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Studies on quantitative inheritance in *Nicotiana tabacum* L.

II. Components of genetic variation for flowering time, leaf number, grade performance and leaf burn

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With 1 figure

For the evaluation of different breeding techniques for the improvement of a crop, there is need for information concerning the nature of the gene action involved, particularly for the quantitatively inherited characters. A knowledge of the relative contribution of the additive and dominance effects of the genes responsible for the expression of the characters involved in comparison to the environmental variation, is also essential. The notion of partitioning the total genetic variance into the additive and non-additive genetic components for certain characters, particularly plant height and flowering time, was utilised by MATHER (1949), SMITH (1952), ROBINSON et al. (1954) and in the subsequent work at North Carolina and Birmingham using diallel crosses in *N. tabacum* and *N. rustica*. In flue-cured tobacco, improvement of the quality of the cured leaf is the most important, while practically little significance is attached to the gross yield, flowering time and leaf number. However, genetic information on quality characters such as leaf burn, bright grade percentage and the body of the leaf, is not so far available. From the limited variability for certain quality characters encountered in flue-cured tobacco in our previous studies, it was felt that an assessment of the different components of genetic variability in the hybrid material developed from the varieties which performed well during the past few seasons for the quality characters, is essential, and this study was undertaken with that purpose. Data on flowering time and number of curable leaves were also collected to find out the relationship of these characters with the above two.

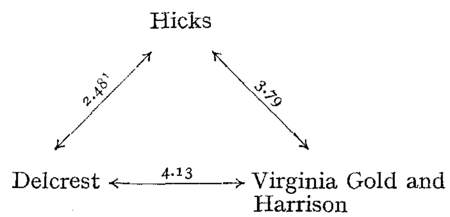
The choice of the parental material was based on a discriminatory analysis using Mahalanobis's generalised distance, selecting parents with different degrees of genetic divergence (MURTY and PAVATE, 1962). The approach of MATHER (1949) and the theory of diallel crosses by HAYMAN (1954 a and b, 1960) and JINKS (1954, 1956) were utilised for estimating the genetic parameters. A comparison also was made of the estimates of the possible genetic advance by this method with that expected using the discriminatory analysis mentioned above. The results of the first year of this study are presented in this paper.

Material and Methods

The material consisted of four flue-cured parents, Harrison Special, Delcrest, Hicks and Virginia Gold, F_1 s, F_2 s, reciprocal F_1 s and reciprocal F_2 s, and back crosses in all possible combinations in a replicated trial of 88 × 3 replicates in a r.c.b. design. The plot size was 5 plants. The number of plots allotted to each treatment in each cross in each replicate is given below:

P_1	1
P_2	1
F_1 and reciprocal F_1	2
F_2 and reciprocal F_2	6
Back cross to P_1	3
Back cross to P_2	3

The nature of genetic divergence as estimated by the discriminatory analysis (D) between the four varieties, is given below:



Planting and other field operations were done as usual for flue-cured tobacco. Nitrogen was applied at 22.2 Kg./hectare in the form of ammonium sulphate.

Observations were taken on each individual plant for the date of first flowering, leaf burn, green and cured leaf weight, bright grade percent and the number of curable leaves in each priming.

The flowering time was recorded in days from the date of planting to the date of first flower opening. For the character curable leaf number, all leaves less than 1 ft. in length were omitted. As there was heavy rain after second priming, which obliterated results, the bright grade percentage was calculated only on the basis of the first and second pickings. Leaf burn test was conducted and scored in seconds as described by VENKATARAMAN and TEJWANI (1957).

Statistical analysis

The estimation of genetic components was limited to D, H, E_1 and E_2 (using MATHER's notation). The estimation of the other parameters, namely, additive × additive, dominance × dominance and additive × dominance, will be taken up from the data of the next season when F_3 s, BIPs and second back crosses will also be available for more precise estimation. The parameters were estimated by the method of least squares. The analysis was on the lines reported by MATHER and VINES (1952).

The negative values obtained for certain components were tested for deviations from zero so as to be sure that they were only due to sampling variation. The possible explanation for such negative values could be due to the existence of negatively correlated effects between adjacent plots.

Since this study at present was for one year and in one location only, the estimates may be biased due to interaction of genotypes with environment within a year and between seasons.

Genetic co-efficients of variability were calculated using the formula:

$$100 \times \frac{D/2}{\bar{x}}$$

where D is the additive component and $\bar{x}$ is the mean of the population. The proportions $D/D + H$ and

$$\frac{D+H}{D+H+E}$$

were estimated using only absolute values of D and H.

Experimental Results

The data on the means and second degree statistics were collected for the characters flowering time, bright grade percentage, leaf burn and number of curable leaves, and are presented in Tables 1 and 2 for the six combinations of crosses. It was also observed from the experience of the previous workers (Smith and Robson, 1959) that a transformation was not essential, since the estimates of E were more or less uniform over all the six crosses.

Table 1. *Parent, F_1 and F_2 array means for the characters flowering time, number of curable leaves, bright grade percent and leaf burn in crosses of flue-cured tobacco.*

	Harrison Special	Delcrest	Hicks	Virginia Gold
A. Flowering time (in days)				
Parent	78	71	72	77
F_1	77	73	78	76
F_2	76	70	73	75
B. Number of curable leaves per plant				
Parent	24	19	17	21
F_1	20	19	17	20
F_2	22	19	18	20
C. Bright grade percentage				
Parent	57.1	67.2	64.1	58.2
F_1	60.3	64.1	66.6	69.5
F_2	61.7	70.3	67.6	63.4
D. Leaf burn in seconds				
Parent	2.44	2.45	2.17	1.92
F_1	2.36	2.13	2.07	2.28
F_2	2.15	2.17	2.18	2.24

Flowering time

The range of plot means for flowering time in the segregating generations of the different crosses is given below:

Cross	Days to flower
Harrison Special × Delcrest	64.0—88.0
Harrison Special × Hicks	64.2—87.2
Harrison Special × Virginia Gold	69.4—90.4
Delcrest × Hicks	61.6—82.0
Delcrest × Virginia Gold	57.8—83.6
Hicks × Virginia Gold	63.0—97.0

It will be noted that the range of variation was high in crosses with Virginia Gold, as expected, since this variety is comparatively late. It is interesting that the crosses between Delcrest and Hicks, both of which are early varieties, exhibited transgressive segregation indicating that the genes for earliness in both of them are different and that it is possible to select plants earlier than either of them.

An examination of the components of variation for this character shows that some of the D and H components are negative. However, an examination of their standard errors indicates that such negative values did not significantly differ from zero. The additive variance is comparatively low in all the crosses except in the cross Delcrest × Virginia Gold. In the other five crosses, it was not significantly different from zero. Consequently, any advance by selection for this character can be accomplished only in the cross Delcrest × Virginia Gold. It is interesting that the dominance variance is quite high in all the crosses except Delcrest × Virginia Gold. The environmental variation as reflected in the E_1 and E_2 components accounted for nearly 30 to 50 per cent of the total variation which cannot be considered very high for a quantitative character like this. There are large differences in the degree of the genetic component of variance between the crosses. This is to be expected since the choice of the parental material was based on the genetic diversity. It is significant that the cross Delcrest × Virginia Gold which has parents with a maximum divergence has the highest additive variance, whereas Harrison Special × Delcrest in which also the parents belong to similarly divergent groups had practically little additive part. Therefore, the degree of genetic divergence alone of the parents may not indicate the amount of additive component in a cross between them and consequently the degree of advance one can make. Thus, it appears that a discriminatory analysis has to be used in conjunction with an analysis of the components of genetic variability in segregating populations.

Bright grade percentage

As mentioned earlier, bright grade percentages were vitiated due to heavy rain after second picking, resulting in low grades for all the treatments.

Cross	Bright grade %
Harrison Special × Delcrest	21.7—81.3
Harrison Special × Hicks	43.3—85.8
Harrison Special × Virginia Gold	33.1—81.7
Delcrest × Hicks	53.7—91.1
Hicks × Virginia Gold	43.1—86.1
Delcrest × Virginia Gold	50.5—86.3

The upper limits of variation were similar in all the crosses as can be seen in the above statement. In none of the crosses was the additive variance significantly different from zero except in Harrison Special × Virginia Gold. The magnitude of the dominance variance was very high in all cases except in the cross Harrison Special × Virginia Gold. The above observations indicate that the high genetic variability of nearly 80 per cent in this cross was more due to the variation in increasing the lower limit than by the improvement of the mean performance compared to the other crosses. The high dominance variance suggests that hybrids between these varieties may perform better than the individual parents. The environmental components are quite high in all the cases and account for nearly 50 to 75 per cent of the total variation.

Table 2. *Components of genetic variation in some crosses of flue-cured tobacco.*

(1)	D (2)	H (3)	E_1 (4)	E_2 (5)	$\frac{D}{D+H} \times 100$ (6)	$\frac{D+H}{D+H+E} \times 100$ (7)	Genetic coefficient of variability (8)
A. Flowering time							
(1) Harrison Special	— 89.74	190.40	44.94	26.83	32.04	86.18	76.81
× Delcrest	±100.106	±155.083	± 38.771	± 38.771			
(2) Harrison Special	1.70	88.16	21.83	22.05	1.89	80.45	3.33
× Hicks	± 46.43	± 71.93	± 17.98	± 17.98			
(3) Harrison Special	— 41.90	142.52	20.21	13.71	22.72	90.12	51.90
× Virginia Gold	± 61.07	± 94.61	± 23.65	± 23.65			
(4) Delcrest × Hicks	— 67.98	75.72	55.93	28.89	47.30	85.78	66.40
	± 58.90	± 91.25	± 22.81	± 22.81			
(5) Delcrest	78.08	— 93.16	53.23	25.27	45.70	76.29	72.30
× Virginia Gold	± 66.93	±103.69	± 25.92	± 25.92			
(6) Hicks	—199.16	401.00	32.92	30.87	33.18	94.80	114.00
× Virginia Gold	±105.206	±162.99	± 40.75	± 40.75			
B. Bright grade percentage							
(1) Harrison Special	—613.64	1106.20	269.35	135.59	35.68	86.46	217.00
× Delcrest	±245.17	±397.81	± 54.82	± 54.82			
(2) Harrison Special	—147.80	477.48	220.05	76.43	23.64	73.97	105.00
× Hicks	±208.142	±322.43	± 46.54	± 46.54			
(3) Harrison Special	336.92	44.92	244.63	192.60	88.24	60.95	166.00
× Virginia Gold	±341.94	±529.72	± 76.46	± 76.46			
(4) Delcrest × Hicks	—175.68	347.84	234.84	136.59	33.43	69.03	115.00
	±311.84	±483.11	± 69.73	± 69.73			
(5) Delcrest	— 75.48	300.20	180.29	91.33	20.04	67.57	76.10
× Virginia Gold	±182.96	±283.45	± 40.91	± 40.91			
(6) Hicks	21.52	606.96	171.10	132.90	3.42	78.60	41.20
× Virginia Gold	±334.43	±518.09	± 74.78	± 74.78			
C. Leaf burn							
(1) Harrison Special	0.0992	— 0.7192	0.5133	0.2743	1.21	61.46	4.67
× Delcrest	± 0.7942	± 1.2304	± 0.1776	± 0.1776			
(2) Harrison Special	2.8516	— 2.6820	0.4315	0.5673	51.53	92.77	111.95
× Hicks	± 0.0441	± 1.6175	± 0.2335	± 0.2335			
(3) Harrison Special	0.5752	— 1.7144	0.6020	0.2295	25.12	79.18	35.55
× Virginia Gold	± 0.7283	± 1.1283	± 0.1629	± 0.1629			
(4) Delcrest × Hicks	0.6254	— 1.0252	0.4819	0.3085	37.88	77.40	37.00
	± 0.5411	± 0.8382	± 0.1210	± 0.1210			
(5) Delcrest	— 0.7668	2.1352	0.4287	0.3904	26.42	87.13	41.20
Virginia Gold ×	± 2.1788	± 3.3754	± 0.4872	± 0.4872			
(6) Hicks	— 1.5954	3.8028	0.4095	0.5363	29.55	92.95	59.21
× Virginia Gold	± 0.9612	± 1.4891	± 0.2149	± 0.2149			
D. Number of curable leaves							
(1) Harrison Special	3.88	14.08	6.44	3.50	21.60	73.61	31.60
× Delcrest	± 14.2084	± 22.0115	± 3.1771	± 3.1771			
(2) Harrison Special	— 16.76	18.24	10.80	3.22	47.89	76.42	66.30
× Hicks	± 8.6321	± 13.3725	± 1.9303	± 1.9303			
(3) Harrison Special	— 10.08	13.52	10.83	5.43	42.71	68.54	50.90
× Virginia Gold	± 14.35	± 22.24	± 3.21	± 3.21			
(4) Delcrest × Hicks	— 2.14	22.00	6.78	4.85	8.86	78.07	30.00
	± 8.18	± 12.68	± 1.83	± 1.83			
(5) Delcrest	22.70	— 21.72	9.13	4.62	51.10	82.95	76.80
× Virginia Gold	± 16.82	± 26.05	± 3.76	± 3.76			
(6) Hicks	24.40	— 15.64	8.80	5.35	60.94	81.98	77.40
× Virginia Gold	± 14.30	± 22.15	± 3.20	± 3.20			

Leaf burn

A study of this character was primarily undertaken to know if detectable genetic differences really exist between varieties. The variation within a leaf itself was so high in the previous studies that it was difficult to predict the performance of any known variety. However, only the first and second grade leaves were taken for burn test to reduce the sampling variation to the minimum and to permit empirical estimation of the heritability of this character.

Cross	Burn in seconds
Harrison Special × Delcrest	1.24—3.24
Harrison Special × Hicks	1.04—4.36
Harrison Special × Virginia Gold	1.14—3.30
Delcrest × Hicks	1.32—3.32
Delcrest × Virginia Gold	1.12—3.64
Hicks × Virginia Gold	1.18—3.50

From the above statement, it can be seen that all the crosses exhibited similar range of variability for this character. The additive component was high in the crosses Harrison Special × Hicks, Hicks × Virginia Gold and Delcrest × Hicks, indicating that Hicks has better genes which combine well with others for this character, whereas Delcrest was not so. This confirms the unique position occupied by Hicks in the discriminatory analysis done earlier by two of us (MURTY and PAVATE, 1962). The dominance component was high in Delcrest × Virginia Gold and Hicks × Virginia Gold which indicates that Virginia Gold has genes for specific combining ability for this character. The magnitude of environmental variation was similar in all the crosses. The data indicated that the genetic variation is not as low as anticipated in discriminatory analysis, but that the additive component was comparatively low. The crosses with Hicks are likely to perform better for this character due to their high additive components.

Number of curable leaves

The varieties chosen widely differed for this character. The range of variation of the plot means in the different crosses was as follows:

Cross	No. of curable leaves
Harrison Special × Delcrest	16.0—22.4
Harrison Special × Hicks	15.4—23.2
Harrison Special × Virginia Gold	13.2—23.4
Delcrest × Hicks	15.2—21.6
Delcrest × Virginia Gold	13.4—23.2
Hicks × Virginia Gold	10.4—23.6

The upper limits of variation were more or less similar in all the crosses. An interesting feature is that the cross between Delcrest and Hicks has segregants which have nearly the same leaf number as the best among other crosses, although both these parents have lower leaf number compared to the other varieties. These results point out that the cumulative action of favourable genes from both the parents has increased the leaf number. The cross Harrison Special × Virginia Gold, both of which have higher number of curable leaves, has thrown out segregants which have as low a leaf number as 13.2 per plant, indicating that these two varieties are genetically distinct from each other.

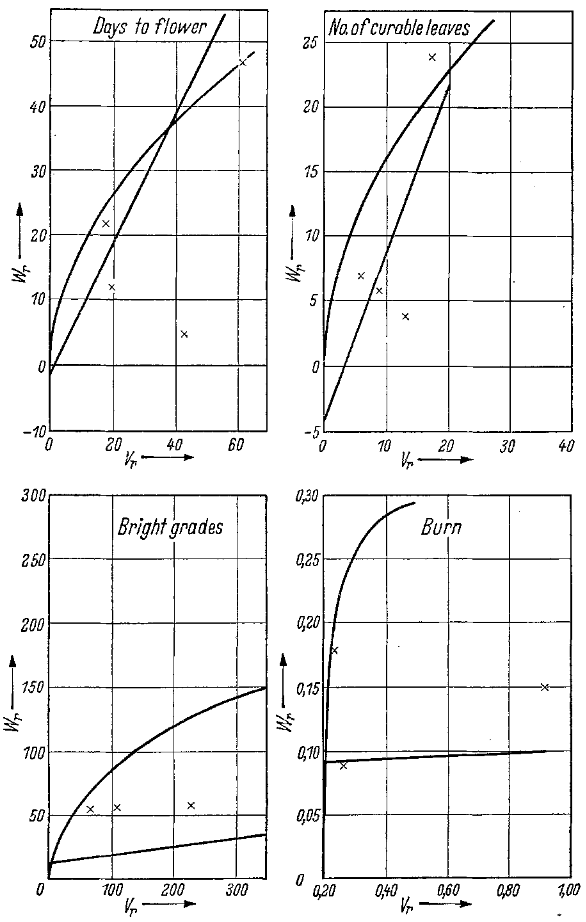


Fig. 1.

The additive component was high only in the crosses Delcrest × Virginia Gold and Hicks × Virginia Gold. The environmental components were not high. The dominance components were much larger than the additive components in four of the six crosses. In the studies of Robinson et al. (1954) the additive component was higher than the dominance component. It is possible that the balancing effects of certain genes might have reduced the additive component to an insignificant value. The results also confirm the conclusion based on the discriminatory analysis.

Analysis of the diallel material

Since the combination under study constituted a complete diallel, the analysis of the F_1's and F_2's along with the parents was done on the model of Hayman (1954 a and b). The results of the analysis are given in the following Tables 3a to 3d, and Figs. 1a and b.

V_r stands for the variance of arrays belonging to that variety used as a common parent. W_r stands for the covariance of the parents with their off-spring in their respective arrays. The V_r W_r graphs are plotted in Figs. 1a and 1b. The parabola represents $W_r^2 = V_{\bar{p}} V_r$ and the linear regression of W_r over V_r is the straight line. The limits of the parents are marked by the parabola. For an understanding of the graph, the basis given by Hayman (1954 a and b) is given below: (1) If the regression line has a slope of one, the effects of the genes is considered to be additive without interaction. (2) The dominance of the gene system could be measured by the intercept and the proximity of the regression line to the parabola. With complete dominance, the regression line would pass through the origin. In the absence of dominance the points cluster near the tangent of the parabola. For overdominance the regressional line will cut the W_r axis below this origin. (3) Regarding the distribution of the dominance or recessive alleles among the parents, low variances (V_r) and covariances (W_r) of an array denote the presence of most dominance alleles in the common parent, while those with most recessive alleles will have high variances and covariances. (4) The amount of non-allelic interaction will be great if there is no common point of intersection of the lines joining the corresponding points of F_1 and F_2 in the $V_r W_r$ graph.

Flowering time

For flowering time, the slope of regression line in the F_1 data, is only half, indicating that there is gene interaction. The F_2 graphs also confirmed the F_1 data about gene interaction, although the slope differed in the direction from that of the F_1. In the F_1, the regression line passes through origin indicating dominance to be complete. However, the F_2 data do not agree with that of F_1 in the degree of dominance. Since the segregating generation gives more information, it can be concluded that dominance is not complete. More recessive genes are present in Delcrest, whereas Harrison Special and Virginia Gold have more number of dominant genes. Since both of these varieties (Harrison Special and Virginia Gold) are later than the other parents it appears that

Table 3a. *V_r — W_r data for flowering time.*

Character Days to flower	♀ \ ♂	Harrison Special	Delcrest	Hicks	Virginia Gold	Mean	V_r	W_r	
F_1	Harrison Special	78	76	75	81	77	17	22	
	Delcrest	73	71	67	83	73	61	47	$V_{\bar{p}} = 37$
	Hicks	77	82	72	81	78	43	5	$bW_r = 0.5114$
	Virginia Gold	78	76	75	77	76	19	12	
	Mean	76	76	72	80				
F_2	Harrison Special	78	78	72	75	76	25	8	
	Delcrest	71	71	67	72	70	15	12	$V_{\bar{p}} = 37$
	Hicks	72	72	72	76	73	12	10	$bW_r = -0.4815$
	Virginia Gold	76	74	72	77	75	15	20	
	Mean	74	74	71	75				

Table 3b. *V_r — W_r data for number curable leaves.*

Character No. of curable leaves	♀ \ ♂	Harrison Special	Delcrest	Hicks	Virginia Gold	Mean	V_r	W_r	
F_1	Harrison Special	24	20	17	19	20	17	24	
	Delcrest	20	19	18	18	19	9	6	$V_{\bar{p}} = 27$
	Hicks	19	17	17	16	17	6	7	$bW_r = 1.3913$
	Virginia Gold	19	21	20	21	20	13	4	
	Mean	20	19	18	19				
F_2	Harrison Special	24	21	20	21	22	9	14	
	Delcrest	19	19	19	18	19	1	—1	$V_{\bar{p}} = 27$
	Hicks	20	18	17	18	18	5	11	$bW_r = 1.8462$
	Virginia Gold	20	19	20	21	20	2	2	
	Mean	21	19	19	20				

Table 3c. *V_r — W_r data for bright grade percentage.*

Character Bright grade %	♀ \ ♂	Harrison Special	Delcrest	Hicks	Virginia Gold	Mean	V_r	W_r	
F_1	Harrison Special	57.14	67.20	58.19	58.68	60.30	1.8107	1.7256	
	Delcrest	64.80	67.24	68.77	55.64	64.11	2.0157	1.7403	$V_{\bar{p}} = 69.50$
	Hicks	69.81	58.90	64.13	73.70	66.64	2.1007	1.9445	$bW_r = .0700$
	Virginia Gold	74.51	77.91	67.25	58.22	69.47	2.3581	1.7599	
	Mean	66.57	67.81	64.59	61.56				
F_2	Harrison Special	57.14	63.61	64.30	61.71	61.69	1.4942	1.5759	
	Delcrest	65.99	67.24	78.72	69.13	70.27	2.0008	1.4351	$V_{\bar{p}} = 69.50$
	Hicks	68.88	71.37	64.13	66.00	67.60	1.4836	1.1668	$bW_r = -0.0149$
	Virginia Gold	62.44	66.22	66.72	58.22	63.40	1.6696	1.6636	
	Mean	63.61	67.11	68.47	63.75				

Table 3d. *V_r — W_r data for leaf burn.*

Character Leaf burn	♀ \ ♂	Harrison Special	Delcrest	Hicks	Virginia Gold	Mean	V_r	W_r	
F_1	Harrison Special	2.44	2.23	2.41	2.37	2.36	0.4145	0.0181	
	Delcrest	1.91	2.45	2.31	1.81	2.13	0.2734	0.0967	$V_{\bar{p}} = .1913$
	Hicks	2.10	2.33	2.17	1.67	2.07	0.2385	0.1816	$bW_r = 0.0080$
	Virginia Gold	2.75	2.04	2.39	1.92	2.28	0.9201	0.1512	
	Mean	2.30	2.26	2.32	1.95				
F_2	Harrison Special	2.44	2.05	2.09	2.01	2.15	0.1173	0.0860	
	Delcrest	2.08	2.45	2.14	1.99	2.17	0.1197	0.1006	$V_{\bar{p}} = .1913$
	Hicks	2.22	2.14	2.17	2.20	2.18	0.0037	0.0062	$b\,W_r = 0.0687$
	Virginia Gold	2.16	2.18	2.71	1.92	2.24	0.3333	0.0410	
	Mean	2.23	2.20	2.28	2.03				

earliness is mostly contributed by recessive genes. Since the points of F_1 and F_2 do not seem to have a common point of intersection, non-allelic interaction appears to be high.

Number of curable leaves

In both the F_1's and F_2's, the data indicate a slope closer to one which suggests that the gene action is mostly additive. The regression line also passes through origin in the F_2, but cuts the W_r axis below the origin in the case of F_1. Therefore, there appears to be predominant influence of dominance, and some overdominance is also suspected. Harrison Special has mostly recessive genes whereas Delcrest has a preponderance of dominant genes. It is likely that less number of leaves is dominant over high number of leaves. The crosses of both Delcrest and Hicks with Virginia Gold will be useful for the improvement of this character.

Bright grades

The absence of any relationship between V_r and W_r, as reflected in the slope of the regression line, indicates a high degree of interaction. The F_1 and F_2 data are in conformity with this view. Therefore, most of the variation should be non-additive. This is reflected in the heritability estimates obtained from the components of variance (Table 2). The degree of interaction for this character appears to be the highest compared to the other three. The distribution of the array points indicates that Hicks carries more dominant genes, whereas Virginia Gold has comparatively more recessive genes. However, due to the absence of consistency in the increase of variances and covariances, it is likely that the genes for this character are not concentrated in any one parent. It is clear from the examination of the array means, that crosses with Harrison Special will not be fruitful for this character. Transformation of the data to a log scale to see if the observed interaction could be reduced on the new scale, did not improve the slope of the regressional line. Probably a more powerful transformation may be needed to overcome the interaction.

Leaf burn

This character also appears to have a high degree of interaction. Absence of dominance also is indicated. The non-additiveness implies that selection for this character is very difficult. Virginia Gold appears to have comparatively more recessive genes and Hicks mostly the dominant genes. For future work, it is not possible to suggest which cross would be the best, from the study of $V_r - W_r$ graphs only. However, the proportion of D and H components (Table 2) indicates that the crosses with Hicks are likely to be more productive since they have higher additive components.

Discussion

The analysis of continuous variation in some of the characters that have influence on the quality and commercial value of flue-cured tobacco is attempted in this study. Flowering time has an indirect influence on quality since early flowering varieties would gain in the body of the leaf due to early topping. The number of curable leaves directly affect yield whereas bright grade percentage and burn have considerable influence over the price. All these characters except the first are highly influenced by the environment. The last two characters do not seem to have been included in studies of this kind by previous workers.

The study revealed that the present methods of generalising the gene effects estimated from one cross cannot have wider application for the characters in tobacco. It can be seen that the estimates of heritability $\frac{D}{D+H}$ (Table 2) varied with each cross which indicates that the genotype of the parents and the degree of divergence between them are primarily responsible for the advance one can make. It is interesting that in certain cases for the same character, dominance component formed the predominant part of the genetic variation, while in others the additive part was predominant. This indicates that, for certain characters, by proper choice of the parents, fixation of transgressive types is possible in spite of high dominance variations. For instance in the cross Harrison Special × Virginia Gold the additive component formed nearly 60 per cent of the total variation whereas in other cases it did not exceed 30 per cent. A higher proportion of the genetic variation in the four characters studied was accounted by the H component which includes interaction also. The $V_r - W_r$ graphs also indicate a high degree of non-allelic interaction. However, the appearance of transgressive types in some cases is suggestive of a complementary type of gene interaction.

In a majority of the cases the F_1 data agreed with F_2 data suggesting that the $W_r - V_r$ analysis is a potent supplementary to the components of variance analysis. Since the material presented in the study belongs to one season only, the conclusions are preliminary. However, the wide array of crosses does permit reasonable deductions from the data.

In each of the cases except curable leaves the gene action was non-additive. From analysis of the diallel Tables 3a, 3b, 3c and 3d, it could be concluded that non-allelic interaction is very high in all the four characters under study. No attempt has been made in this study to ascertain whether the interactions are specific to certain genotypes or of a more generalised nature, by omitting certain arrays and test the improvements in the regression slope. However, visual observation of the dispersion of the points in the $V_r - W_r$ graphs indicates that the interaction is of a generalised type. This is also reflected by its effects in causing heterogeneity of the components. Because of the non-allelic nature of interaction, test for linkage is difficult and therefore, is not attempted. In a majority of the cases either dominance was absent or over-dominance was operating but never was the dominance complete. The distribution of the dominance and recessive genes is non-random for flowering time and number of curable leaves. But they appear to be equally distributed for the other two characters in all the parents. Therefore one cannot rely on only one cross to obtain the most desirable combination for quality characters, in particular. The general type of interaction could not be removed by scaling as attempted by us for the character of bright grade percentage.

The analysis of the heritability for each character as measured by the function $\frac{D}{D+H}$ and the degree of dominance as measured by $\frac{H}{D}$ is examined below (see also Table 2). For flowering time there is significant over-dominance consistently in all the crosses. Similar was the case with bright grade percentage, except in the cross Harrison Special × Virginia Gold which gave incomplete dominance. The number of curable leaves as well as leaf burn also showed overdominance. However, the degree of complementary type of interaction observed in this study, suggest that any conclusions about the dominance relations may have to be reexamined after a study

Table 4. *D^2 Statistic and heritability (additive component %) estimates in crosses between four flue-cured varieties.*

		Hicks and Delcrest	Hicks and Harrison Special	Hicks and Virginia Gold	Delcrest and Harrison Special	Delcrest and Virginia Gold	Harrison Special and Virginia Gold
Pooled D^2 (Murty et al.)		6.13	14.39	14.39	17.04	17.04	2.21
Bright Grade %	A	0.65	10.51	10.51	6.63	6.63	—
	B	33.43%	23.64%	3.42%	35.68%	20.04%	88.24%
Curable leaves	A	—	—	—	—	—	—
	B	8.86%	47.89%	60.94%	21.6%	51.1%	42.7%
Burn	A	1.12%	0.34	0.34	2.05	2.05	—
	B	37.88%	51.53%	29.55%	1.21%	26.42%	25.12%
Maturity	A	4.20	0.15	0.15	3.52	3.52	—
	B	47.30%	1.89%	33.18%	32.04%	45.70%	22.72%

A = D^2 Statistic; B = additive component % (heritability).

of advanced segregating generations. These observations agree with only some of the cases in the V_r — W_r analysis. Since some of the components of genetic variation showed negative signs, the heritability estimates should be viewed with caution. Ignoring the signs, the proportion $\frac{D}{D+H}$ was used as the measure of heritability. $\frac{D+H}{D+H+E}$ was considered as the proportion of genetic variation to the total variation.

For flowering time, Delcrest × Hicks and Delcrest × Virginia Gold have high heritability. The crosses with Harrison Special have in general, low additive components. Actually in all the crosses involving Harrison Special, heritability was low indicating non-allelic interaction of an unpredictable nature, although the genetic portion of the total variation is quite high. For the character, number of curable leaves, crosses with Virginia Gold have greater heritability and also have the highest genetic variability. For the quality character bright grades Harrison Special × Virginia Gold has a heritability of 88 per cent. However, it is pertinent to note that the total genetic variability itself is low in this cross being 61 per cent compared to a maximum of 86 per cent in the other crosses. Leaf burn has high genetic variability but very low heritability. Only the crosses Hicks × Harrison Special and Hicks × Delcrest show indications of some improvement. These crosses also have a good deal of genetic variability.

This study was a sequence of the classification of the collection at this Institute by the D^2 statistic of Mahalanobis (Murty and Pavate, 1962). It can be seen from Table 4, that in a majority of the cases the degree of genetic divergence was reflected in the heritability component also. Thus, it appears that discriminatory analysis followed by the partition of genetic variation is helpful in plant breeding programme particularly for characters which have low heritability. However, it is not always possible to predict that the most genetically divergent lines will be the most productive for fixing transgressive types because, the dominance component which can be very high and unfixable might be playing a large part in the divergence. This is borne out by the results of our study. The high epistatic effects indicate that some residual variability should be retained in the populations. The fact that desirable genes are distributed over several parents suggests the need for multiple crosses. The heritability estimates for flowering time and leaf number were high as observed by previous authors (Robinson et al. 1954, Matzinger et al. 1960; Oka, 1959). A comparison of the heritability estimates from our data with those of other authors are presented in Table 5. The data suggest that the estimates of the latter authors were probably overestimates. The estimates for flowering time were comparable with those obtained by others but not the estimates for the other characters. As suggested by Hayman (1960) it is possible that the presence of epistatics, detected in our study, is responsible for the differences in the heritability values obtained by us compared to the previous workers. Robinson et al. (loc. cit.) consider that accumulation of maximum number of favourable genes in homozygous genotypes, rather than hybrid vigour in F_1, offers greater promise in tobacco improvement. Such a situation appears to hold good for the characters studied by us also in spite of the high epistatic variation.

The use of W_r — V_r graphs which are very sensitive to complementary type of interaction is normally quite effective in choosing a proper scale before analysis of the variance components. The use of multiple crosses is recommended after desirable lines are isolated from the early segregating generations of single crosses. Since the nature of gene interaction has nothing special about any particular part of genotype, accumulation of favourable genes is recommended.

In all the characters, the variety Hicks appears to stand out both as a superior genotype as well as a variety with high general combining ability. In particular, the crosses with Hicks have consistently shown greater additive genetic variance whereas those with Harrison Special were the reverse. This confirms the unique position occupied by Hicks in the discriminatory analysis done by Murty and Pavate (1961).

Table 5. *Comparison of heritability estimates from different authors.*

	H. H. Smith (1952) *N. rustica*	Robinson et al. (1954)	Oka (1959)	Range of heritability in our study
1. Days to flower	62.7% (plant height)	94.4	66.7	1.89—47.3%
2. Leaf number	21.1%	90.1	72.1	8.86—60.94%
3. Bright grades	—	61.8	—	3.42—88.24%
4. Leaf burn	—	—	—	1.21—37.88%

To examine the magnitudes of additive × additive, dominance × dominance and additive × dominance interactions in the next season with BIPs, F_3s and second backcrosses, studies are being continued. It is also evident that some of the phenotypically similar parents could be genetically different to a high degree. This study had indicated a contrast to the nature of the gene action of the quality characters in tobacco as compared to the gross yield components such as leaf number and leaf size.

There is considerable confusion due to the use of expressions like "heritability in the narrow sense" and "heritability in the broad sense" by authors like WARNER (1952), LUSH (1945), ROBINSON et al. (1954) and ALLARD (1960). The ratio $\frac{D}{D+H}$ is a more appropriate definition of heritability unless E which is subject to high sampling errors is estimated from several environments. FISHER (1918) who originally used this term, defined it as $\frac{D}{D+H}$. This view is again strongly expressed by KEMPTHORNE (1957). Therefore it is proposed that $\frac{D}{D+H}$ shall be termed heritability, $\frac{D+H}{D+H+E}$ as the coefficient of genetic variation and the product of these two as the rate of advance under selection.

Summary

The components of genetic variation for two characters, flowering time and the number of curable leaves, which influence the gross yield, and two quality characters, grade performance and burning quality of the cured leaf, were examined in the F_2 and back-cross generations of a set of diallel crosses between four flue-cured varieties selected on the degree of divergence as measured by Mahalanobis's D^2 statistic.

Differences in the relative proportions of D and H components were observed, in different crosses, for the same character. These differences were parallel to the degree of divergence between the parents concerned. Significant non-allelic interaction of a generalised nature was detected for each of the four characters. Additive component formed a substantial purt of the total genetic variation for the character curable leaf number only.

A comparison of the degree of divergence between the parents and the heritability estimates for the characters concerned, indicated that in a majority of the cases, the use of D^2 statistic for the choice of the parents would be useful for evaluating the potential of a cross.

Analysis of the diallel material for V_r and W_r components confirmed the existence of a high degree of non-allelic interaction. The distribution of the desirable genes, for quality characters, over several parents, suggests the need for multiple cross for the accumulation of a maximum number of favourable genes. A contrast in the nature of gene action between quality characters and gross yield components was also indicated in the study.

A variety Hicks was found to be unique in its high general combining ability and high additive variance for all the four characters, in its crosses, whereas another variety Harrison Special was a consistently poor combiner. A comparison of the components of genetic variability estimated by other workers with those of the present investigation was made with reference to the limitations of conclusions from one or few crosses.

The utility of the combined use of D^2 statistic, the analysis of $V_r - W_r$ components and the partition of the components of genetic variation was discussed with reference to the future breeding work in flue-cured tobacco for the characters under study.

Zusammenfassung

Zwischen vier Sorten von Röhrentrocknungs-Tabak (flue-cured tobacco), die anhand des Divergenzgrades (ermittelt mit der D^2-Statistik nach MAHALANOBIS) ausgewählt worden waren, wurden diallele Kreuzungen durchgeführt. An den F_2 und den Rückkreuzungsgenerationen wurden die genetischen Variationskomponenten von 2 den Ertrag beeinflussenden Merkmalen (Zeitpunkt der Blüte und Anzahl der nutzbaren Blätter) und 2 Qualitätsmerkmalen (Anteil hellfarbener Blätter und Brennbarkeit des getrockneten Blattes) analysiert.

Bei verschiedenen Kreuzungen ergaben sich für jeweils das gleiche Merkmal Unterschiede in den relativen Anteilen der Komponenten D und H. Diese Unterschiede entsprachen dem Grad der Divergenz zwischen den betreffenden Eltern. Für jedes der 4 Merkmale wurde signifikante nicht-allele Interaktion allgemeiner Art beobachtet. Die additive Komponente bildete nur für das Merkmal Blattzahl einen wesentlichen Teil der gesamten genetischen Variation.

Ein Vergleich des Divergenzgrades zwischen den Eltern und den Schätzungen der Erblichkeitsanteile für die betreffenden Merkmale zeigte, daß sich in den meisten Fällen die Anwendung der D^2-Statistik bei der Auswahl der Eltern für die Vorausberechnung der Kreuzungsergebnisse bewähren dürfte.

Die Analyse der Komponenten V_r und W_r in dem diallelen Material bestätigte das Vorhandensein starker nichtalleler Interaktion. Die Verteilung der erwünschten Gene für Qualitätsmerkmale auf verschiedene Eltern macht mehrfache Kreuzungen notwendig, um eine größtmögliche Anreicherung dieser Gene zu erreichen. Auf unterschiedliche Genwirkungen bei Qualitätsmerkmalen und Ertragskomponenten wird hingewiesen.

Die Sorte Hicks erwies sich in ihren Kreuzungen als bemerkenswert bezüglich ihrer hohen allgemeinen Kombinationseignung und der hohen additiven Varianz bei allen 4 Merkmalen, dagegen hatte die Sorte Harrison Special eine durchweg geringe Kombinationseignung. Die Ergebnisse anderer Autoren bei der Schätzung der Variationskomponenten werden mit denen der vorstehenden Untersuchung verglichen. Es wird dabei darauf hingewiesen, daß Schlüssen auf Grund nur einer oder weniger Kreuzungen Grenzen gesetzt sind.

Die Brauchbarkeit der kombinierten Anwendung der D^2-Statistik, der Analyse der Komponenten V_r und W_r sowie der Trennung der genetischen Variationskomponenten wird für die untersuchten Merkmale im Hinblick auf künftige Züchtungsarbeiten mit Röhrentrocknungs-Tabak diskutiert.

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Beobachtungen zur phänotypischen Variabilität der Genotypen: Resistenz und Anfälligkeit am Beispiel der Rippenbräune des Tabaks

Von **G. KOELLE**

Mit 2 Abbildungen

Unsere Kenntnis von der Genetik eines Erbmerkmals beruht zumeist nur auf der Analyse einer Aufspaltung, und zwar der Aufspaltung von Nachkommen der in diesem Merkmal Heterozygoten. Wir schließen dabei aus der Verteilung der Phänotypen auf einen genau definierten Unterschied im Genotypus, können aber daraus, wenn es sich um ein physiologisches Merkmal handelt, nichts ableiten über eine absolute Reaktionsnorm dieser Genotypen. Im Falle der Erbmerkmale Resistenz und Anfälligkeit heißt das, daß, solange die stofflichen Grundlagen der Resistenz nicht bekannt sind, ein genetisch bedingter Unterschied aber nachgewiesen ist, wir nur sagen können, daß aller Voraussicht nach dieser Unterschied sich in einem stärkeren Befall der Anfälligen gegenüber den Resistenten äußern wird, aber nicht mit Sicherheit wissen, wie ihre Reaktion auf eine Infektion absolut gesehen verlaufen wird. Der Verlauf einer Krankheit hängt ja, abgesehen von der genetischen Disposition, noch von vielen außergenetischen Faktoren ab, wie Anzahl der Vektoren, Klima, Düngung, Wasserversorgung usw., die ich, ohne im einzelnen auf sie einzugehen, in dem Sammelbegriff Milieu zusammenfassen möchte, um sie als variable Größe dem konstanten Genotypus zuzuordnen.

Die üblichen Erfahrungen über Resistenz oder Anfälligkeit einer Tabaksorte stammen meist nur aus einem für den Verwendungszweck dieser Sorte optimal abgestimmten Milieu. Von den vielen denkbar möglichen Milieus ist damit aber nur ein kleiner Teil erfaßt und damit auch nur ein kleiner Ausschnitt aus der möglichen Reaktionsbreite dieser Sorte verwirklicht. Ich habe den Versuch gemacht, durch Befallsbeobachtungen an möglichst vielerlei Standorten die phänotypische Variationsbreite der Genotypen Resistenz und Anfälligkeit für Rippenbräune (Y-Virus) abzustecken, wobei unter Resistenz nur gewöhnliche Feldresistenz verstanden sein soll. Meinen Ausführungen liegt als Arbeitshypothese folgende Vorstellung zu Grunde: Beide Genotypen, Anfällige wie Resistente, haben die Fähigkeit, krank zu werden oder gesund zu bleiben, nur sind die Resistenten, wenn sie befallen sind, es weniger stark als die Anfälligen. Es kann auch der Fall eintreten, daß ein Unterschied zwischen beiden Typen nicht mehr zum Ausdruck kommt, und zwar einmal dann, wenn bei fehlendem Erreger beide Typen gesund bleiben, und andererseits dann, wenn bei extrem starkem Infektionsdruck auch die Resistenten nahezu 100%ig befallen werden. In der nachstehenden Abbildung ist versucht, diese Hypothese in einem einfachen Diagramm zu veranschaulichen.

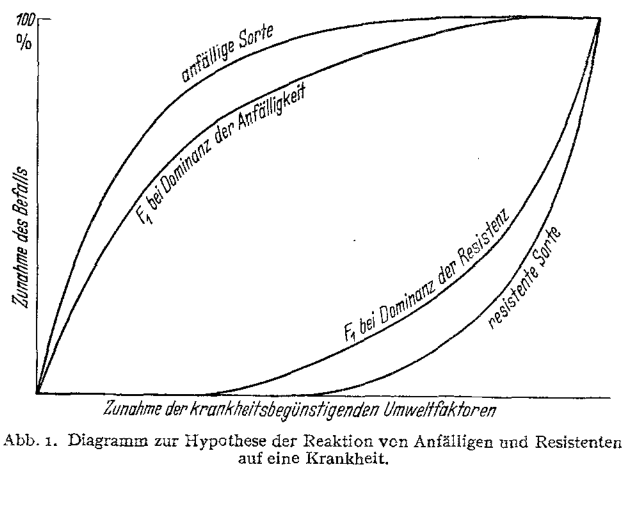

Abb. 1. Diagramm zur Hypothese der Reaktion von Anfälligen und Resistenten auf eine Krankheit.