |
| | No. Leaves | Per cent. | No. Leaves | Per cent. | No. Leaves | Per cent. | No. Leaves | Per cent. | No. Leaves | Per cent. | | |
| 5-2-1-3 | .. | ... | 40 | 9.9 | 201 | 49.5 | 137 | 33.7 | 28 | 6.9 | | |
| 6-2-1-4 | .. | ... | 42 | 9.3 | 222 | 49.2 | 179 | 39.7 | 8 | 1.8 | | |
| 12-1-1 | 2 | .4 | 32 | 7.0 | 132 | 28.9 | 225 | 49.1 | 67 | 14.6 | | |
| 12-2-1 | .. | ... | 21 | 5.0 | 252 | 59.7 | 141 | 33.4 | 8 | 1.9 | | |
| 27-1-1 | 36 | 8.1 | 73 | 16.5 | 93 | 21.0 | 174 | 39.3 | 67 | 15.1 | | |
| 27-2-1 | .. | ... | 43 | 9.5 | 185 | 40.8 | 183 | 40.4 | 42 | 9.3 | | |
| 41-1-2 | 17 | 5.8 | 57 | 19.6 | 56 | 19.2 | 129 | 44.4 | 32 | 11.0 | | |
| 41-2-1 | .. | ... | 40 | 8.9 | 185 | 41.2 | 159 | 35.4 | 65 | 14.5 | | |
| 73-2-3-3 | .. | ... | 21 | 5.5 | 176 | 46.0 | 171 | 44.6 | 15 | 3.9 | | |
| 76-2-1-1 | 10 | 2.2 | 49 | 10.7 | 169 | 36.8 | 201 | 43.8 | 30 | 6.5 | | |
| 77-1-1-2 | .. | ... | 63 | 14.6 | 182 | 42.3 | 168 | 39.1 | 17 | 4.0 | | |
| 77-2-1 | .. | ... | 43 | 10.3 | 170 | 40.6 | 179 | 42.7 | 27 | 6.4 | | |
| K-1-1-2 | 31 | 7.1 | 44 | 10.1 | 114 | 26.1 | 149 | 34.1 | 99 | 22.6 | | |
| K-2-1-6 | 26 | 5.9 | 56 | 12.8 | 186 | 44.8 | 192 | 46.3 | 6 | 1.4 | | |
| Havana | .. | ... | 56 | 12.8 | 104 | 23.8 | 180 | 41.1 | 72 | 16.4 | | |

These data were taken in such a manner that any possible correlation with the grain classes of the previous discussion could be determined, and while no correlation coefficients have been figured we feel justified in concluding from inspection that there is no correlation between grain and the characters here discussed.

While there was no great difference between the selections in texture, there is no question but that some selections were better than others, and several of them gave a somewhat larger percentage of better leaves than the Havana.

Results of Sorting Test.

The results of the actual sorting test are given in Table VIII. For convenience they are calculated to an acre basis, since by this means one can easily compare the value of one selection with another. During the actual sorting, the various lengths of each picking were kept separate, but for convenience they are grouped in the table.

The tobacco was sorted into five different grades: Light Wrappers, Medium Wrappers, Dark Wrappers, Binders and Tops. The Light Wrappers comprise those leaves which have a light even color and thin texture with good body and good vein. Medium Wrappers are a little darker and heavier than the Light Wrappers but must also have good texture and vein. Dark Wrappers are heavier than Medium Wrappers and of a darker color. A great many leaves, which under ordinary circumstances would have been classed as Mediums, are placed in the Dark Wrapper class because of white veins. Binders are thin leaves which are either off-colored, have white veins, or have a tear in them, such faults not permitting them to be graded as Light Wrappers. Tops are heavy, dark, oily leaves.

Table VII gives the prices used in computing the comparative values. These figures were obtained by consulting tobacco men who handled primed sun-grown tobacco in 1911 and 1912, and taking the averages of the prices so obtained. These prices refer to the packed value after fermentation.

The computations for actual packed value were made as follows: First, the yield per acre for a perfect stand of plants was calculated from the healthy plants in a measured row.

Second, the total amount and percentage of each grade was figured to this basis by utilizing the actual sorting data. It was then assumed that these grades could be sold at the prices quoted in Table VII.

TABLE VII.
PRICES PER POUND USED IN COMPUTING VALUES.

| Grade | Prices per Pound for Leaf Lengths and Grades | | |
|----------------|--|-----------|-----------|
| | 12 in. | 13-14 in. | 15-20 in. |
| Light wrappers | 20 cents | 30 cents | 80 cents |
| Medium " | 10 " | 18 " | 50 " |
| Seconds | 8 " | 10 " | 22 " |
| Dark wrappers | 8 " | 10 " | 25 " |
| Tops | 5 " | 7 " | 12 " |

Deductions were made for harvesting an extra number of leaves, as many of the selections produced a larger number of leaves per plant than Havana. These deductions were made as follows:

Taking an actual case, for example (5-2)-1-3 averages 29 leaves per plant, by count, and our standard Havana averages about 20 leaves. If we assume that all leaves have an equal weight, 9/29 of 2,813 pounds of tobacco, or 873 pounds must be handled because of the nine extra leaves. One of our best-known growers said that it actually cost him 28 cents per pound to put primed Havana into bales. Thus, the extra cost of handling nine leaves, after growing, and fertilizing the land, would be about 20 cents a pound, and for 873 pounds would amount to \$174.60.

If we take the Havana, which averages about 20 leaves per plant, as the standard, and compare its relative value with that of (5-2)-1-3, we must first deduct \$174.60 from the packed value of (5-2)-1-3. Assuming the value of Havana as 100, we can then obtain relative values of our other selections by dividing their packed value, after deducting the extra cost for larger leaf number, by the calculated packed value of Havana. Relative values so computed appear in the last column of Table VIII.

TABLE VIII.
SORTING TEST AND RELATIVE VALUES OF THE HALLADAY TYPES.

| No. | Mean Leaf Production | Yield in Pounds per Acre | Light Wrappers | | Medium Wrappers | | Binders | | Dark Wrappers | | Tops | | Relative Value |
|----------|----------------------|--------------------------|----------------|-----------|-----------------|-----------|---------|-----------|---------------|-----------|--------|-----------|----------------|
| | | | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | |
| 5-2-1-3 | 29.0 | 2813 | 271 | 9.7 | 176 | 6.2 | 718 | 25.5 | 990 | 35.2 | 658 | 23.4 | 108.3 |
| 6-2-1-4 | 30.5 | 2822 | 582 | 20.7 | 266 | 9.4 | 771 | 27.0 | 497 | 17.6 | 704 | 25.0 | 137.1 |
| 12-1-1-1 | 29.1 | 3370 | 575 | 17.0 | 87 | 2.6 | 893 | 26.5 | 935 | 27.8 | 880 | 26.1 | 147.3 |
| 12-2-1-1 | 29.0 | 3085 | 365 | 11.9 | 28 | 0.9 | 785 | 25.4 | 805 | 26.1 | 1102 | 35.7 | 104.7 |
| 27-1-1-1 | 25.9 | 2766 | 414 | 15.0 | 22 | 0.8 | 935 | 33.8 | 643 | 23.2 | 752 | 27.2 | 115.1 |
| 27-2-1-1 | 25.0 | 2736 | 677 | 24.7 | 100 | 3.6 | 889 | 32.5 | 573 | 20.9 | 497 | 18.2 | 157.3 |
| 41-1-1-2 | 27.4 | 2196 | 240 | 11.0 | 44 | 2.0 | 710 | 32.3 | 509 | 23.2 | 693 | 31.5 | 83.3 |
| 41-2-1-1 | 26.9 | 2694 | 553 | 20.5 | 54 | 2.0 | 1034 | 38.4 | 415 | 15.4 | 637 | 23.7 | 132.8 |
| 41-2-3-2 | 17.8 | 1936 | 362 | 18.7 | 9 | 0.5 | 612 | 31.6 | 203 | 10.5 | 750 | 38.7 | 111.3 |
| 73-2-3-3 | 26.7 | 2645 | 308 | 11.7 | 0 | 0.0 | 785 | 29.6 | 256 | 9.7 | 1296 | 49.0 | 74.2 |
| 76-2-1-1 | 26.9 | 2721 | 456 | 16.8 | 126 | 4.6 | 557 | 20.5 | 714 | 26.2 | 868 | 31.9 | 114.1 |
| 77-1-1-1 | 18.4 | 2271 | 481 | 21.2 | 40 | 1.7 | 521 | 22.9 | 494 | 21.8 | 735 | 32.4 | 144.7 |
| 77-2-1-1 | 25.8 | 2341 | 445 | 19.0 | 39 | 1.7 | 380 | 16.2 | 689 | 29.4 | 788 | 33.7 | 111.7 |
| K-1-1-2 | 21.5 | 2332 | 508 | 21.8 | 45 | 1.9 | 540 | 23.2 | 621 | 26.6 | 618 | 26.5 | 131.5 |
| K-2-1-6 | 22.8 | 2740 | 617 | 22.5 | 65 | 2.3 | 787 | 28.7 | 737 | 26.9 | 534 | 19.5 | 162.6 |
| Havana | 20.0 | 2119 | 201 | 9.5 | 80 | 3.9 | 485 | 22.8 | 612 | 28.8 | 740 | 35.0 | 100.0 |

A glance at the percentages of Light Wrappers received shows in no case a very favorable result. Selection (27-2)-1, which gave a relative value of 157.3, leads all the selections by producing a total of 24.7% of Light Wrappers. As the Havana which was grown on the same field produced only 9.5% Light Wrappers, the results seem more favorable. There is certainly a wide range of value for these Halladay selections. The poorest, (73-2)-3-3, which also was the selection which produced the shortest leaves of the lot, had a relative value of 74.2, while the most favorable, (K-2)-1-6, gave a relative value of 162.6 as compared with Havana.

It has already been mentioned that before the tobacco was sorted it was examined by three tobacco men. These three men examined the same hands which had been used for the grain and texture results, each working independently and without prejudice of any kind other than some diversity of opinion as to what constitutes an ideal tobacco. None of the three men were very favorably impressed, the general criticism of each being that the tobacco lacked a bright finish. The different selections, however, were given relative placings, at our request. After the placings had been roughly made, each man was then given the second picking of the six selections which, in preliminary judgment, were rated the highest. With these second pickings final placings were then made, and the results are given in the table below, the gradings being placed in sequence with the better type at the top.

| Judge 1 | Judge 2 | Judge 3 |
|------------|------------|------------|
| (77-1)-1-2 | (K-2)-1-6 | (K-2)-1-6 |
| Havana | (73-2)-3-3 | Havana |
| (77-2)-1 | Havana | (27-2)-1 |
| (76-2)-1-1 | (77-2)-1 | (77-2)-1 |
| (K-1)-1-2 | (77-1)-1-2 | (41-2)-1 |
| (6-2)-1-4 | (27-2)-1 | (76-2)-1-1 |

It will be noted that (K-2)-1-6 appears first twice and it is also of interest to know that this selection gave a high relative value by the sorting test. Commercial Havana ranks second twice and third once. The only other selection which appears three times in the judges' table is (77-1)-1-2. (27-2)-1, which gave the second highest relative value, appears twice in this table.

As the crop was of such an inferior nature no hard and fast conclusions can be drawn as to the commercial value of the selections. It is encouraging that under similar conditions several types gave much higher relative values than Havana.

Conclusions.

Our results show conclusively that the Halladay Havana was not a mutation or sport, but that it resulted from a recombination of parental characters, in which the number of leaves and leaf shape of the Sumatra were united with the leaf size and habit of growth of the Havana. That the general Halladay Havana type as it appears in the field can be reproduced whenever desired is an undoubted fact.

The apparent uniformity of the Halladay type in 1908 has proved to be of only superficial nature. By selection we have been able to produce several strains which differ very widely in number of leaves, leaf size and vigor. In other families of this cross, selection has as yet given no results of appreciable value. It seems only fair to conclude that by selection we have been able simply to isolate different lines that approach a homozygous condition, and that in those cases where selection has given no results the lines were already in a nearly homozygous condition.

Quality of cured leaf is, without a doubt, due to both external and internal factors. Environment, of which we may mention physical characters of soil, moisture, temperature and soil fertility, and methods of handling, such as time of harvesting, are of great importance. These may be roughly classed as external factors.

In our experiments we have eliminated, as far as possible, unfavorable external factors, but the total elimination of unfavorable conditions is a physical impossibility. All that we have been able to do is to give all selections as nearly an equal chance under as favorable conditions as possible. The relative values of the experimental selections were compared with Havana grown under similar conditions. Assuming the value of Havana as 100, the experimental types have ranged in value from 74.2 to 162.6.

Previous experiments have shown that the Sumatra parent lacks wrapper quality when grown in Connecticut. It has,

however, a large leaf number and a good leaf shape. The Havana parent, while widely grown, is not an ideal type. The leaf is too pointed in shape and there are also possibilities of improving its quality. A leaf which is of intermediate weight between Sumatra and Havana and which shows the bright appearance and elasticity of the Havana parent would be of commercial value. Nearly all of our Halladay strains have good leaf size and an improved leaf shape. Some of the types are very inferior in quality, others are of intermediate value, and a few closely resemble Havana. The better selections will be further tested as they show promise of being of commercial value.

FAMILY (403×401), SUMATRA×BROADLEAF.

In 1909 a cross was made between Sumatra (403) and the Connecticut out-door type of tobacco known as Broadleaf (401). The Sumatra had been grown under tent from inbred seed for four years and appeared uniform. The Broadleaf parent was a commercial variety, and as seed of the same type has proved very uniform we feel justified in saying that this cross was made between types which, as to external characters, were in a nearly homozygous condition.

The objects of this cross were to study the inheritance of certain characters as a check on the Halladay Havana results, and to produce a type of tobacco which had the desirable quality of the Broadleaf parent together with more desirable morphological characters, and it was thought that a recombination of factors from both the Broadleaf and the Sumatra might furnish such a variety. The leaves of the Broadleaf are long and drooping, and for this reason the tobacco is hard to cultivate and harvest. The shape of the leaf, with its narrow pointed tip, is such that considerable waste is made in cutting wrappers. A shorter, rounder, more erect leaf of as good quality as the Broadleaf would be of material value. It has not been produced as yet but the results are of interest as some facts of importance have been obtained.

The first generation of the cross together with its parents was grown in New Haven in 1910, though a few plants of the F_1 generation were also grown in Bloomfield.

In 1911 the parents and two F_2 generations were grown in New Haven and large cultures of three F_2 generations were grown in Bloomfield. It was our intention to harvest the Bloomfield selections and to examine them for quality, but there was a heavy hail storm a few weeks before harvesting time, and as only about half the leaves were worth harvesting, the tobacco was sold in the bundle and no actual sorting data were taken. However, some leaves were of good quality.

A number of F_3 generations were grown in Bloomfield in 1912, and others, together with further generations of the parents, were grown in New Haven. The Bloomfield selections were assorted in the same manner as the Halladay Havana types.

Inheritance of Leaf Number.

The inheritance of number of leaves per plant for this family has been considered in a previous paper (Hayes, 1912) and the F_1 and F_2 hybrid generation results were then given.

Table IX gives the results of three generations of the parents, the first generation of the cross which was grown in New Haven, two F_2 generations, and nine F_3 generations, which were grown in Bloomfield. This table gives the number of leaves of the parent, the total number of variates, the means, and the coefficients of variability.

The Broadleaf parent (401) has shown little variation in mean leaf number in the three years grown, the means being $19.2 \pm .05$ leaves in 1910 and $19.9 \pm .07$ in 1912. The coefficient of variability is slightly higher in 1912 than in 1910.

The mean leaf number of the Sumatra variety was $28.2 \pm .08$ in 1910, $26.5 \pm .11$ in 1911, and $26.2 \pm .12$ in 1912. The duplication of the results in the last two years indicates an error of counting in 1910, since such an error might arise by not discarding the three basal leaves uniformly as was done in the later years.

The coefficient of variability for the Sumatra parent was $5.27 \pm .21$ in 1910, $6.64 \pm .28$ in 1911, and $8.28 \pm .32$ in 1912. The cause of this rise in variability in 1912 is not clear. It may be due to a small mutation in one of the germ cells of the 1910 plant that gave rise to the 1911 population. The population in 1912 would then be the F_2 generation of the

TABLE IX.
 INHERITANCE OF LEAF NUMBER IN CROSS (403 X 401) SUMATRA X BROADLEAF.

| No. | Year Grown | Generation | Leaves of Parent | Range of Variation | Total | A. | C. V. |
|-----------------|------------|----------------|------------------|--------------------|-------|------------|-------------|
| 403, Sumatra | 1910 | P ₁ | .. | 24-31 | 150 | 28.2 ± .08 | 5.27 ± .21 |
| 403-1 | 1911 | P ₂ | 29 | 23-31 | 125 | 26.5 ± .11 | 6.64 ± .28 |
| 403-1-2 | 1912 | P ₃ | 29 | 21-32 | 151 | 26.2 ± .12 | 8.28 ± .32 |
| 401, Broadleaf | 1910 | P ₁ | .. | 17-22 | 150 | 19.2 ± .05 | 5.00 ± .19 |
| 401-1 | 1911 | P ₂ | 20 | 16-22 | 108 | 19.1 ± .08 | 6.54 ± .30 |
| 401-1-1 | 1912 | P ₃ | 22 | 17-23 | 145 | 19.9 ± .07 | 6.03 ± .24 |
| (403 X 401) = B | 1910 | F ₁ | .. | 19-26 | 150 | 23.6 ± .07 | 5.51 ± .21 |
| B-1 | 1911 | F ₂ | 25 | 17-32 | 2402 | 22.7 ± .03 | 8.99 ± .11 |
| B-3 | 1911 | F ₂ | 24 | 17-35 | 1632 | 22.5 ± .03 | 9.51 ± .10 |
| B-1-4 | 1912 | F ₃ | 25 | 16-29 | 179 | 22.5 ± .12 | 10.84 ± .39 |
| B-1-7 | 1912 | F ₃ | 22 | 17-28 | 207 | 21.5 ± .10 | 10.14 ± .34 |
| B-1-8 | 1912 | F ₃ | 28 | 19-33 | 82 | 26.3 ± .20 | 10.38 ± .55 |
| B-1-10 | 1912 | F ₃ | 26 | 19-27 | 151 | 23.1 ± .10 | 7.75 ± .30 |
| B-1-12 | 1912 | F ₃ | 25 | 18-30 | 209 | 23.7 ± .14 | 10.51 ± .41 |
| *B-1-14 | 1912 | F ₃ | 25 | 19-29 | 56 | 21.8 ± .14 | 7.18 ± .46 |
| B-3-5 | 1912 | F ₃ | 27 | 17-28 | 159 | 21.7 ± .11 | 9.45 ± .36 |
| B-3-6 | 1912 | F ₃ | 28 | 16-27 | 229 | 22.5 ± .09 | 8.71 ± .27 |
| B-3-8 | 1912 | F ₃ | 25 | 17-23 | 85 | 20.6 ± .12 | 8.25 ± .43 |

* 131 plants were grown at New Haven, the calculated coefficient of variability being 6.44 ± .27.

mutating germ cell with a normal cell. On the other hand, though, we have data on another cross that indicate that the field environment has but little effect in determining the number of leaves, it may be that this effect is somewhat greater on the Sumatra variety with its different habit of growth.

Cross (403×401) has been designated as B in Table IX, and as such it will be described in the text. An inspection of the table will show that the first generation of the cross is no more variable than the parents, although intermediate in leaf number, whereas the F_2 generations, B-1 and B-3, of which large cultures were grown, are extremely variable, giving coefficients of variability of $8.99 \pm .11$ and $9.51 \pm .10$, and ranging in value from the leaf number of the Broadleaf to that of Sumatra.

Of the nine F_3 generations, B-1-8 has a mean for leaf number of $26.3 \pm .20$, which is about the same as Sumatra, while the remainder show means of intermediate value, although that of B-3-8, $20.6 \pm .12$, is only slightly greater than the Broadleaf parent.

B-1-14 shows a coefficient of variability of $7.18 \pm .46$, which is only slightly higher than the parents. This same selection was also grown in New Haven and gave a coefficient of variability of $6.44 \pm .27$. For this reason, if one is to attach any value to this biometrical constant, it seems only fair to conclude that this type is in a homozygous condition for leaf number. B-1-10 also proved rather uniform since it had a variability coefficient of only $7.75 \pm .30$. These two types were both of intermediate value for leaf number.

On the other hand, five of the remaining populations have coefficients of variability of practically the same value as the F_2 generation, and two show an intermediate value. This difference in the variability of F_3 populations grown from individuals from various F_2 classes is exactly what should be expected if several Mendelian factors have recombined in the F_2 generation.

Shape and Size of Leaf.

In the data on inheritance of leaf size in cross B, which were given in an earlier paper, there were no F_2 plants with as large an average leaf area as the extreme variates of the Broadleaf.

TABLE X.
 BREADTH INDEX OF F₁, F₂ GENERATIONS AND PARENTS OF CROSS (403×401), SUMATRA×BROADLEAF.

| No. | Year grown | Generation | Breadth Index Classes | | | | | | | | | | | | | | | | Total | A. | C. V. |
|---|------------|----------------|-----------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|------------|-------------|-------|
| | | | 36 | 39 | 42 | 45 | 48 | 51 | 54 | 57 | 60 | 63 | 66 | 69 | | | | | | | |
| 403, Sumatra 401, Broadleaf (403×401) = B B-1 B-2 | 1910 | P ₁ | .. | .. | .. | 2 | 15 | 47 | 43 | 30 | 12 | 1 | .. | .. | .. | .. | .. | 150 | 53.5 ± .19 | 6.60 ± .26 | |
| | 1910 | P ₁ | .. | 2 | 13 | 41 | 46 | 32 | 13 | 3 | .. | .. | .. | .. | .. | .. | .. | 150 | 47.9 ± .20 | 7.62 ± .30 | |
| | 1910 | F ₁ | .. | .. | .. | 5 | 15 | 34 | 62 | 28 | 6 | .. | .. | .. | .. | .. | .. | 150 | 53.2 ± .18 | 6.18 ± .24 | |
| | 1911 | F ₂ | 1 | 2 | 9 | 21 | 30 | 15 | 16 | 9 | 2 | 1 | .. | 1 | .. | .. | .. | 107 | 49.3 ± .35 | 10.81 ± .50 | |
| | 1911 | F ₂ | 2 | 17 | 40 | 65 | 57 | 40 | 15 | 3 | 2 | .. | .. | .. | .. | .. | .. | 241 | 46.5 ± .19 | 9.40 ± .30 | |
| | | | | | | | | | | | | | | | | | | | | | |

This was explained by the fact that the environmental conditions for F_2 were poorer than the parents or F_1 had enjoyed. While no statistical records were taken, the large size of leaves of numerous plants of several of our F_3 generations grown at Bloomfield in 1912 has shown this explanation to be the correct one.

Size of leaf, as perhaps should be expected, is greatly influenced by environment, which made proper analysis of our breeding results a difficult task; but shape of leaf, which is the basis of our next study, is fortunately less subject to such modification.

The method of determining leaf shape which has been used is called breadth index. It is obtained by dividing the breadth by the length and expressing the result in per cent.

The same variates which showed no distinct segregation in leaf size have been considered, the results of this method of treatment appearing in Table X. The middle leaf of each plant was used in computing breadth index.

The table shows that the average breadth index of the Sumatra is $53.5 \pm .19$, which means that, on the average, the breadth of leaf of the Sumatra is a little more than half the length. The Broadleaf gave an index of $47.9 \pm .20$, and the F_1 generation an index of $53.2 \pm .18$. The indexes of the two F_2 generations are shown by the table to be $49.3 \pm .35$ and $46.5 \pm .19$. The conditions for the F_2 generations were very unfavorable and the indexes are smaller than one would expect. That there is some sort of segregation of leaf shape seems very evident, as the coefficients of variability of the F_2 are much larger than those of the parents, or F_1 .

Table XI gives comparative results for length of leaf of the F_3 selections grown at Bloomfield in 1912. This table gives the average number of leaves per plant, by actual count, the yield of cured tobacco per acre, and the number of pounds of cured tobacco of leaf length classes, which range from 12 to 20 inches. It is regretted that no Broadleaf selection was grown to compare with the hybrids.

TABLE XI.

COMPARATIVE LENGTH OF LEAVES OF THE F₃ GENERATIONS OF CROSS (403×401), SUMATRA×BROADLEAF.

| No. | Mean Leaf Production | Yield in Pounds per Acre | Yield in Pounds for Leaf Length Classes in Inches | | | | | | | |
|--------|----------------------|--------------------------|---|-----|-----|-----|-----|-----|-----|-----|
| | | | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 |
| B-1-4 | 22.0 | 2030 | 130 | 220 | 295 | 350 | 350 | 330 | 299 | 55 |
| B-1-7 | 21.5 | 2476 | 63 | 126 | 213 | 281 | 352 | 399 | 567 | 475 |
| B-1-8 | 26.3 | 2579 | 305 | 291 | 410 | 388 | 298 | 276 | 410 | 201 |
| B-1-10 | 23.1 | 2517 | 41 | 133 | 233 | 388 | 484 | 443 | 653 | 142 |
| B-1-12 | 23.7 | 2405 | 46 | 101 | 150 | 261 | 362 | 421 | 545 | 519 |
| B-1-14 | 21.8 | 2629 | .. | 159 | 265 | 361 | 520 | 392 | 583 | 350 |
| B-3-5 | 21.7 | 3206 | .. | 152 | 190 | 262 | 410 | 512 | 982 | 698 |
| B-3-6 | 22.5 | 2927 | 58 | 173 | 203 | 275 | 323 | 405 | 643 | 845 |
| B-3-8 | 20.6 | 2566 | 36 | 154 | 190 | 298 | 361 | 425 | 669 | 434 |

In considering these results it is important to note that only medium size and large leaved plants were used as parents of the F₃ generations. There is considerable variation in leaf lengths, as shown by this table. Thus, B-1-4 produced a large number of leaves on classes 15 and 16. B-1-8 and B-1-14, while producing the greater weight of leaves on class 18, also produced a large number of leaves on classes 15 and 16. B-3-6 is the only selection which produced the most leaves by weight in class 20. The selections, then, show considerable variation in leaf length when compared with each other and show that there are probably a number of factors affecting leaf size.

Some general notes on the leaf conditions of these F₃ generations of cross B are given in Table XII. Three general features—uniformity, color of leaves and type of leaf—were considered. Uniformity refers to the leaf characters of the selection as a whole. Those marked “good” in the table were uniform in all characters, while the remainder showed considerable variation. These facts are mentioned here, as our results point to the conclusion that the different characters, such as leaf number, shape of leaf and type of leaf, in which the parents differ, are in a large measure inherited independently. One other purpose was to determine if any single external character could be correlated with quality.

TABLE XII.

GENERAL NOTES ON THE LEAF CONDITION OF THE F_3 GENERATIONS OF CROSS (403×401), SUMATRA×BROADLEAF.

| No. | Uniformity | Color of Leaves | Type of Leaf |
|--------|------------|------------------------|----------------------|
| B-1-4 | Good | Light green | Moderately crinkled |
| B-1-7 | Fair | Medium green | Smooth to crinkled |
| B-1-8 | Good | Light green | Very crinkled |
| B-1-10 | Fair | Medium green to bluish | Slightly crinkled |
| B-1-12 | Fair | Somewhat bluish | Leaves mostly smooth |
| B-1-14 | Good | Medium green | |
| B-3-5 | Fair | Light to medium green | Slightly crinkled |
| B-3-6 | Fair | Medium to dark green | Moderately crinkled |
| B-3-8 | Fair | Medium green | Moderately crinkled |

Quality of the F_3 Selections.

Data on texture and grain were not taken for the F_3 Sumatra × Broadleaf crosses, with the exception of two selections which were examined for grain, the leaves being classified into seven grain classes as for the Halladay types. The selections used were B-1-10, which proved uniform for number of leaves per plant, giving a variability coefficient of $7.75 \pm .30$, and B-1-7 which was not uniform for leaf number and which gave a variability coefficient of $10.14 \pm .34$.

If there were a correlation between grain and leaf number we should expect the classes for B-1-10 to be more uniform than those for B-1-7. A glance at Table XIII indicates that such is not the case, since both selections were about equally variable and both have a large amount of grain. At the same time it is realized that the method of determining grain is exceedingly arbitrary.

TABLE XIII.

COMPARISON OF GRAIN OF B-1-7 AND B-1-10.

| No. | Leaves per Plant | Picking | Grain Classes | | | | | |
|--------|------------------|---------|---------------|-----|-----|----|----|----|
| | | | 1 | 2 | 3 | 4 | 5 | 6 |
| B-1-7 | 21.5 | 1 | 37 | 41 | 42 | 25 | 13 | 4 |
| | | 2 | 32 | 51 | 40 | 26 | 11 | .. |
| | | 3 | 32 | 39 | 53 | 23 | 10 | .. |
| | | Total | 101 | 131 | 135 | 74 | 34 | 4 |
| B-1-10 | 23.1 | 1 | .. | 35 | 40 | 31 | 10 | 1 |
| | | 2 | 30 | 40 | 46 | 26 | 9 | 1 |
| | | 3 | 29 | 44 | 44 | 34 | 5 | .. |
| | | Total | 59 | 119 | 130 | 91 | 24 | 2 |

TABLE XIV.
SORTING TEST AND RELATIVE VALUES OF F₃ BROADLEAF SELECTIONS.

| No. | Mean Leaf Production | Yield in Pounds per Acre | Light Wrappers | | Medium Wrappers | | Binders | | Dark Wrappers | | Tops | | Relative Value |
|--------|----------------------|--------------------------|----------------|-----------|-----------------|-----------|---------|-----------|---------------|-----------|--------|-----------|----------------|
| | | | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | |
| B-1-4 | 22.0 | 2030 | 468 | 23.0 | 4 | 0.2 | 287 | 14.2 | 622 | 30.6 | 649 | 32.0 | 100.0 |
| B-1-7 | 21.5 | 2476 | 583 | 23.5 | 5 | 0.2 | 457 | 18.5 | 819 | 33.1 | 612 | 24.7 | 141.8 |
| B-1-8 | 26.3 | 2579 | 469 | .. | .. | .. | 335 | .. | 224 | .. | 715 | .. | .. |
| B-1-10 | 23.1 | 2517 | 502 | .. | 41 | 1.6 | 407 | 16.2 | 690 | 27.4 | 877 | 34.8 | 122.6 |
| B-1-12 | 23.7 | 2405 | 587 | 24.4 | 16 | 0.7 | 428 | 17.8 | 633 | 26.3 | 741 | 30.8 | 113.6 |
| B-1-14 | 21.8 | 2629 | 297 | 11.3 | 21 | 0.8 | 329 | 12.5 | 1028 | 39.1 | 954 | 36.3 | 102.7 |
| B-3-5 | 21.7 | 3206 | 558 | 17.4 | 30 | 0.9 | 812 | 25.3 | 998 | 31.3 | 808 | 25.2 | 162.6 |
| B-3-6 | 22.5 | 2927 | 699 | 23.9 | 13 | 0.4 | 491 | 16.8 | 966 | 33.0 | 758 | 25.9 | 159.5 |
| B-3-8 | 20.6 | 2566 | 416 | 16.2 | .. | .. | 659 | 25.7 | 750 | 29.2 | 741 | 28.9 | 127.4 |

Relation of Havana to B-1-4 = 100:105.1.

Table XIV gives the sorting test and relative values of the F_3 selections. The yield ranged from 2,030 pounds per acre in B-1-4 to 3,206 pounds in B-3-5. This seems to be good evidence that a selection can be produced which would give a much higher yield per acre than the commercial Broadleaf now grown. The success of our experiment does not depend so largely on yield factors as it does on quality values, however, and on this subject no very definite conclusions can be drawn until the selections are more uniform for external plant characters and have been tested for quality another season.

B-1-4 has about the same relative value as the Havana type given in Table VIII, the relation of B-1-4 to Havana being 105.1 to 100. For the relative values given in the last column of Table XIV, B-1-4 has been used as the standard (100), the actual prices for grades being assumed to be the same as for the Halladay types which were given in Table VII. B-1-14 gave about the same relative value as B-1-4, although it gave a yield of 2,629 pounds per acre while B-1-4 only gave a yield of 2,030 pounds. B-3-5 gave the highest yield, and also the highest relative value of any of the selections.

The attempt to discover some external character or characters which are correlated with quality has not, as yet, proved successful. It seems very probable that, although it may be necessary to have all characters in a nearly homozygous condition in order to produce tobacco that is of uniform quality, this is not because there is a close relation between quality and any one external character. If the type is in a complex hybrid condition, variation in time of maturity, venation, etc., will be the rule. Such conditions will not be favorable to producing a uniform quality of tobacco.

Conclusions.

The results obtained from the Broadleaf \times Sumatra cross show that, as a rule each character, such as leaf size, leaf shape, number of leaves and type of leaf, are inherited independently. Hence the difficulty of producing a uniform strain after crossing will depend largely on the gametic condition of the parents. If the parents differ in a large number of factors the difficulties will be much greater than if there are but a small number with which to deal.

The really important feature is that there is a segregation of quantitative characters in the F_2 generation of tobacco crosses and that some segregates will breed true in F_3 . As this is the case, there seems to be no need of using a different method when working with quantitative characters than for qualitative or color characters.

Since quality of cured leaf depends on many factors, external as well as internal, it is probably unreasonable to expect a single external character to be closely correlated with quality, but as homozygosis produces uniformity in both quantitative and qualitative characters it must tend to produce uniform quality.

The important matter in practice is simply to grow a sufficient number of F_3 and later generations to run a fair chance of testing out all the combinations of factors possible to the parental varieties used.

FAMILY (402×405), HAVANA×CUBAN.

This cross was made in 1909 between strains of Havana and Cuban which had been grown for several years from inbred seed. The P_1 generation of the Cuban parental type given in the tables was not grown from inbred seed of a single plant, but from commercial seed saved under tent covering. The plants from which this seed was saved were grown from seed of direct descendants of the inbred Cuban type used as the male parent. The P_1 generation of Havana given in our tables was also grown from commercial seed.

This cross has been designated as C in our discussion. The parents and different generations of this cross have been grown under shade covering at the Windsor Tobacco Growers' Corporation in Bloomfield, with the exception of C-1-5 and C-1-6, which were grown outdoors on the same field as the Halladay and F_3 Broadleaf selections. The conditions for this cross grown under cloth shade are more uniform than for the previous experimental selections which were grown in the open, due to the protection the covering affords from heavy winds and storms.

The parents and F_1 were grown in 1910, further generations of the parents and F_2 in 1911, and the third generation of parents and five F_3 generation families in 1912.

TABLE XV.
 INHERITANCE OF LEAF NUMBER IN CROSS BETWEEN (402 X 405), HAVANA X CUBAN

| No. | Year grown | Generation | Leaves of Parent | Range of Variation | Total | Mean | C. V. |
|-----------------|------------|----------------|------------------|--------------------|-------|------------|-------------|
| 405, Cuban | 1910 | P ₁ | .. | 16-25 | 150 | 19.9 ± .08 | 7.53 ± .28 |
| 405-1 | 1911 | P ₂ | 21 | 18-23 | 124 | 20.6 ± .07 | 5.29 ± .23 |
| 405-1-1 | 1912 | P ₃ | 23 | 17-25 | 150 | 20.9 ± .07 | 6.17 ± .24 |
| 402, Havana | 1910 | P ₁ | .. | 17-24 | 143 | 19.8 ± .07 | 6.98 ± .27 |
| 402-1 | 1911 | P ₂ | 20 | 16-25 | 150 | 20.3 ± .10 | 8.87 ± .35 |
| 402-1-1 | 1912 | P ₃ | 20 | 15-25 | 150 | 19.4 ± .05 | 4.59 ± .18 |
| (402 X 405) = C | 1910 | F ₁ | .. | 15-25 | 150 | 19.8 ± .07 | 6.10 ± .24 |
| C-1 | 1911 | F ₂ | .. | 14-33 | 192 | 20.9 ± .16 | 15.84 ± .54 |
| C-1-2 | 1912 | F ₃ | 20 | 13-29 | 112 | 19.7 ± .18 | 14.67 ± .67 |
| C-1-3 | 1912 | F ₃ | 20 | 15-22 | 142 | 18.4 ± .09 | 9.02 ± .36 |
| C-1-4 | 1912 | F ₃ | 28 | 20-35 | 148 | 26.6 ± .16 | 11.20 ± .44 |
| C-1-5 | 1912 | F ₃ | 30 | 22-34 | 45 | 28.0 ± .28 | 10.00 ± .72 |
| C-1-6 | 1912 | F ₃ | 22 | 13-29 | 201 | 20.1 ± .15 | 16.17 ± .56 |

Inheritance of Leaf Number.

The inheritance of number of leaves per plant is given in Table XV. The Cuban selection gave a range of variation of 16 to 25 leaves in 1910 and from 17 to 25 in 1912. The mean number of leaves per plant was $19.9 \pm .08$ in 1910, $20.6 \pm .07$ in 1911, and $20.9 \pm .07$ in 1912. There has been a slight progressive change in leaf number for the three years, but whether this is due to an actual germinal change or to unavoidable errors in our leaf counts is impossible to say. No wide changes are shown by the coefficients of variability, which were $7.53 \pm .28$ in 1910, $5.29 \pm .23$ in 1911, and $6.17 \pm .24$ in 1912.

The Havana selection gave a mean of $19.8 \pm .07$ leaves in 1910, $20.3 \pm .10$ in 1911, and $19.4 \pm .05$ in 1912. This selection shows no great change for leaf number. The coefficient of variability shows considerable variation, as it was $6.98 \pm .27$ in 1910, $8.87 \pm .35$ in 1911, and $4.59 \pm .18$ in 1912.

The F_1 gave about the same mean and variability coefficient as the parent types, the mean being $19.8 \pm .07$ and the coefficient of variability $6.10 \pm .24$.

If the parents both contained the same inherited factors for leaf number, which one might expect from their having about the same average number of leaves per plant, no increased variability over F_1 should be obtained in F_2 . The range of variation, 14 to 33 leaves, and the coefficient of variability of the F_2 generation, $15.84 \pm .54$, both show that such is not the case. Plants appeared which bore a higher and also a lower number of leaves than in F_1 .

The counts of leaf number for the five F_3 generations show conclusively that the increased variability in F_2 was a germinal one. These five F_3 selections were grown from F_2 plants which bore 20, 20, 22, 28 and 30 leaves respectively. Progeny from one of the 20-leaved F_2 plants, C-1-3, gave rather uniform results in F_3 , the mean being $18.4 \pm .09$ and the coefficient of variability $9.02 \pm .36$. Progeny from the other 20-leaved parent plant, C-1-2, and also the 22-leaved plant, C-1-6, gave means of about 20 leaves per plant and large variability coefficients, $14.67 \pm .67$ and $16.17 \pm .56$ respectively.

The two remaining selections, C-1-4 and C-1-5, with coefficient of variability values of $11.20 \pm .44$ and $10.00 \pm .72$ were more variable than the F_1 and less variable than the F_2 .

TABLE XVI.
BREADTH INDEX OF F₁, F₂, F₃ GENERATIONS AND PARENTS OF CROSS (402×405), HAVANA×CUBAN.

| No. | Year grown | Generation | Breadth Index Classes | | | | | | | | | | | | | | | | Total | A. | C. V. |
|---------------|------------|----------------|-----------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|------------|------------|-------|
| | | | 36 | 39 | 42 | 45 | 48 | 51 | 54 | 57 | 60 | 63 | 66 | 69 | 72 | | | | | | |
| 402, Havana | 1910 | P ₁ | .. | 4 | 29 | 69 | 38 | 9 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 150 | 45.4 ± .15 | 6.04 ± .24 | |
| 402-1-1 | 1912 | P ₃ | .. | 3 | 21 | 74 | 48 | 4 | .. | 56 | 56 | 14 | 1 | .. | .. | .. | .. | 150 | 45.6 ± .13 | 5.13 ± .20 | |
| 405, Cuban | 1910 | P ₁ | .. | .. | .. | .. | .. | 3 | 19 | 56 | 56 | 14 | 1 | .. | .. | .. | .. | 150 | 58.3 ± .16 | 5.09 ± .20 | |
| 405-1-1 | 1912 | P ₃ | .. | .. | .. | .. | .. | .. | 1 | 30 | 76 | 34 | 9 | .. | .. | .. | .. | 150 | 60.4 ± .14 | 4.09 ± .16 | |
| (402×405) = C | 1910 | F ₁ | .. | .. | 1 | 13 | 38 | 69 | 25 | 3 | 1 | .. | .. | .. | .. | .. | .. | 150 | 50.3 ± .16 | 5.73 ± .22 | |
| C-1 | 1911 | F ₂ | 1 | 1 | 10 | 15 | 37 | 57 | 34 | 26 | 10 | 1 | .. | .. | .. | .. | .. | 192 | 51.2 ± .23 | 9.18 ± .32 | |
| C-1-2 | 1912 | F ₃ | .. | .. | .. | .. | .. | 3 | 8 | 19 | 35 | 38 | 8 | 1 | 1 | .. | .. | 113 | 57.5 ± .23 | 6.40 ± .29 | |
| C-1-3 | 1912 | F ₃ | .. | 6 | 25 | 56 | 35 | 19 | 1 | .. | .. | .. | .. | .. | .. | .. | .. | 142 | 45.8 ± .18 | 6.92 ± .28 | |
| C-1-4 | 1912 | F ₃ | .. | 6 | 10 | 50 | 55 | 24 | 3 | 2 | .. | .. | .. | .. | .. | .. | .. | 150 | 47.0 ± .18 | 7.00 ± .27 | |

TABLE XVII.
INHERITANCE OF LEAF SIZE IN CROSS BETWEEN (402×405), HAVANA×CUBAN.

| No. | Year grown | Generation | Classes in Sq. Dcms. | | | | | | | | | | | | Total | A. | C. V |
|---------------|------------|----------------|----------------------|----|----|----|----|----|----|----|----|----|----|-----|-----------|------------|------|
| | | | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | | | | | |
| 402, Havana | 1910 | P ₁ | .. | 1 | 23 | 42 | 41 | 35 | 8 | .. | .. | .. | .. | 150 | 6.7 ± .06 | 17.1 ± .68 | |
| 402-1-1 | 1912 | P ₃ | .. | 2 | 47 | 65 | 33 | 3 | .. | .. | .. | .. | .. | 150 | 4.9 ± .05 | 16.6 ± .67 | |
| 405, Cuban | 1910 | P ₁ | 3 | 26 | 58 | 54 | 9 | .. | .. | .. | .. | .. | .. | 150 | 5.3 ± .05 | 16.7 ± .67 | |
| 405-1-1 | 1912 | P ₃ | 4 | 41 | 87 | 18 | .. | .. | .. | .. | .. | .. | .. | 150 | 4.8 ± .04 | 14.1 ± .56 | |
| (402×405) = C | 1910 | F ₁ | .. | 6 | 27 | 46 | 39 | 27 | 5 | .. | .. | .. | .. | 150 | 6.5 ± .07 | 18.4 ± .74 | |
| C-1 | 1911 | F ₂ | 3 | 10 | 32 | 32 | 45 | 33 | 24 | 8 | 4 | 1 | .. | 192 | 7.0 ± .09 | 25.3 ± .92 | |
| C-1-2 | 1912 | F ₃ | 5 | 22 | 43 | 31 | 8 | 1 | .. | .. | .. | .. | .. | 110 | 5.2 ± .07 | 19.3 ± .91 | |
| C-1-3 | 1912 | F ₃ | .. | 3 | 45 | 46 | 34 | 13 | .. | .. | .. | .. | .. | 141 | 6.1 ± .06 | 16.5 ± .68 | |
| C-1-4 | 1912 | F ₃ | 4 | 33 | 58 | 31 | 12 | 10 | 2 | .. | .. | .. | .. | 150 | 5.3 ± .07 | 23.4 ± .96 | |

The means for leaf number were $26.6 \pm .16$ and $28.0 \pm .28$. Thus, from crossing two types bearing an average of about 20 leaves per plant, a new type has been produced with a larger leaf number.

Size and Shape of Leaf.

It was pointed out in an earlier paper that Cuban and Havana have about the same average leaf width but that Havana has somewhat longer leaves than Cuban. The breadth indexes of the parental varieties and crosses are given in Table XVI. As in the other cross, the middle leaf of each plant was used for these computations. The Havana leaf is shown to be proportionally much narrower for its length than the Cuban. The F_1 was of intermediate value for breadth index, and in F_2 there was an increase of variability. The F_3 strain, C-1-2, bred comparatively uniformly for the Cuban shape of leaf, giving a mean breadth index of $57.5 \pm .23$. This is slightly lower than the index of the 1910 Cuban selection, which is $58.3 \pm .16$, but the difference between these values is slightly less than four times the probable error. The parent F_2 plant of C-1-3 resembled Havana in all particulars and the progeny was of Havana type in both leaf size and breadth index value. The breadth index of C-1-4 was also of Havana type, and the coefficient of variability showed this selection to be uniform in leaf shape.

Table XVII gives the inheritance of leaf size for this cross. For this work, the areas of the fourth leaf from the bottom, the middle leaf, and the last leaf at the top below the bald sucker were taken. The area of leaf used in the table is the average of these three measurements.

The table shows that in 1910 the average Havana leaf area was greater than the Cuban and that the F_1 generation had nearly as large an average leaf area as Havana. The average leaf area of the F_2 generation was slightly greater than in F_1 and the variability was also much greater.

It is true that none of the shade selections grew as vigorously in 1912 as in previous years, but this does not explain the proportionally greater decrease in leaf size of the Havana as compared with the Cuban. It is of interest to know that selection C-1-3, which was not very variable for leaf number and

which was of uniform leaf shape, gave a variability coefficient of about the same value as the parental selections. The coefficient of variability of C-1-2 was only slightly greater than that of the parents, while C-1-4 seemed to be more variable.

It should be mentioned that the coefficient of variability is not a very safe criterion by which to judge when dealing with a character such as area of leaves. It is to be expected that a selection which is heterozygous in other plant characters will be more variable in a character such as leaf area than a completely homozygous selection, as stimulus to development is greater in a heterozygous than in a homozygous state, and when segregation is taking place some plants of a generation are homozygous and others complex hybrids.

The comparative length of leaves of the parents and F₃ generations is given in Table XVIII. As in previous tables of this kind, one must remember that these computations are made on the acre basis and that the figures in the table under the heading "leaf classes in inches" refer to pounds and not to number of leaves.

TABLE XVIII.

COMPARATIVE LENGTH OF LEAVES OF THE PARENTS AND F₃ GENERATIONS OF CROSS (402×405), HAVANA×CUBAN.

| No. | Mean Leaf Production | Yield in Pounds per Acre | Leaf Classes in Inches | | | | | | | |
|----------|----------------------|--------------------------|------------------------|-----|-----|-----|-----|-----|-----|------|
| | | | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 20 |
| 405-1-1* | 20.9 | 1493 | 186 | 193 | 142 | 350 | 328 | 218 | 76 | .. |
| 402-1-1† | 19.4 | 1508 | 51 | 29 | 208 | 113 | 164 | 273 | 499 | 171 |
| C-1-2 | 19.7 | 1635 | 102 | 137 | 183 | 218 | 295 | 355 | 279 | 66 |
| C-1-3 | 18.4 | 1369 | 44 | 36 | 33 | 120 | 153 | 127 | 517 | 339 |
| C-1-4 | 26.6 | 2036 | .. | 6 | 51 | 93 | 93 | 206 | 556 | 1032 |
| C-1-5 | 28.0 | 1709 | .. | 100 | 168 | 200 | 302 | 369 | 469 | 101 |
| C-1-6 | 20.1 | 2206 | 98 | 151 | 214 | 351 | 292 | 411 | 538 | 151 |

*Cuban.

† Havana.

This table shows that the Cuban produces a larger percentage of short leaves than the Havana. C-1-2, which it will be remembered was of Cuban shape except that its leaves are average slightly larger, shows a population similar to 405-1-1. C-1-

3, the F₃ Havana type, shows a population more nearly like Havana. Selection C-1-4 is of interest as it produced a much larger number of leaves per plant than the other shade selections. It also produced a large proportion of leaves of 20 inch length, averaging 1032 pounds per acre. The results given for C-1-5 and C-1-6 should not be given much weight in the discussion of comparative leaf lengths as they were grown out of doors. The interesting feature of these results is that one of the five F₃ generations closely resembled the Havana parent in leaf size and shape while another F₃ generation produced leaves that were of the shape and size of the Cuban parent.

Inheritance of Quality.

The results of a sorting test for quality are given in Table XIX, and the prices per pound which were used in computing relative values are given in Table VII. It is, of course, true that the selections which were grown under shade are worth more per pound than the prices used indicate; however, for our purposes these prices are probably as valuable as any other. No corrections were made for leaf number except for C-1-4, which produced 26.6 leaves per plant, this being reduced to a 20 leaf basis. The fourth picking of C-1-5 was lost, so the figures given for this selection represent the first three pickings only. Selection C-1-6 was weighed before sizing and the yield given in the table is correct. During the warehouse work the third picking of C-1-6 was mixed with a Broadleaf selection. The Broadleaf selection was discarded, but in the case of the C-1-6 the value per pound of the third picking was estimated, as we knew the actual value of the first, second, and fourth pickings.

The results of this sorting test throw some light on the problem of quality inheritance. Both parental varieties in this cross are tobaccos which produced a good quality of wrapper leaf. The percentages of light wrappers are 31.9 for 405-1-1, Cuban, and 39.8 for 402-1-1, Havana. For the computation of the relative values, Havana is again taken as the standard and the ratio of the shade selection 402-1-1 to the out-door Havana given in Table IX is 118.3:100.

TABLE XIX.
SORTING TESTS AND RELATIVE VALUES OF THE PARENTS AND F₂ GENERATIONS OF CROSS (402 X 405),
HAVANA X CUBAN.

| No. | Mean Leaf Production | Yield in Pounds per Acre | Light Wrappers | | Binders | | Dark Wrappers | | Tops | | Relative Value |
|---------|----------------------|--------------------------|----------------|-----------|---------|-----------|---------------|-----------|--------|-----------|----------------|
| | | | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | Pounds | Per cent. | |
| 405-1-1 | 20.9 | 1493 | 477 | 31.9 | 382 | 25.6 | 470 | 31.5 | 164 | 12.0 | 81.0 |
| 402-1-1 | 19.4 | 1508 | 601 | 39.8 | 317 | 21.0 | 452 | 30.0 | 138 | 9.2 | 100.0 |
| C-1-2 | 19.7 | 1635 | 640 | 39.1 | 325 | 19.9 | 477 | 29.2 | 193 | 11.8 | 106.5 |
| C-1-3 | 18.4 | 1428 | 601 | 42.0 | 390 | 27.3 | 324 | 22.7 | 113 | 7.9 | 104.7 |
| C-1-4 | 26.6 | 2036 | 905 | 44.5 | 553 | 27.1 | 414 | 20.4 | 164 | 8.0 | 142.9 |
| C-1-5 | 28.0 | 1709 | 837 | 49.0 | 486 | 28.4 | 336 | 19.6 | 50 | 3.0 | 133.0 |
| C-1-6 | 20.1 | 2206 | 189 | 15.2 | 523 | 41.8 | 183 | 15.0 | 355 | 28.4 | 86.1 |

C = cross between Havana and Cuban, 405-1-1 being Cuban and 402-1-1 being Havana.
The comparative value of the shade Havana to the outdoor Havana of Table IX is 118.3:100.

That the increase of leaf number does not cause an increase of dark and top leaves is clearly shown by selections C-1-4 and C-1-5. These selections both produced a high percentage of light wrappers and gave a high relative value.

The yields of the shade tobacco are much less than they would be if they were grown in the open, as the shade covering produces a thin leaf. A sample of Havana shade-grown light wrappers was shown to a well-known buyer who was in the warehouse when the experimental tobacco was being assorted and he was asked what they were. He immediately replied, "A fine quality of Havana." On the other hand, an out-door Cuban selection retained its distinctive character, although the percentage of dark leaves was greater and the leaves were heavier in the out-door tobacco. Thus we must come to the conclusion that quality, while decidedly affected by environment, is nevertheless greatly dependent on heredity.

The relative value of C-1-6 is only 86.1 although this selection gave a yield per acre of 2,206 pounds. This seems most easily explained by the fact that this selection was in a heterozygous condition for many characters. The variation in leaf number per plant was very high, as is shown by Table XV, and we know from observation that the variation in leaf shape and size was also very large. Hence, though some leaves of this selection were of high quality, the percentage was very low, and a large percentage of off-colored and dark leaves was produced. These results show that uniformly high quality cannot be expected if many characters are in a heterozygous condition.

Conclusions.

The results obtained from this cross show clearly that an external similarity of size characters in tobacco varieties does not necessarily mean a genetic similarity. Havana and Cuban both produced about the same average number of leaves per plant, yet when they were crossed together an increased variability occurred in F_2 . The five F_3 generation selections show that this increased variability was germinal, two of the five F_3 selections giving a much higher leaf average than the parents.

Similar results have been obtained frequently in inheritance

of qualitative characters. The general basis of the Mendelian conception of heredity depends on the fact that the somatic appearance of a plant is not a correct expression of its breeding nature. Of two red-flowered plants in the second generation of a cross between white and red-flowered races in which complete dominance is the rule, the one may breed true for the red color, giving only red progeny, and the other may give both red and white progeny. Advances may be disguised and may appear in crosses as well as simple recessives, although advances due to crossing are as a rule less frequent than simple recessives. In such cases as the purple aleurone color of maize, which depends on the presence of at least two color factors we may receive purple aleurone seeds on crossing white races if one white race contains one of the necessary color factors and the other white race contains the other. That similar results are obtained when dealing with size characters and that in both quantitative and qualitative characters it is impossible to know the germinal characters except by a breeding test seems further proof of the belief that both are inherited in a similar manner.

The results of the sorting test of the parents and third generation crosses show that heterozygosis affects quality and that uniformity of external characters tends to produce uniformity of quality in the cured leaves. Some of the hybrids gave increased yields and good quality and look promising from a commercial standpoint. It will be necessary, however, to continue the selections in row cultures until all characters are in a homozygous condition or nearly so.

INTERPRETATION OF RESULTS.

In a previous paper (Hayes, 1912) the data obtained from the first and second hybrid generations of size studies of tobacco were given a strict Mendelian interpretation by assuming a multiplicity of factors, each inherited independently and capable of adding to the character, the effect of the heterozygous condition of each factor being half the homozygous. The data on the third generations and on the Halladay reported in this paper show no need of a change of interpretation.

In order that the above interpretation may be justified,

certain results must be obtained. The first generation of a cross between two homozygous varieties which differ in a quantitative character, such as number of leaves per plant, must be of intermediate value and no more variable than the parents; the F_2 generation should give an increase in variability and, when sufficient individuals are studied, should give a range of variability equal to the combined range of the parents. Certain selected F_2 plants should breed true giving no greater variability than the parents; others should give a variation as great as the F_2 generation, and others should give variabilities intermediate between the value of the F_1 and F_2 . All of these conditions are fulfilled in our crosses.

The exact number of factors involved in any cross is difficult of determination, due to the obscuring effects of fluctuating variability. It might be possible to determine the number accurately by growing the parents, the F_1 and F_2 generations and a large number of F_3 generations under as uniform environmental conditions as possible. But even when only a limited number of F_3 generations are grown, it is possible to obtain an approximate idea of the factorial condition.

For the sake of illustration, let us first consider the inheritance of leaf number in the cross between Sumatra and Broadleaf given in Table IX. In this cross the parents differ by about six leaves per plant, the Broadleaf producing an average of about 20 leaves and the Sumatra an average of about 26 leaves. The F_1 generation was of intermediate value and no more variable as determined by the coefficient of variability than the parents, while the F_2 generation gave a range of variability equal to the combined range of the parents.

Of the nine F_3 generations, B-1-14 is comparatively uniform. Only 56 variates of B-1-14 were grown at Bloomfield, the calculated coefficient of variability being $7.18 \pm .46$, but 131 variates of this same selection were grown in New Haven and a variability coefficient of $6.44 \pm .27$ was obtained. Considering the large probable errors of these determinations it seems only fair to conclude that the coefficients of variability are really identical and that B-1-14 is in a homozygous condition for leaf number. B-1-10 is also rather uniform giving a variability coefficient of $7.75 \pm .30$. Of the remaining selections,

four show coefficients of variability slightly greater than in F_2 , one has about the same coefficient value as F_2 and two are of intermediate variability.

The results of this cross can be explained by supposing that the parental varieties are each pure for the same basal factorial formula for 20 leaves and that in addition the Sumatra has three independently inherited factors, each adding two leaves when homozygous and one when heterozygous.

Our gametic conditions for Broadleaf will be 20 aabbcc and for Sumatra 20 AABbCC. The F_1 formula will be 20 AaBbCc or 23 leaves, and in F_2 there will be a germinal variation from 20 to 26 leaves. With these gametic formulas we should expect one out of every eight F_3 generations to breed true. Of the nine F_3 generations given in Table IX, one gave a coefficient of variability of about the same value as the parents. That the F_3 generations gave different averages for leaf number may be seen by consulting our results.

All crosses cannot be explained in as simple manner as this one. In the case of inheritance of leaf number of cross (402×405) Havana×Cuban, the conditions are apparently more complex. Here both parents and F_1 gave an average of about 20 leaves per plant and about the same coefficients of variability. The F_2 generation was very variable, and of the five F_3 generations grown two proved as variable as the F_2 , two were of intermediate variability, and one showed a coefficient of variability slightly larger than the parents or F_1 . As selections were grown in F_3 which gave higher and lower leaf averages than the parents, the variability of F_2 must have been germinal. As only about 150 variates were counted and only five F_3 generations grown it is impossible to say definitely how many factors are involved.

If we suppose our parental formulas for leaf number to be 14 AABbCC and 14 DDEEFF, we will obtain a condition in F_1 of 14 AaBbCcDdEeFf or 20 leaves, and a germinal variation of 14 to 26 leaves in F_2 . While this hypothesis may not be correct, the results can be explained by some such means.

In the inheritance of leaf shape of the cross between Havana and Cuban, the conditions are very simple. The data from this cross are given in Table XVI. The F_1 generation is shown to be intermediate in leaf shape and in F_2 there is segregation. Of the three F_3 generations given in the table, all are comparatively

uniform, two having the Havana leaf shape and one the Cuban leaf shape. Two other F_3 generations were grown and although no statistical results can be given we know by observation that one selection had the Cuban leaf shape and the other had a variable leaf shape. These results can probably be explained by the use of a single factor.

It is not assumed that the factorial formulas here given are necessarily correct, as the conditions may be of a more complex nature, but we wish to show that some such mathematical description simplifies the breeding results in a manner that is helpful in actual practice.

GENERAL CONCLUSIONS.

Our results show that the F_1 generations of size crosses in tobacco are as uniform as the parents and of an intermediate value; that there is an increase of variability in F_2 and where sufficient variates are studied, a range of variation equal to the combined range of the parents; that certain F_2 individuals breed true in F_3 , and that others give variabilities ranging in value from the parents to that of the F_2 generation.

These results can be explained in essentially the Mendelian manner — by the segregation of potential characters in the germ cells and their chance recombination — therefore, from the plant breeding standpoint there seems good reason for believing that quantitative characters are inherited in the same manner as qualitative characters.

The production of fixed forms which contain certain desirable plant characters is not, however, a simple problem, due to the large number of factors in which plants of different races differ and because a superficial resemblance does not necessarily mean a genetical resemblance. It is necessary to grow large F_2 generations and to save seed from those plants which most nearly conform to the desired type. Progeny of these F_2 plants should be grown in row tests in F_3 and selection continued in later generations until the desired form has been obtained. The length of time which it takes to produce a uniform type will depend largely on the number of variates which can be grown in F_2 and the number of row tests which can be grown in F_3 .

Quality of cured leaf is a complex character and due to many conditions, environmental as well as inherited. There is also the added difficulty that the quality of leaf must conform to the trade ideals. The experiments here reported indicate that a good quality of leaf can more generally be expected in a hybrid, if the parents are both of high quality, than if one parent is a good variety and the other somewhat lacking.

It should be realized that the production of improved cigar wrapper types is not an easy problem and that desirable results cannot be obtained without the outlay of considerable time and money.

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PLATE I.



a. 403-1-1, Sumatra, averaged 26.2 leaves per plant. New Haven, 1912.



b. Havana type plant, averages about 20 leaves per plant.



c. (403 x 402)-1, F₂ of cross between Sumatra and Havana. This plant could not be distinguished from pure Sumatra. New Haven, 1912.

PLATE III.



a. (403 x 402)-1, F_2 of cross between Sumatra and Havana. Plant of Havana type. New Haven, 1912.



b. (403 x 402)-1, F_2 of cross between Sumatra and Havana. Plant resembling F_1 generation. New Haven, 1912.



c. (403 x 402)-1, a tall vigorous plant of the F_2 of a cross between Sumatra and Havana bearing 30 leaves. New Haven, 1912.



a. (403 x 402)-1, F_2 of cross between Sumatra and Havana. Plant bearing 28 leaves and short internodes. New Haven, 1912.



b. (403 x 402)-1, F_2 of cross between Sumatra and Havana. Plant bearing 19 leaves of Havana character. New Haven, 1912.

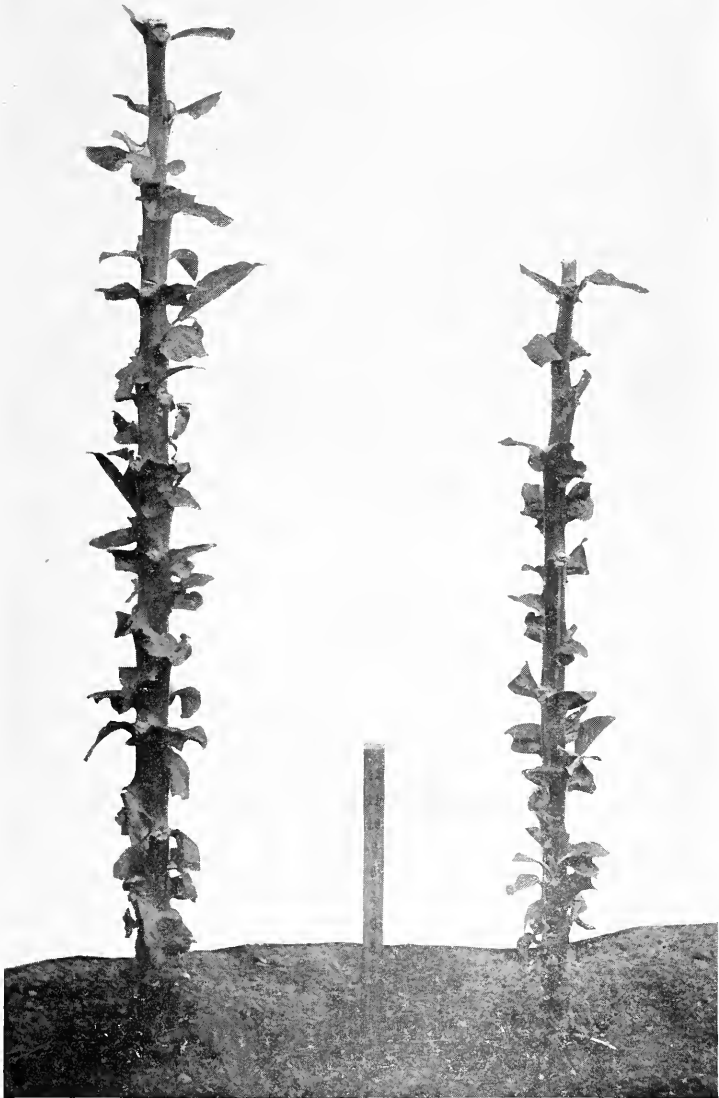
PLATE IV.



a. (403 x 402)-1, an F_2 plant of the cross between Sumatra and Havana, bearing 27 leaves and short internodes. A "Halladay Havana" type. New Haven, 1912.

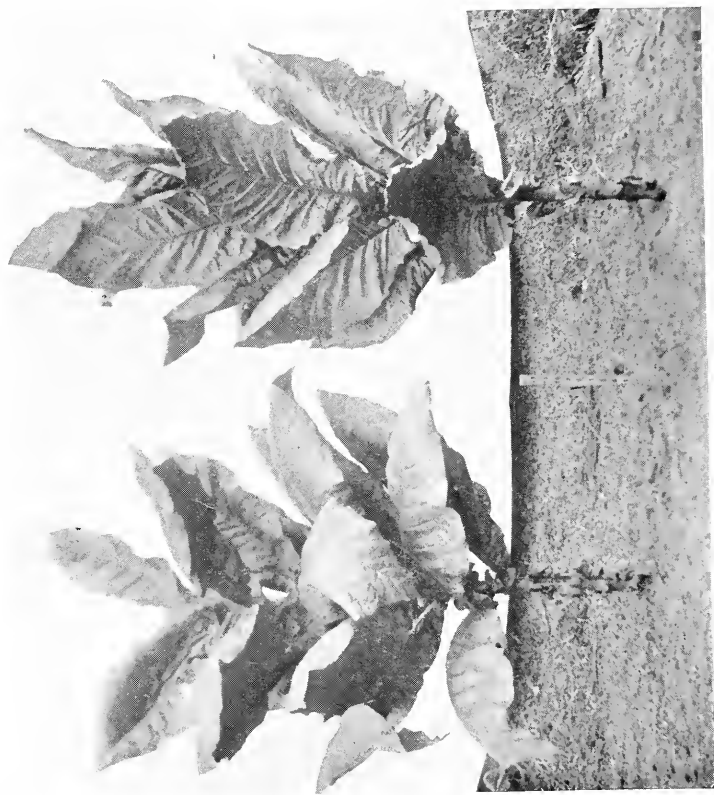


b. (403 x 402)-1, an F_2 plant of the cross between Sumatra and Havana, bearing 26 leaves. Another "Halladay" type. New Haven, 1912.

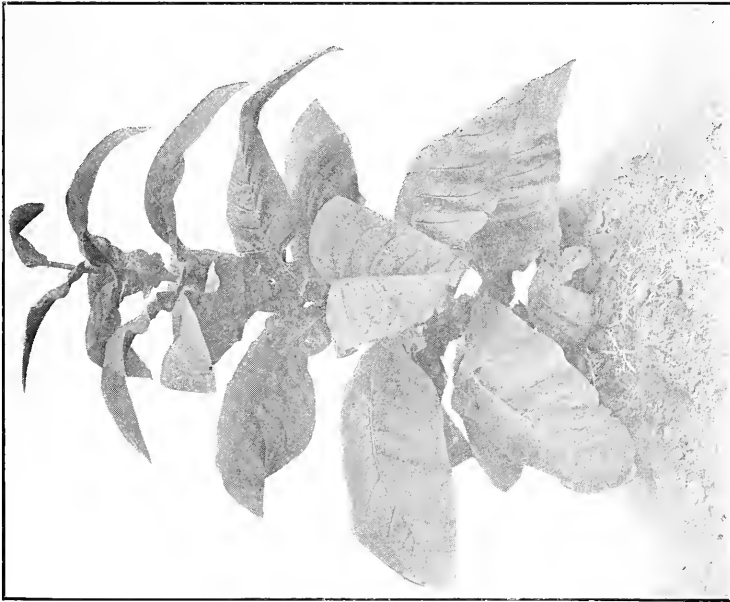


At left, 12-1-1, a vigorous strain and at right, K-1-1-2, non-vigorous strain of Halladay Havana. Bloomfield, 1912.

PLATE VI.



At right (12-2)-1 which has erect, crinkly leaves, and at left (12-1)-1 which bears smooth, drooping leaves. These strains were produced from family No. 12 and are absolutely distinct. Bloomfield, 1912.



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

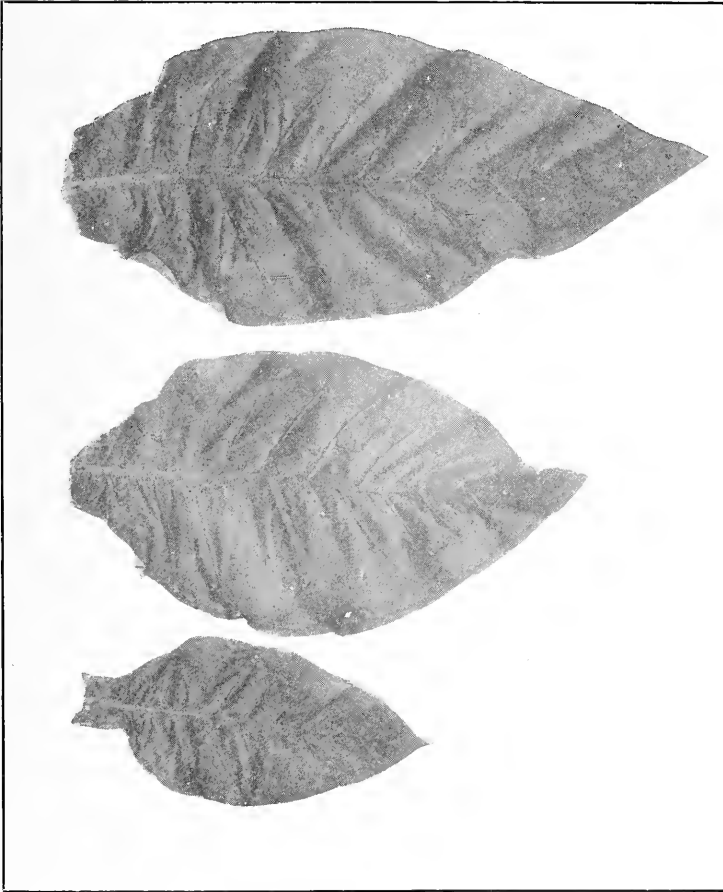


b. (403 x 401)-1-5, an F_3 generation of a cross between Sumatra and Broadleaf which bred true for an intermediate leaf size and for the drooping leaf habit of the Broadleaf, and gave a mean leaf number of $22.0 \pm .08$ and a C.V. of $7.54 \pm .27$. New Haven, 1912.

PLATE VIII.

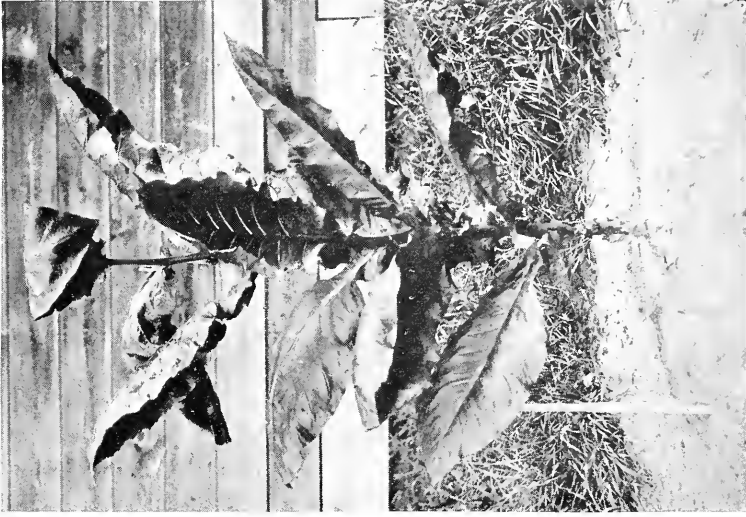


(403 x 401)-1-6, an F_3 generation of a cross between Sumatra and Broadleaf which gave a mean leaf number of $23.9 \pm .08$ and a C.V. of $6.61 \pm .23$. The size of leaf is as yet very variable. New Haven, 1912.

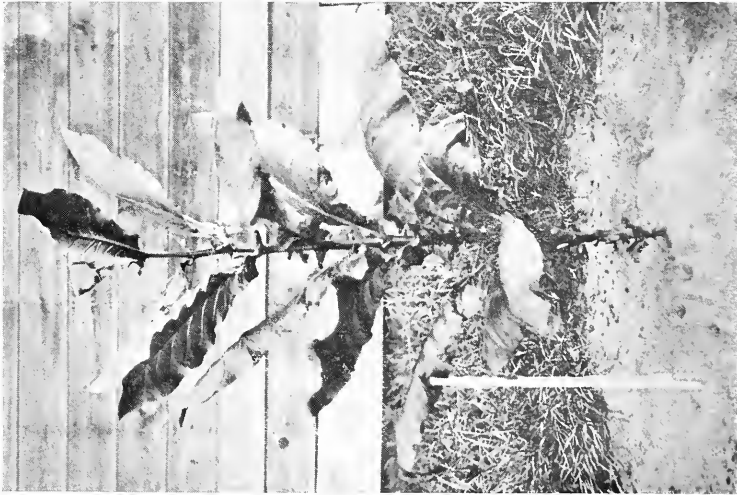


Average middle leaf of No. 403, Sumatra at left, of No. 401, Broadleaf at right and F_1 in center.

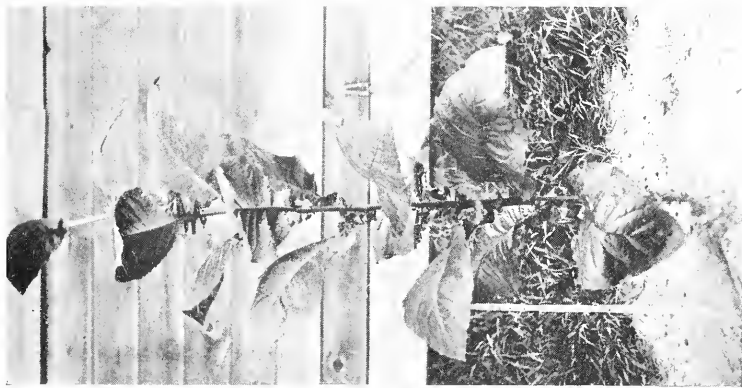
PLATE X.



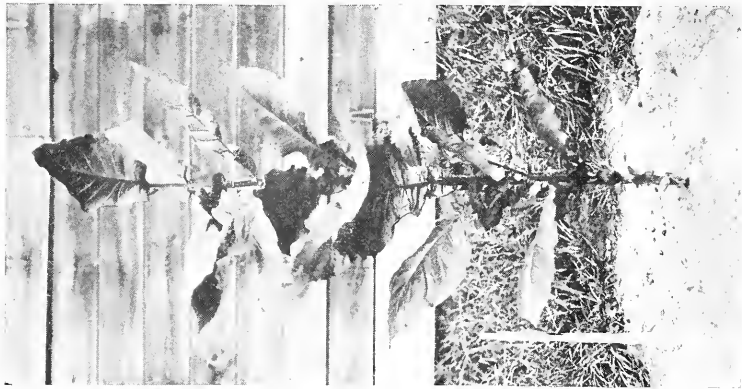
b. (402 x 405)-1-3. An F_2 generation of a cross between Havana and Cuban which gave a mean leaf number of 18.4 and which bred true for the Havana leaf characters. Grown under cloth shade. Bloomfield, 1912.



a. 402-1-1, Havana. Averages about 20 leaves per plant. Grown under cloth shade. Bloomfield, 1912.



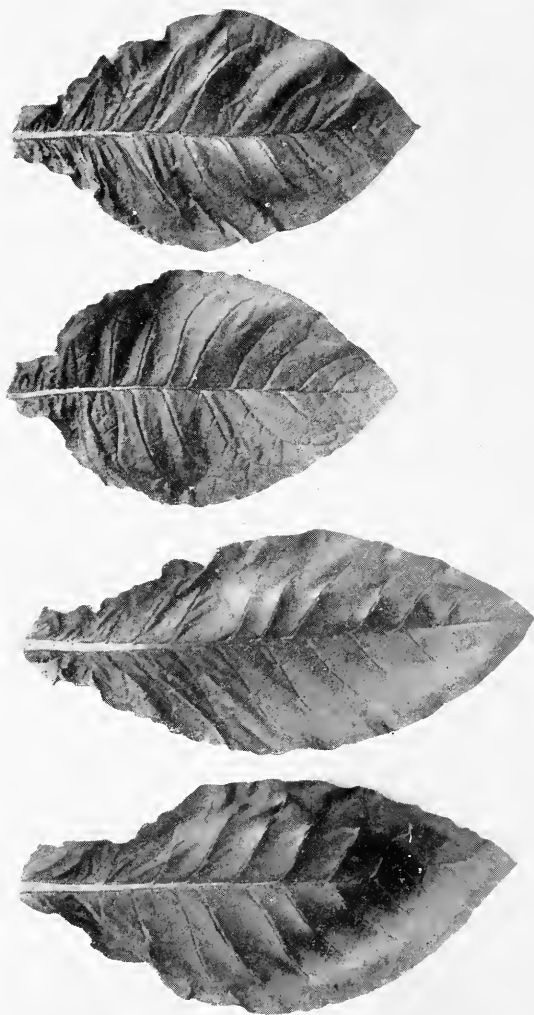
a. 405-1-1, Cuban. Averages about 20 leaves per plant. Grown under cloth shade. Bloomfield, 1912.



b. (402 x 405)-1-2, an F_3 generation of a cross between Havana and Cuban which bred true for the Cuban leaf size and shape but was very variable for leaf number. Grown under cloth shade. Bloomfield, 1912.



c. (402 x 405)-1-5, a 30 leaved plant of the F_3 of a cross between Havana and Cuban. Grown under cloth shade at Bloomfield, 1911. The progeny of this plant gave a mean leaf number of $28.0 \pm .28$ leaves in 1912.



Middle leaves of the F_3 generation plants shown in plates X and XI. From left to right (402 x 405)-1-3, Havana segregate; 402-1-1, Havana; 405-1-1, Cuban; and (402 x 405)-1-2, which bred true for the Cuban leaf size and shape.



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