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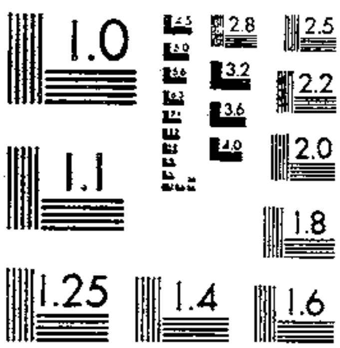

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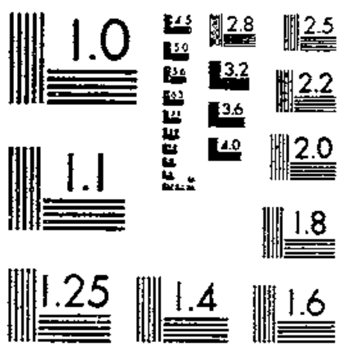

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BREEDING TOBACCO FOR RESISTANCE TO THIELAVIA ROOT ROT

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In Cooperation with the Wisconsin Agricultural Experiment Station

CONTENTS

INTRODUCTION

The black root-rot disease of tobacco caused by *Thielavia basicola* (B. and Br.) Zopf is a common and important disease of tobacco in the United States and in many foreign countries. A remarkable difference in the varietal susceptibility of tobacco to this disease has been shown to exist, and the value of resistant strains in the commercial culture of tobacco has been recognized for some time. Several distinct types of tobacco, however, are grown commercially, and consequently resistant strains of the respective types must necessarily be developed before the standard strains can be replaced. An increasing demand for such resistant strains is anticipated, especially on account of the rapidly growing evidence that the rotation of tobacco with other crops, hitherto regarded as a desirable control measure for black root rot, frequently introduces other factors injurious to the production of the crop.

Some degree of resistance to root rot has apparently been empirically developed within certain types through mass selection of seed by the growers themselves. Some progress has also been made by the selection of chance individuals for resistance and by submitting these to progeny-row trials, but progress by this method is also limited. More rapid and satisfactory progress undoubtedly may be made in most instances by crossing strains most likely to yield the desired results as to resistance, yield, and quality. It is of primary

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importance in such a procedure that the characteristics and degree of resistance of the existing varieties and strains of tobacco and their value for breeding purposes be known. A knowledge of the genetic behavior of the characters of disease resistance in crosses is equally important to the best progress in the development of resistant commercial types.

This bulletin reports an attempt along these lines of tobacco breeding. The relative resistance of a considerable number of commercial varieties has been determined. Some new resistant commercial strains of tobacco which are desirable have been developed, but progress in the more strictly genetical aspects has been more uncertain and incomplete. The general conclusions as to the genetic behavior of disease resistance in tobacco to Thielavia root rot have been set forth elsewhere.[1]

THE THIELAVIA ROOT-ROT DISEASE

The root-rot disease of tobacco is caused by the ascomycetous fungus *Thielavia basicola*. The lesions of this disease are practically confined to the roots, except on young seedlings, where the base of the stalk may be affected. The roots are reduced in number and the function of the remaining ones more or less interfered with, according to the severity of the attack. The result is a starvation of the aerial part of the plant due to reduced food and water supply. The plants are not killed as a direct result of the disease, since a surprisingly small proportion of the normal root system is sufficient to enable the plants to survive, although they may make no appreciable growth during a period of several months in cases of severe attack. On the other hand, growth may be only temporarily interfered with, and no economic injury may result in cases of light attack. Stages intermediate to these extremes are, of course, of more common occurrence. All other conditions being equal, therefore, the relative weight or height of the plants is a good index of the relative amount of disease in a soil infested with black root rot. (Fig. 1.)

In connection with studies on resistance to the Thielavia root-rot disease it becomes of special importance to recognize the influence of environmental conditions on the results secured. In a previous paper[2] it has been shown experimentally that soil temperature is the most important environmental factor affecting the amount of injury resulting from black root rot. Low soil temperatures (18°–22° C.) favor the disease, whereas high soil temperatures (26° and above) greatly reduce or prevent injury. Furthermore, badly diseased plants are able to make a decided recovery as a result of rising soil temperatures. That variations in soil temperatures comparable to the above occur in the field was shown by soil-temperature readings. The average soil temperature for June, July, and August for the year 1915, for instance, was found to be 20.3° C., whereas for the corresponding period in 1916 the average was 27.7°. These

[1] JOHNSON, J. INHERITANCE OF DISEASE RESISTANCE TO THIELAVIA BASICOLA. (Abstract.) Phytopathology 11: 49. 1921.

[2] JOHNSON, J., and HARTMAN, R. E. INFLUENCE OF SOIL ENVIRONMENT ON THE ROOT-ROT OF TOBACCO. Jour. Agr. Research 17: 41–86, illus. 1919.

conditions were clearly reflected in the amount of disease occurring in the field, i. e., heavy infection in 1915 and light infection in 1916.

VARIETAL RESISTANCE

Earlier work, of a preliminary nature, on varietal resistance in tobacco to Thielavia root rot was reported in 1916.[3] Similar trials for the standard American varieties of tobacco were continued for several years thereafter, together with trials for a considerable number of subvarieties or strains. In addition, several foreign varieties

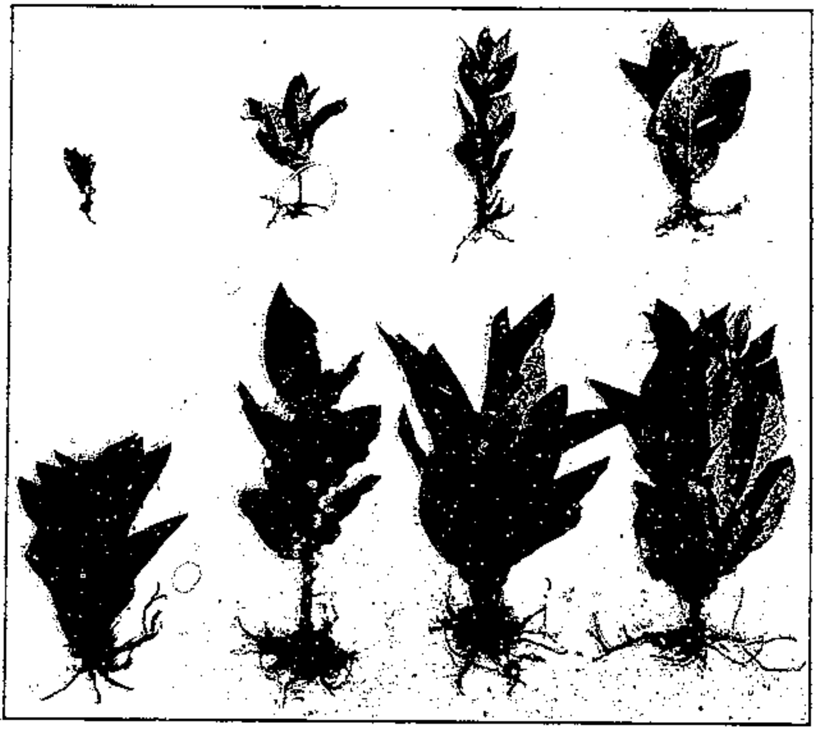

FIGURE 1.—Representative plants of eight varieties of tobacco grown in Thielavia-infested soil, with roots carefully removed from the soil for the purpose of illustrating the correlation between the amount of root rot and the weight and height of the plants

have now been studied sufficiently to be placed in their relative positions for disease resistance. Many of these varieties, furthermore, have been grown in widely different locations, namely, Kentucky, Connecticut, Wisconsin, and Ontario, Canada. In no case has there been any evidence that the inherent resistance of these varieties has been broken down or changed in any way. Furthermore, where soil conditions were uniform the growth of the plants in the trials has been remarkably uniform in the commercial strains tested. The apparent relative changes in behavior which occur in strains from

[3] JOHNSON, J. RESISTANCE IN TOBACCO TO THE ROOT-ROT DISEASE. Phytopathology 6: 167–181, illus. 1916.

year to year may be attributed largely to the influence of environmental factors.

As previously stated, the most important of these environmental factors is the soil temperature. Soil-temperature records over a long period of years are not available, but it is known that these are closely correlated with air temperatures. In Table 1 is shown the distribution of the mean air temperatures at Madison, Wis., for the months of June, July, and August, during a period of years as supplied by the Weather Bureau records. In general, it has been found that the relative resistance of a variety is fairly closely correlated with the mean temperature.

TABLE 1.—*Distribution of mean air temperatures at Madison, Wis., for years shown*

[From records of U. S. Weather Bureau]

Month	Temperature (° F.) and years																
	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	78	80
								1922									
								1920									
				1912	1918			1913									
				1908	1905			1910									
			1927	1907	1904	1914	1925	1899	1901	1923							
June	1928		1924	1906	1897	1909	1900	1898	1893	1919							
	1917	1926	1903	1892	1885	1891	1888	1896	1887	1911							
	1916	1902	1875	1883	1882	1881	1884	1886	1880	1895							
	1915	1889	1860	1863	1878	1879	1876	1871	1859	1894	1921						
	1869	1874	1854	1858	1877	1872	1861	1862	1853	1890	1870	1873	1857				
										1926	1928						
										1925	1917						
										1913	1899	1911		1919			
									1927	1912	1896	1898		1897			
									1922	1908	1895	1893	1923	1894			
July								1920	1918	1907	1892	1888	1914	1881			
							1924	1905	1909	1903	1890	1885	1910	1879			
							1915	1904	1906	1902	1880	1877	1886	1878			
							1882	1884	1900	1889	1873	1875	1876	1874	1887	1921	
						1891	1853	1869	1883	1871	1858	1872	1870	1857	1859	1916	1901
									1928	1926							
									1921	1925							
						1917			1914	1922							
						1912			1892	1913							
						1907	1924	1920	1889	1910	1906						
August						1904	1923	1919	1875	1905	1901						
						1902	1868	1911	1872	1896	1899	1918					
						1897	1891	1908	1871	1882	1894	1910					
					1927	1884	1888	1893	1858	1880	1886	1909					
					1903	1870	1877	1887	1857	1879	1878	1895		1900			
			1915	1885	1890	1869	1861	1863	1853	1874	1873	1876		1881			

Certain other factors, however, tend to upset the uniformity of results from season to season. Late-maturing varieties, for instance, have a better opportunity to recover from the disease and from other unfavorable conditions than the early maturing varieties. (Fig. 2.) Time of planting, seasonal distribution of rainfall, and other soil conditions influence the experimental results in some degree. These influences are best eliminated as far as breeding trials are concerned by repeating the trials over a period of years.

The procedure in the varietal tests has been fairly simple. The seed used has in all cases come from individual self-fertilized plants except when grown for the first time without the previous history being known. In all cases the seedlings have been grown in sterilized soil so as to prevent any root-rot infection in the seed beds, in addition to insuring strong, uniform plants for transplanting. For all ordinary or preliminary trials about 50 plants of each variety or strain were transplanted in the field and the final green weights of 25 consecutive plants from such rows determined. Usually these plantings were duplicated in the same or in other infested fields for comparison during the same season. Even more important, however, is the duplication of the planting on uninfested soil, which has usually been on fertile plots not previously grown to tobacco. Different varieties of tobacco vary greatly in their habit of growth and in the yield produced, so that it has been necessary always to take into consideration the normal plant for each strain grown under similar seasonal conditions although under different soil conditions.

The relative resistance of the various types in any one experiment is computed on the basis of their yields on infested and uninfested

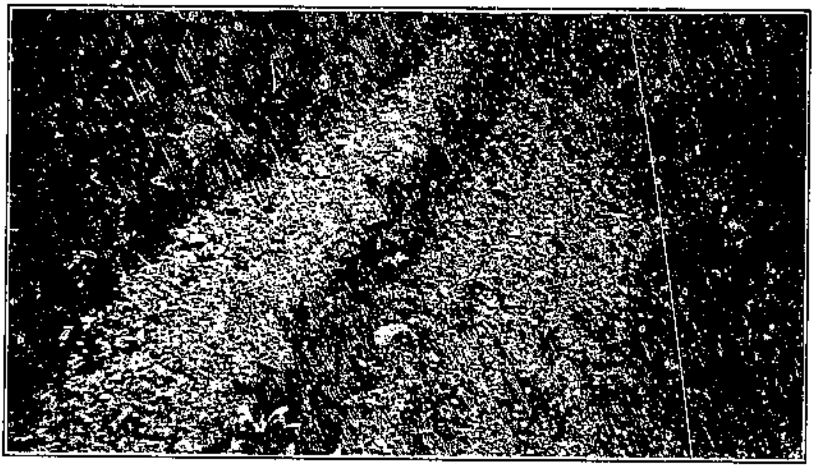

FIGURE 2.—An early maturing susceptible tobacco variety (Chilean) topping out in center row, compared with a late-maturing susceptible variety (White Burley), at right. The development of the Chilean variety is already limited, but the Burley variety still has some possibility of further growth

soil, i. e., relative resistance is the percentage of normal yield. Estimates of relative growth were also made at frequent intervals throughout the season, and although these data are too voluminous to present they serve to show the relative behavior of the types during the growing period. This may be far from constant, thus accounting in large measure for the change in the relative position of resistance in certain varieties as determined by final weights.

The results of seven years' trials with the common American varieties are shown in Table 2. If the relative resistance for each year is noted it will be seen that a very considerable range exists, the minimum being 3.8 per cent for Maryland Broadleaf in 1915, and the maximum being reached by the Little Dutch variety in 1921 with 84.3 per cent. The table, however, shows that while the relative resistance of the Maryland Broadleaf was 3.8 per cent in the cool season of 1915 it reached the high figure of 51.6 per cent in the warm season of 1921. The Little Dutch, on the other hand, with a maximum of 84.3 per cent in 1921, reached the high minimum of 50.3 per cent in 1915. Manifestly we can not compare the relative resistance shown in one season with that shown in another without taking soil environmental conditions into consideration. The figures for any one year are, however, to be regarded as quite significant in indicating relative resistance, at least for that year and for other years having similar seasonal conditions. From both the genetic and economic standpoints, the relative resistance secured in a normal year is to be regarded as being most significant, and the relative resistance in the years 1917 or 1918 is more likely to represent the normal genetic behavior of the various types, as regards resistance, than is that in the years 1915 or 1916.

TABLE 2.—*Relative resistance of some of the principal varieties of tobacco to Thielavia root rot during different seasons*

Variety	Relative resistance during—							
	1915	1916	1917	1918	1919	1920	1921	Average
White Burley	4.5	19.7	4.7	11.3	10.7	11.1	32.2	13.4
Maryland Broadleaf	3.8	8.2	12.0	16.9	27.2	19.8	51.6	19.9
Pryor	4.2	13.0	24.3	27.2	44.0	26.3	55.2	27.7
Orinoco	5.2	16.7	19.2	26.6	50.8	34.8	58.6	30.2
Connecticut Havana	46.1	52.6	32.6	42.9	52.0	28.2	65.5	45.7
Pennsylvania Broadleaf	16.9	44.0	36.4	58.4	48.8	50.2	72.1	46.7
Connecticut Broadleaf		40.0	32.8	60.5	43.5	49.0	64.2	48.5
Little Dutch	50.3	70.0	55.3	58.9	58.9	53.0	84.3	61.7
Shade-Grown Cuban			51.6	77.4	63.3	44.5	79.7	63.3

In the years 1917 and 1918 the White Burley was the most susceptible variety, followed by varieties showing increasing resistance in approximately the following order: Maryland Broadleaf, Orinoco, Pryor, Connecticut Havana, Connecticut Broadleaf, Pennsylvania Broadleaf, Little Dutch, Shade-Grown Cuban. If the relative resistance over the entire period of the tests is averaged a fairly relative position of the varieties is obtained. (Table 2.) It should be noted in this connection that although standard strains of the various basic types have been used in these tests it is not unlikely that in the case of a few of them other commercial strains of the same type may be more or less resistant than the ones used. This matter would have to be tested by growing a large collection of the various strains from each tobacco district. This has been done in connection with these experiments with only certain of the varieties, especially the White Burley, Havana Seed, and Pryor groups. In these varieties no striking strain differences in the ordinary commercial varieties morphologically true to type have been found. For purposes of ordinary comparison, the basic strains and their subvarieties can be roughly divided into five classes, namely: (1) Very resistant, (2) resistant, (3) intermediate, (4) susceptible, and (5) very susceptible. Such a classification is illustrated in Table 3 for some of the main varieties and subvarieties tested, together with other miscellaneous varieties. This list could be considerably lengthened, but would not be significant without an explanation of the commercial or genetical relationships of the strains.

TABLE 3.—*Varieties and strains of tobacco classified according to resistance to root rot*

Very resistant	Resistant	Intermediate	Susceptible	Very susceptible
Shade-Grown Cuban.	Connecticut Broadleaf.	Havana Seed.	Maryland Broadleaf.	White Burley (14 strains).
Little Dutch.	Resistant White Burley.	Comstock Spanish.	Orinoco (6 strains).	Chilean.
Halladay Havana.	Wisconsin No. 1801.	Zimmer Spanish.	Pryor (12 strains).	
Havana No. 142.	Porto Rican.	Connecticut Havana No. 38.	Big Cuban.	
Brasile Beneventano (Italy).	Yara Cuban.	Pennsylvania Broadleaf.	Maryland Mammoth.	
Xanthia (Turkey).[1]	Wisconsin No. 2901.	Stewart Cuban.	Sumatra.	
	Northern Hybrid.	Brazilian.	Mexican (3 strains).	
		Bagdad (Turkey).		

[1] Practically immune.

GENETIC BEHAVIOR OF RESISTANT CHARACTER

The studies on crosses between resistant and susceptible types of tobacco have been carried on for the most part simultaneously with the varietal studies and in the same fields. The work was done chiefly in the years 1917 to 1920, inclusive, and the seasons of extreme temperature—1915, 1916, and 1921—therefore have been avoided. That the soil used was thoroughly infested with Thielavia root rot and at the same time was in other respects in a good state of fertility is evident from the results obtained from the variety studies.

The crosses were made in the usual manner, and since the varieties crossed differ markedly in various morphological characteristics no difficulty has been experienced in readily distinguishing them. That the parents used were pure strains with respect to the resistant character was evident from their uniformity of growth on infested soil in repeated trials.

When the seedlings (grown on sterilized soil) attained the proper size in the seed beds they were transplanted to progeny rows in the field, strains on which comparative results were most important being placed in close proximity. On account of the number of selections grown each season, it has not been possible to grow many of them in great numbers. Usually only 50 to 60 plants from each selection were employed in the trials, except in the F_2 generations, in which 200 or more were usually planted. In many cases, however, the plantings on infested soil were duplicated, together with controls on uninfested soil.

It is evident that in a disease such as Thielavia root rot no practical method of determining the actual amount of infection on the roots is available, and that even if there were, by its application the usefulness of the plant for further study and seed production would be lost. It has been repeatedly noted that the growth of the plant is an excellent criterion of the development of disease, and in the variety tests the green weight has been used as a basis of calculation.

In the inheritance studies with crosses it has not been advisable to sacrifice potentially important seed plants by harvesting, and consequently plant height has been used as a basis of measurement for resistance. While this method has obvious limitations in cases where the differences are not marked, it has been found applicable in cases where the extremes of the parents differ by as much as 2 or 3 feet in height on infested soil. Measurements were made at about the time when the majority of the plants to be compared were well headed out. Many of the selections, of course, never headed out, and in this case the height from the soil line to the bud was recorded. In the case of plants in the flowering stage the height to the "crow's-foot," i. e., the base of the main inflorescence, was taken. The plants in all cases were measured to the nearest inch and were then placed in 5-inch classes in the frequency-distribution tables.

For convenience the plants were numbered by a system illustrated as follows: White Burley, 6; Little Dutch, 3; the F_1 generation then being 6×3 or 3×6, the female parent being given first. The F_2 generations were designated as 631, 632, etc., for the separate crosses

FIGURE 3.—Growth of susceptible White Burley parent (A), resistant Little Dutch parent (C), and the F_1 generation of the cross between the two (B) on Thielavia-infested soil. Compare with Figure 4

made. The types selected for growing in the F_3 were denoted by letters of the alphabet following 63, as 63–A, 63–B, etc. The succeeding generations were designated by adding a digit for each generation, i. e., F_4 as 63–A–1, etc.

LITTLE DUTCH AND WHITE BURLEY CROSS

The major portion of the genetic studies on crosses between varieties of tobacco resistant and susceptible to the Thielavia root-rot disease has been concerned with the cross between the Little Dutch (resistant) and White Burley (susceptible). (Fig. 3.) The Little Dutch is a very vigorous-growing, narrow-leaved type with an upright habit of growth, and was at one time grown extensively in Ohio as a filler type. The White Burley strain used in the first crosses was known as Halley's White Burley, a semiupright, vigorous, large type, but, like most Burley types, not growing so rapidly nor maturing so soon as the Little Dutch, though finally yielding as well on an average, and normally reaching a greater height in the absence of disease.

In Table 4 is compiled a portion of the data secured in 1918 for the Little Dutch and White Burley cross. The calculated means for height, the standard deviations, and the coefficients of variability are given on both infested and uninfested soil for the parents, F_1, F_2, and for two F_3 generations.

TABLE 4.—*Height of plants in the White Burley (susceptible) and Little Dutch (resistant) cross on uninfested and Thielavia-infested soil in 1918*

Designation	Generation	Uninfested soil				Infested soil			
		Plants	Mean height	Standard deviation	Coefficient of variability	Plants	Mean height	Standard deviation	Coefficient of variability
		No.	*Inches*			*No.*	*Inches*		
White Burley (6)	P_1	100	[1] 48.6±0.8	5.0±0.2	10.3±0.5	46	3.0±0.0	0	0
Little Dutch (3)	P_2	122	41.9±0.4	6.7±0.3	16.1±0.7	37	34.5±0.5	4.5±0.3	13.0±1.0
6 × 3	F_1	111	45.1±0.7	11.1±0.5	24.7±1.2	50	26.4±0.7	7.6±0.5	28.8±1.8
631	F_2	121	44.8±0.6	10.8±0.5	24.1±1.1	328	19.2±0.4	10.5±0.3	54.7±1.8
63-H	F_3	111	44.0±0.5	8.4±0.4	19.2±0.9	50	26.5±0.6	6.5±0.4	24.5±1.7
63-R	F_3	93	48.7±0.6	8.7±0.4	17.9±0.9	56	4.4±0.8	2.9±0.2	65.0±5.9
63-B	F_3	----	----	----	----	57	39.2±0.7	7.5±0.5	19.1±1.2

[1] Measured one week later than others in order to secure approximately the same stage of maturity.

In 1918 the planting on uninfested soil was grown under somewhat unfavorable conditions, and the variation is somewhat above normal. The measurements on the White Burley variety were made later that year than those on the other varieties, on account of the fact that White Burley is a somewhat later maturing type. The true condition is represented more accurately by this delayed measurement than by the earlier measurement made in 1919, as shown in Table 5. The terminal inflorescence represents almost one-third of the height of the plant and develops quickly in healthy, vigorous plants when once the flowering stage has been reached. On uninfested soil the White Burley variety normally is considerably taller than the Little Dutch type, with the F_1 intermediate in height, but quite as large a type as the Burley in other respects. In general, however, the difference in growth as expressed by the height of the plants is comparatively small in the parents and in the F_1, F_2, and F_3 generations grown on uninfested soil. (Fig. 4.) Striking morphological segregation occurs in the F_2 and succeeding generations in all these crosses, but this is much less commonly expressed in height of plant than in shape and size of leaf and habit of growth. No serious discrepancies are to be expected, therefore, in using plant height as a measure of resistance on infested soil as a consequence of morphological variation.

TABLE 5.—*Height of plants in the White Burley (susceptible) and Little Dutch (resistant) cross on uninfested and Thielavia-infested soil in 1919*

Designation	Generation	Uninfested soil				Infested soil			
		Plants	Mean height	Standard deviation	Coefficient of variability	Plants	Mean height	Standard deviation	Coefficient of variability
		No.	*Inches*			*No.*	*Inches*		
White Burley (6)	P_1	52	[1] 29.0±0.6	6.3±0.4	21.7±1.5	45	6.5±0.4	3.6±0.2	55.2±4.9
Little Dutch (3)	P_1	71	45.3±0.3	3.2±0.2	7.1±0.4	43	34.1±0.9	8.6±0.6	25.3±1.9
6 × 3	F_1	73	47.4±0.7	8.7±0.5	18.9±1.4	47	15.5±0.6	6.3±0.4	40.6±3.3
631	F_2	284	43.4±0.3	8.6±0.2	19.9±0.6	418	25.4±0.4	10.9±0.2	42.9±1.2
63-J	F_3	74	44.2±0.7	9.2±0.5	20.9±1.2	53	27.3±0.8	8.6±0.6	31.6±2.3
63-O	F_3	68	46.8±0.6	7.5±0.4	16.0±0.9	50	14.1±0.6	6.7±0.4	47.5±3.9

[1] Slow growing, not topped out. Mean 63.4 inches two weeks later.

By comparing the growth of these strains on infested soil as given in Table 4 it may be seen that the White Burley parent did not extend beyond the 3-inch class, as compared with 34.5 inches

FIGURE 4.—The growth of the susceptible White Burley (A), the resistant Little Dutch (B), and the F_1 generation of the cross between these on soil free from disease (C). Compare with Figure 3

for the Little Dutch parent, a difference in height of over 2½ feet. The F_1 is intermediate in height, as is the F_2, but the latter shows a considerably higher coefficient of variability. One F_3 selection (63–R) is almost as susceptible as the susceptible White Burley parent, whereas on uninfested soil it is a vigorously growing type. Another F_3 selection (63–B) is, on the other hand, more resistant than the most resistant parent. The standard deviations are limited in their significance in a comparison of the variations on uninfested soil with those on infested soil. On uninfested soil the normal fluctuating variation of large, rapidly growing, healthy plants is obtained in the parent types, together with that which may be due to heterozygosis for height in the crosses.

In the infested soil the additional variation due to disease is introduced, but with the greatly reduced vigor of growth (from a height of 44.8 to 19.2 inches in the F_2) it is to be expected that the variation due strictly to ordinary heterozygosity for height is correspondingly reduced, whereas that due to differences in resistance is predominant. (Fig. 5.) This can best be illustrated by the standard deviation for 63–R, which is 8.7 ± 0.4 on uninfested soil but only 2.9 ± 0.2 on infested soil. Manifestly the inherent normal heterozygosity for height is as great on the infested as on the uninfested soil, but as a result of the susceptibility to root rot of the variety all other variation is overshadowed. Theoretically, the coefficient of variability of these types on infested and uninfested soil more accurately represents the true state of affairs, because it takes into consideration the relative mean heights. With very susceptible types, however, the coefficient of variability apparently gives too much weight to the relative variability actually occurring, and

FIGURE 5.—A portion of a row of the F_2 generation of the White Burley and Little Dutch cross, illustrating the degree of segregation for disease

conclusions can be drawn from these statistical methods only in so far as they do not interfere with the actual biological principles involved.

Results of a nature similar to those shown in Table 4 are presented in Table 5 for the 1919 season. The measurements for the White Burley parent on uninfested soil are again not strictly comparable on account of the delayed flowering of this variety.

The mean heights of some F_3 and succeeding generations in comparison with the parental strains are shown in Tables 6 and 7. It may be noted that certain of these strains, F_3 to F_6, are continuing to vary and may be modified in resistance by continued selection, as, for instance, strains 63–C and 63–D. Strains more resistant than the resistant parent and fairly uniform in this characteristic, as, for example, strain 63–K–1, may be secured as early as the F_3 or F_4 generation. (Fig. 6.) On the other hand, strains as susceptible as the most susceptible parent may be isolated, as is illustrated by strain 63 D. That such strains breed approximately true to type is indicated by the behavior of the F_4 and F_5 generations of this strain.

FIGURE [illegible].—Growth of F and F generation strains of the White Burley and Little Dutch cross on root-rot-infested soil. Note the early tendency toward uniformity [illegible]

TABLE 6.—*Height of plants in the White Burley (susceptible) and the Little Dutch (resistant) cross grown on Thielavia-infested soil in 1929*

Designation	Generation	Plants	Mean height	Standard deviation	Designation	Generation	Plants	Mean height	Standard deviation
		No.	*Inches*				*No.*	*Inches*	
White Burley	P	[illegible]	[illegible]	[illegible]	63 C	F	44	20.9±1.1	11.2±0.8
Little Dutch	P	24	[illegible]	[illegible]	63 C 2	F_4	44	19.2±1.0	10.4±0.7
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	63 C 22	F	46	11.9±0.7	7.6±0.5
[illegible]	[illegible]	72	[illegible]	[illegible]	63 D 4	F_4	44	10.4±0.7	6.7±0.5
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	63 K 1	F_4	49	10.1±0.3	3.5±0.2
[illegible]	[illegible]	250	[illegible]	[illegible]					

TABLE 7.—*Height of plants in the Little Dutch (resistant) and White Burley (susceptible) cross grown on Thielavia-infested soil in 1929*

Designation	Generation	Plants	Mean height	Designation	Generation	Plants	Mean height
		Number	*Inches*			*Number*	*Inches*
Little Dutch	P	[illegible]	30.3	63 C 25	F	50	21.1
White Burley	P	[illegible]	[illegible]	63 D	F	47	14.5
[illegible]	F_1	[illegible]	[illegible]	63 D [illegible]	F_4	45	24.0
[illegible]	F_2	[illegible]	16.1	63 D 12	F_5	48	33.8
[illegible]	[illegible]	[illegible]	[illegible]	63 D 122	F_6	51	41.2
[illegible]	[illegible]	[illegible]	[illegible]	63 G	F	52	4.7
[illegible]	[illegible]	[illegible]	[illegible]	63 G [illegible]	F_4	26	4.1
[illegible]	[illegible]	[illegible]	[illegible]	63 G 17	F_5	52	6.2
[illegible]	[illegible]	78	[illegible]	63 P	F	53	17.8
[illegible]	[illegible]	54	14.6				

It appears from these and other data obtained, as well as from observational evidence, that some resistant individuals breeding true can be obtained from the F_2, but that the majority of selections from this generation are variable in this respect. Selected susceptible individuals from F_2 or succeeding generations yield only susceptible strains, as far as observations have gone in this cross. The evidence, therefore, seems to indicate that resistance is the dominant factor and susceptibility the recessive factor in relation to Thielavia root rot. No evidence of segregation in any simple Mendelian ratio was evident in this case.

The White Burley variety of tobacco used in this cross differs very strikingly from other varieties of tobacco in that the plant is normally much lighter in color, often becoming yellow or "white" as

FIGURE 7.—Fourth-generation families of the White Burley and Little Dutch cross. Note the combination of the resistant character of the Little Dutch with the "white" character of the Burley in the rows to the right. Susceptible strains in the foreground

it nears maturity, as compared with the ordinary varieties of tobacco. This low-chlorophyll-content type is completely obscured by the dominant normal green condition in the F_1. In the F_2 the ratio of "white" to "green" is approximately 1 to 25. The whites always reproduce whites, and the white character is, therefore, the recessive condition. This interesting inheritance of plant color in tobacco has not been studied in detail in the present connection. Resistant White Burley types are readily secured in the F_2 generation, and, while those selected in this case possessed no commercial value, the results suggest the origin of resistant White Burley strains in the field[4] and demonstrate the possibilities of combining resistance with other commercial characters of tobacco. (Fig. 7.)

[4] JOHNSON, J. Op. cit. (See footnote 3.)

OTHER CROSSES OF RESISTANT AND SUSCEPTIBLE VARIETIES

The data presented for the Little Dutch and White Burley cross are supported by the results obtained from several other crosses between resistant and susceptible types. Some of the results of a cross between Connecticut Broadleaf (semiresistant) and White Burley (susceptible) are shown in Table 8. The mean height for the Connecticut Broadleaf variety on infested soil is 37.1 inches, as compared with only 3.6 inches for the White Burley variety.

The F_1 generation, with a mean of 14.5 inches, more nearly approaches the intermediate condition than the mean of either parent. The range of variation in the F_2 generation extends almost to the extremes of the two parents. This F_2 generation is, on the whole, more susceptible than the F_2 generations of the Little Dutch cross with White Burley, indicating that the Connecticut Broadleaf variety, as is to be expected, is not able to transmit as high a degree of resistance in hybridization as the Little Dutch variety.

TABLE 8.—*Height of plants in the Connecticut Broadleaf (resistant) and White Burley (susceptible) cross grown on Thielavia-infested soil in 1918*

Designation	Generation	Plants	Mean height	Designation	Generation	Plants	Mean height
		Number	*Inches*			*Number*	*Inches*
Connecticut Broadleaf (4)	P_1	52	37.1	64-C-2	F_4	57	9.3
White Burley (6)	P_2	53	3.6	64-C-23	F_5	47	7.7
6 × 4	F_1	55	14.5	64-K	F_3	55	16.7
641	F_2	248	14.1	64-L	F_3	50	8.1
64-B-11	F_3	49	26.4	64-N	F_3	48	16.3
64-C	F_3	57	9.0	64-R	F_3	41	30.9

The most resistant plants of the F_2 generation were selfed and grown in the F_3, but none of those selected reached the degree of resistance of the resistant parent 64-R, the nearest approach being made with a mean height of 30.9 inches. Strain 64-C possessed the White Burley character of chlorophyll color and was quite susceptible. Further selection for resistance in the F_3 and F_4 generations failed to increase the relative resistance.

The remainder of the crosses made between resistant and susceptible types were made largely with the purpose of developing resistant commercial varieties of tobacco. This naturally involved considerably more attention to the other desirable characteristics of tobacco in the respective types and less attention to the behavior of inheritance. A general similarity, however, to the results previously described was observed in the following crosses:

Resistant White Burley×White Burley (susceptible).
Resistant Wisconsin strain 2901×Connecticut Havana No. 38 (intermediate).
Resistant Wisconsin strain 1207×Connecticut Havana No. 38 (intermediate).
Resistant Wisconsin strain 1207×Yellow Pryor (susceptible).
Resistant Shade Cuban×Big Cuban (susceptible).
Resistant White Burley×Orinoco (susceptible).

The statistical data secured upon the inheritance in these crosses are too limited to be profitably presented. The first two crosses named have yielded commercial varieties, however, which are briefly described in the following pages. (Fig. 8.)

RESISTANT STAND-UP WHITE BURLEY

The selection of resistant White Burley strains for commercial purposes has been discussed in an earlier paper.[5] About the time that the earlier resistant strain of White Burley was introduced, "stand-up" or erect-leaved strains of Burley were replacing the original drooping or pendent-leaf strains, to which the original resistant Burley belonged. It was consequently desirable to develop a resistant strain of stand-up White Burley. Field selections from standard stand-up strains offered no hope of a resistant strain. A strain of drooping-leaved resistant White Burley was, therefore, crossed with a strain of susceptible stand-up White Burley (Judy's Pride), and selections were made in the F_2 and succeeding generations for a resistant stand-up White Burley. (Figs. 8 and 9.) Several apparently desirable strains were secured, and the best one of these, all factors being considered, was finally

FIGURE 8.—A drooping-leaved resistant White Burley strain (A), a stand-up susceptible White Burley strain (C), and the F_1 generation of the cross between these (B)

distributed for trial to Burley growers in Kentucky, Ohio, and Canada. This strain may be grown for several years on the same land as far as Thielavia is concerned, whereas ordinary Burley, owing to its susceptibility, would prove a complete failure. Objection to the thinness of the leaf in this strain has been offered in some instances, but excellent crops as to both yield and quality have been reported in others. This strain is now commonly grown in the Burley district of Canada.

The development of additional new strains of root-rot resistant White Burley of commercial value may be expected to come in the future from various sources. It is to be expected, however, that these may vary considerably in the actual degree of resistance exhibited (fig. 10) as well as in relative yield and quality. It will then remain to determine by careful comparative trials, made under

[5] JOHNSON, J., and MILTON, R. H. STRAINS OF WHITE BURLEY TOBACCO RESISTANT TO ROOT-ROT. U. S. Dept. Agr. Bul. 765, 11 p., illus. 1919.

different soil and seasonal conditions, the relative commercial merits of such strains.

RESISTANT HAVANA NO. 142

The Havana Seed variety of tobacco, a type commonly grown in Wisconsin, the Connecticut Valley, and to some extent in New York and Pennsylvania, is fairly susceptible to Thielavia root rot.[6] Repeated efforts were made to secure a resistant strain of this variety of tobacco by field selection, but the resistant strains secured were usually undesirable as to habit of growth of the plant or as to quality of leaf produced. One of these strains, No. 1801, became quite generally grown in Wisconsin under the name of "root-rot resistant cigar binder." This strain was, however, only moderately resistant and met with some objections as to quality. Its distribution, therefore, was discontinued, although it was at one time grown fairly extensively in Wisconsin and is still being grown on a small scale.

FIGURE 9.—Progeny row trials of strains of White Burley

As a consequence of the studies on the crosses between susceptible and resistant strains, it became evident that the most rapid progress in the development of a resistant Havana Seed strain could be made by crossing the latter with the most promising of the undesirable resistant strains. A desirable strain of Havana Seed, known as Connecticut Havana No. 38, previously developed in Wisconsin and widely grown in that State, was crossed with two resistant selections, strains 1207 and 2901. The latter, which was a selection from a strain of seed known as Page's Comstock, but which was quite dissimilar to the well-known Comstock Spanish strain of Wisconsin, proved to be the most desirable parent, and selections in the succeed-

[6] JOHNSON, J. Op. cit. (See footnote 3.)

ing generations were continued largely from this cross. Several strains even more resistant than the resistant parent, with greatly improved habit of growth and leaf number, were secured.

FIGURE 10.—A, A resistant stand-up White Burley strain; B, a susceptible stand-up White Burley strain; C, a so-called resistant strain of Burley distributed commercially by certain seed growers

A few years' trial indicated that strain No. 142, everything being considered, was the most desirable. This strain was consequently distributed to a few growers and was favorably received. The culture of the strain spread very rapidly in Wisconsin and has met with considerable approval in the Connecticut Valley. Havana No. 142 is somewhat later in maturing than Havana Seed, but if it is planted sufficiently early on old tobacco land, for which it is intended, maturity will be reached under ordinary circumstances. On Thielavia-infested soil the strain will greatly outyield ordinary Havana Seed. (Fig. 11.) It has a distinct advantage in that it permits repeated culture of tobacco on the same land, and thereby the possible injurious effects of crop rotation on tobacco are avoided.

DISCUSSION OF RESULTS

It has been shown that varieties of tobacco differ greatly in their degree of resistance to the root-rot disease caused by *Thielavia basicola.* This difference is of such magnitude that it was believed at the outset that it might offer a good opportunity for the study of the inheritance of disease resistance. Certain disadvantages however exist, the most important being the necessity for using an indirect measure of the amount of disease present, the influence of

FIGURE 11.—Connecticut Havana No. 38 (A), the parent strain, with an intermediate degree of resistance, growing on Thielavia-infested soil, in comparison with the very resistant Havana No. 142 strain (B), now grown commercially on an extensive scale

time of flowering or maturity on such measurements, and the influence of environmental conditions, especially soil temperature, on the development of the disease. Similar influences are, of course, encountered to a greater or lesser extent in inheritance studies of all quantitative characters. While these interferences are reflected throughout the data, it is believed that the results secured express satisfactorily the behavior of the root-rot resistant character in tobacco.

The crosses between resistant and susceptible types have in all cases shown the first generation to be more or less intermediate in resistance. The prevailing environmental conditions may naturally influence the relative resistance of the F_1 as it does that of the parents. The second generation of crosses between resistant and susceptible varieties breaks up into types of varying degrees of resistance, certain individuals being as resistant as or more resistant than the resistant parent, and others as susceptible as the susceptible parent. Almost the entire population of individuals is, however, between these extremes. New combinations of the resistant character with other plant characters naturally occur, so that it is possible, by selection, to secure plants of the general type of the susceptible parent, having in addition the resistant factor of the other parent. In the third generation certain individual selections will continue to vary in the same manner as the F_2, whereas others apparently breed true for resistance. Susceptibility appears to be the recessive condition.

During the several seasons in which these crosses have been grown no evidence has been obtained that would indicate a segregation according to any simple Mendelian ratio. The hypothesis of multiple factors as propounded by Nilsson-Ehle [7] and others for the inheritance of certain quantitative characters seems to apply in the case of the inheritance of resistance to Thielavia root rot in tobacco. The inheritance of disease resistance in tobacco is, therefore, much like that found in recent years to occur in the case of many other hosts.

While much remains to be done in the way of a more detailed study of the genetic aspects of disease resistance in tobacco, the results secured in this investigation have demonstrated some of the methods and possibilities relative to the development of root-rot resistant commercial strains of tobacco. That such a line of endeavor is worthy of the effort is illustrated by the development of two strains of tobacco, namely, the root-rot resistant Havana No. 142 and the resistant stand-up White Burley, both of which are extensively grown on a commercial scale. The present understanding of the relative resistance of tobacco varieties, some of which, like Xanthia, are practically immune to root rot, together with a rough idea of the mode of inheritance, the relation of environment to the disease, and the nature of this resistance as suggested by the histological studies made by Conant [8] in this laboratory, should form a basis for more complete genetic researches on disease resistance in tobacco.

SUMMARY

The relative resistance to Thielavia root rot of most of the important commercial varieties and strains of tobacco grown in the United States and in many foreign countries has been studied. Many of these varieties have been placed in one of five classes according to their resistance to the disease.

Environmental conditions, especially soil temperature, influence to a decided extent the apparent relative resistance of any variety to the root-rot disease, low temperatures (18°–22° C.) favoring the disease and high temperatures (above 26°) being unfavorable to it.

The time of maturity of a variety also influences the apparent relative resistance. Early maturing susceptible varieties are usually most seriously affected. Late-maturing susceptible varieties are more likely to recover partially from the effects of the disease.

While these facts do not in any way affect the actual genetic resistance or susceptibility of a variety, it is important that they be taken into consideration in drawing conclusions as to the genetic

[7] NILSSON-EHLE, H. KREUZUNGSUNTERSUCHUNGEN AN HAFER UND WEIZEN. Lunds Univ. Arsskr. (n. F. Afd. 2) 7: 57–82. 1911.

[8] CONANT, G. H. HISTOLOGICAL STUDIES OF RESISTANCE IN TOBACCO TO THIELAVIA BASICOLA. Amer. Jour. Bot. 14: 457–480, illus. 1927.

resistance or susceptibility of varieties or crosses in experimental trials.

The first generation of a cross between root-rot resistant and susceptible types is intermediate in resistance. The second generation yields individuals of all grades of resistance from those even more resistant than the most resistant parent to others as susceptible as the susceptible parent.

In the third generation certain families continue to vary in respect to resistance, while other families apparently breed true for this character. Susceptible F_2 individuals, especially, breed true for susceptibility. Resistance is believed to be the dominant condition and susceptibility the recessive condition.

The inheritance of disease resistance in tobacco does not seem to follow any simple Mendelian ratio, but behaves in a manner that may be more satisfactorily explained by the multiple-factor hypothesis.

The development of two root-rot resistant commercial varieties of tobacco is described, namely, the resistant Havana No. 142 and the resistant stand-up White Burley.

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