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Yield and Yield Components in Flue-Cured Tobacco and Their Genetic Analysis

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Abstract. Five cultivars and the half diallel set of 10 F_1 hybrids of flue-cured tobacco (*Nicotiana tabacum* L.) were grown in two seasons. Highly significant differences were assessed between genotypes as concerns flowering time, plant height, number of leaves, leaf length and width and yield per plot. High to moderate values for heritability in the broad sense were obtained in all cases. Hybrids, in general, flowered earlier, were taller, had fewer but shorter and wider leaves and slightly increased yield when compared with the mean value of all parents. The variance associated with general combining ability (GCA) was highly significant in all characters. The estimates of SCA were significant in most cases. High GCA/SCA ratios which largely exceeded the unity were obtained for most attributes. The negative and positive alleles were unequally distributed in the parents for all the studied traits. A small number of effective genes was obtained for all characters except plant height, where one to two groups of genes were distinguished

Biometrical methods have been used in genetic studies in order to analyse the inheritance of a continuous variation in quantitative characters in terms of the nature of the polygenic system responsible. An analysis of means and variance components applied to data from a series of generations following prescribed breeding programs made it possible to interpret the kinds of gene action, *i.e.* additive, dominance and various non-allelic interactions. Information obtained from such genetic analysis can be utilized in designing breeding methods which would guarantee best results in plant improvement.

The purpose of the present study is to evaluate the estimates of heterosis, general and specific combining ability and genetic parameters for yield and yield components in a half diallel cross of five pure lines of flue-cured tobacco (*Nicotiana tabacum* L.).

MATERIAL AND METHODS

The experiments reported herein were carried out at the Research Institute of Tobacco Industry, Báb, during the two successive seasons 1981 and 1982. Five cultivars of flue-cured tobacco (*Nicotiana tabacum* L.) namely

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LHSE-68, Virginia 71, Coker 139, Virginia 31 and R-1349 were used as parental lines. In 1980 all possible crosses excluding reciprocals were made between the five parental lines giving a total of ten crosses. A randomized complete block design with four replications was used in the present study. Each experimental plot included six rows, three of which were devoted to growth analysis and the rest to the determination of yield and yield components.

The following characters were studied: 1) Flowering time was recorded as the number of days from transplanting until 25% of plants have at least one open flower; 2) plant height was measured from the ground level to the crow-foot flower (just below the first capsule); 3) number of leaves per plant was recorded as the number of harvestable leaves per plant; 4) leaf length was measured along the midrip from the leaf axil up to its apex on the largest leaf in the plant; 5) maximum leaf width was measured on the same leaf which was selected for leaf length measurement; and 6) green leaf fresh mass was determined on three rows in kg and expressed as kg/plot.

The data were first subjected to analysis of variance. Heterosis values were expressed as percent increase of the F_1 hybrids above the average of the parents

$$\text{Heterosis } \% = \frac{F_1 - MP}{MP} \times 100 .$$

The diallel cross analysis for general (GCA) and specific (SCA) combining ability estimates were obtained by using GRIFFING's (1956) diallel cross analysis designated as method 2, model 1. The data were further subjected to diallel analysis proposed by HAYMAN (1954) to obtain more information about the genetic behavior for the traits under study. Heritability estimates in both broad and stricter sense were computed according to MATHER and JINKS (1971). The statistical computational techniques used in this study were run on a computer. Two programs were prepared and written in the standard FORTRAN language and applied on an IBM 380 computer of SVS-UTIA, ČSAV, Praha. The results obtained are given in Tables 1 and 2.

RESULTS AND DISCUSSION

Mean characteristics of all genotypes of the diallel table, *i.e.* parents and their F_1 hybrids in 1981 and 1982 seasons for flowering time, plant height, leaf length, leaf width, number of leaves per plant and yield of green leaves per plant are given in Table 1. Highly significant differences existed between genotypes in all characters, indicating a high variability in the studied traits. Parents and hybrids reached the significant level for most of the traits studied.

The coefficient of heritability is a measure of the efficiency of selection in separating genotypes. High to moderate values of heritability in broad sense were obtained in all cases, revealing that most of the phenotypic variability in each case was due to genetic causes (Table 2). For flowering time in 1982 season and the number of leaves and plant height in both seasons, values in both senses were of nearly equal magnitudes, indicating that the genetic variance associated with those traits was mostly due to additive effects of genes. Therefore, a rapid and effective selection could be made for these traits. High to moderate values of heritability in the broad

TABLE 1

Mean characteristics and average heterosis for yield and yield components in 5 flue-cured tobacco parental cultivars and their F_1's in the two seasons

Genotypes	Flowering time [d]		Plant height [cm]		No. of leaves per plant		Leaf length [cm]		Leaf width [cm]		Yield/Plot [kg/plot]	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
LHSE-68	67.00	67.75	110.7	115.7	20.05	22.95	48.70	52.54	22.95	28.81	14.023	13.910
Virginia 71	67.50	65.25	106.4	114.3	21.80	24.90	46.88	53.48	22.28	28.68	14.403	15.405
Coker 139	68.50	68.50	109.0	125.4	23.13	26.13	48.68	60.63	23.08	32.17	15.528	19.570
Virginia 31	64.50	65.00	107.2	121.4	20.53	22.88	50.65	54.00	25.38	29.70	14.188	14.755
R1349	64.25	65.25	124.1	133.0	19.95	21.65	46.38	56.45	25.58	32.13	11.600	13.745
LHSE-68 × V.71	66.00	65.25	113.6	118.0	20.13	23.50	47.15	55.22	23.68	29.46	13.358	14.813
× C.139	66.50	66.50	113.4	123.3	21.45	24.53	47.95	54.39	23.63	29.26	14.440	16.753
× V.31	66.00	67.75	109.5	121.2	20.03	22.25	45.98	53.91	23.85	30.25	13.808	14.845
× R1349	65.75	64.75	125.3	137.7	20.33	23.00	47.75	60.04	25.75	34.04	14.425	16.265
Virginia 71 × C.139	66.00	66.25	114.4	123.3	22.03	24.58	48.20	53.36	22.10	29.73	15.143	16.145
× V.31	63.00	64.25	110.7	120.7	20.80	23.38	47.25	54.91	24.23	29.43	15.403	15.370
× R1349	63.00	63.00	115.3	127.0	20.03	22.88	45.83	56.50	25.13	31.48	13.433	15.538
Coker 139 × V.31	65.50	69.00	116.3	127.0	21.10	23.83	45.98	54.45	24.68	29.54	14.040	15.915
× R1349	64.50	68.50	125.9	136.9	21.05	24.13	47.20	57.84	25.28	32.89	12.313	15.348
Virginia 31 × R1349	65.50	66.75	125.2	126.1	19.68	21.80	45.93	54.21	26.18	31.70	13.860	15.395
Total mean	65.57**	66.25**	115.2**	124.7**	20.80**	23.49**	47.37**	55.46**	24.25**	30.62**	13.997**	15.585**
L.S.D. 5%	1.11	3.58	4.5	5.8	0.95	1.05	1.07	3.88	1.01	1.05	1.64	1.84
L.S.D. 1%	1.49	4.79	5.9	7.8	1.27	1.41	1.43	5.19	1.35	1.41	2.19	2.46
Parents mean	66.35**	66.35	111.5**	122.0**	21.09**	23.70**	48.26**	55.42**	23.85**	30.30**	13.948**	15.477**
Hybrids mean	65.18**	66.20	117.0**	126.1**	20.66**	23.39**	46.92**	55.48*	24.45**	30.78**	14.022*	15.639
Heterosis %	−1.76**	−0.23	4.93**	3.36**	−2.04*	−1.31	−2.78*	0.11	2.52**	1.58*	0.53	1.05

* = significant differences from zero at 5%;
** = significant differences from zero at 1%.

TABLE 2
Heritability, combining ability analysis and genetic components analysis of yield and yield components in flue-cured tobacco

Component	Traits											
	Flowering time [d]		Plant height [cm]		No. of leaves		Leaf length [cm]		Leaf width [cm]		Yield/Plot [kg/plot]	
	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982	1981	1982
Heritability												
narrow	44.25	34.52	60.25	56.21	63.32	63.82	37.70	19.01	44.79	55.45	37.34	27.55
broad	89.13	47.64	85.46	81.63	98.14	98.04	86.92	53.12	91.48	89.91	67.19	61.99
GCA	16.88**	26.33**	457.83**	509.43**	11.46**	18.97**	5.98**	36.15**	19.40**	25.42**	8.80**	17.69**
SCA	6.47**	7.02	72.47**	67.57	0.63	0.74	7.69**	17.98*	1.64**	5.06**	2.72*	3.47*
GCA/SCA	2.61	3.75	6.32	7.54	18.19	25.64	0.78	2.01	11.83	2.02	3.24	5.10
$\hat{D}$	6.13*	5.59*	55.85*	71.43*	23.82+	9.15+	5.27+	9.14	6.30+	4.59+	2.91+	6.15*
$\hat{F}$	3.68	−0.52	−9.85	−11.67	2.12	1.45	4.95	10.52	4.38	1.30	1.29	6.31
$\hat{H}_1$	11.90*	6.47	70.23*	105.1	37.26	10.81	11.22	29.40	14.35	9.77	6.11+	8.54+
$\hat{H}_2$	9.48*	5.43	61.93+	89.39	30.89	8.85	8.34	21.91	11.00	7.23	4.76	6.06
$\hat{h}^2$	3.94*	−2.68+	71.19**	59.68**	17.80*	4.57	5.49*	−2.63	1.36	0.73	−0.17	−0.57
$\hat{E}$	0.60	6.26	9.67	16.64	0.45	0.54	0.57	7.36+	0.50	0.54	1.31	1.67+
$(\hat{H}_1/\hat{D})^{1/2}$	1.39	1.08	1.12	1.21	1.25	1.09	1.46	1.79	1.51	1.46	1.45	1.17
$\hat{H}_2/4\,\hat{H}_1$	0.20	0.21	0.22	0.21	0.21	0.20	0.19	0.19	0.19	0.19	0.19	0.18
K_D/K_R	1.59	0.92	0.85	0.87	1.07	1.16	1.95	1.95	1.60	1.22	1.36	2.52
K	0.42	−0.49	1.15	0.67	0.58	0.52	0.66	−0.12	0.12	0.12	−0.04	−0.09

+ = significant differences from zero at 10%;
* = significant differences from zero at 5%;
** = significant diferences from zero at 1%.

sense were previously reported by LUTHRA (1964) in tobacco for leaf length, leaf width, earliness and plant height.

In general, hybrids flowered earlier, were taller, had fewer but shorter and wider leaves and slightly increased yield when compared with their parents (Table 1). In the first season, significant negative estimates of heterosis were obtained for flowering time, number of leaves and leaf length, indicating earliness in flowering, a smaller number of leaves per plant and smaller leaf length. However, significant positive estimates of heterosis were obtained for plant height and leaf width in both seasons.

It was observed that the crosses LHSE-68 × R-1349, Virginia 31 × R-1349 and Virginia 71 × Virginia 31 have significantly higher yields than the mid-parents in 1981 and 1982 seasons. It was also found that LHSE-68 parental cultivar has a low yield per plot. Their combinations with Virginia 71, Coker 139 and Virginia 31 have brought up their yield considerably.

The high yield of LHSE-68 × R-1349 cross could be attributed to the heterosis in plant height, number of leaves, leaf length and leaf width. Examination of the components of yield showed that flowering time, leaf length and width were the most important components that contribute to yield heterosis.

Plant breeders are interested in a hybrid which is superior to the better parent. Many hybrids exceeded their respective top parents in yield by a significant amount. These hybrids involved the breeding lines LHSE-68 × × R-1349 in both seasons, Virginia 71 × Virginia 31 in 1981 season and LHSE-68 × Virginia 31, Virginia 71 × R-1349 and Virginia 31 × R-1349 in 1982 season. The most promising hybrids for early flowering cultivars were found in Virginia 71 × Virginia 31 and Virginia 71 × R-1349 crosses.

The heterotic response found in this study for yield and earlier flowering is similar to those previously reported for flue-cured and burley tobacco (AYCOCK *et al.* 1963, CHAPLIN 1966, LEGG *et al.* 1970), but the magnitude of the response was considerably less than that ascertained in oriental tobacco (MARANI and SACHS 1966) and in burley tobacco (MATZINGER *et al.* 1971).

The variance associated with general combining ability (σ^2 g) was highly significant in all cases (Table 2). The estimates of specific combining ability σ^2's were significant for all traits except flowering time in the 1982 season, and the number of leaves in both seasons. The significant estimates of σ^2 g for all characters obtained in the present work are in agreement with the estimates from intercrosses between flue-cured cultivars (MATZINGER *et al.* 1962, CHAPLIN 1966). EPISON and CAPOTA (1976) found that the general combining ability in diallel cross of tobacco was significant for plant height, leaf width, leaf length, number of leaves, distance between leaves, leaf blade weight and days to flowering, while specific combining ability was significant only for leaf length and days to flower.

Except for leaf length in the 1981 season, the σ^2 g was larger than σ^2 s. Significance of the mean squares for general and specific combining ability obtained herein in most characters indicates that in their inheritance both the additivity and nonadditivity of gene effects are important. Therefore, the standard methods of producing new cultivars through development of homozygous lines as well as the methods involving dominance would be effective. Similar results have been previously obtained on flue-cured tobacco (POVILAITIS 1966, SHAMSUDDIN *et al.* 1980).

In most cases, the general combining ability mean squares (GCA) were higher than those of specific combining ability mean squares (SCA), as indicated by the GCA/SCA ratio. This indicates that the largest part of the total genetic variability associated with these cases is a result of additive and additive by additive gene action types.

The components of genetic variation and their proportions for yield and yield components are given in Table 2. With the exception of leaf length in the second season, the additive components $\hat{D}$ reached the significant level of probability for all the traits studied, suggesting that the additive gene action plays an important role in the inheritance of these characters in flue-cured tobacco, particularly of those which had high general and specific combining ability. This finding is in accordance with that reached for GCA analysis. Similar results were previously obtained by POVILAITIS (1966) and LEGG and COLLINS (1971). Insignificant $\hat{D}$ values were obtained for the leaf length in the second season, in spite of high estimates. The dominance may influence GCA estimates as was emphasized by JINKS (1955). Moreover, the computed regression coefficients of the parent-offspring covariance (W_r) on the parental array variance (V_r) were found to be significantly less than the unity in this case, revealing the presence of a complementary type of epistasis. The complementary type of epistasis generally decreased W_r disproportionately more than V_r leading to an inflation in the relative magnitude of dominance to additive components (HAYMAN 1954, HAYMAN and MATHER 1955, MATHER and JINKS 1971). Therefore, the contradiction in magnitude detected here in $\hat{D}$ and GCA estimates for leaf length in the second season could be attributed to the great effect of both allelic and non-allelic gene interactions on the expression of this trait.

The presence of the dominance effects was substantiated by the significant values of $\hat{H}_1$ for flowering time and plant height in 1981 season and for yield in both seasons. Moreover, the values of $\hat{H}_1$ were significantly higher than the respective $\hat{D}$ ones in all cases, contradicting the results reached from combining ability. Similar results were obtained by POVILAITIS (1966) who found the dominance for tobacco yield to be of an overdominance type.

None of the estimates of the genetic parameters for leaf length in the second season was significant. However, the significance of GCA and SCA estimates obtained would indicate that both additivity and dominance are involved in this trait.

The average degree of dominance is measured by $\hat{H}_1/\hat{D}$. The quantity $(\hat{H}_1/\hat{D})^{1/2}$ is a weighted estimate of the average degree of dominance at each *locus*. The values of $(\hat{H}_1/\hat{D})^{1/2}$ were greater than unity for all characters, indicating that full to overdominance may be important in these cases. Regression coefficients of the parent-progeny covariances W_r on variances of the arrays V_r were significantly different from zero for flowering time, plant height and yield in 1981 season and for the leaf length in both seasons, and the slope of the regression lines lay significantly below the points of origin, indicating overdominance at all *loci*. For the other yield components, insignificant coefficient of V_r on W_r was detected; overdominance as indicated by $(\hat{H}_1/D)^{1/2}$ could be associated with complementary gene action (ALLARD 1956, JOHNSON 1963).

The ratio $\bar{H}_2/4\bar{H}_1$ was used to estimate the average frequency of negative *versus* positive alleles in the parents (CRUMPACKER and ALLARD 1962). If the distribution among the parents is equal, the ratio is expected to be 0.25. If not, the ratio will be less than 0.25. The estimated values for the traits studied were all smaller than 0.25, indicating that the positive and negative alleles were not equally distributed in the parents. The parents seemed to carry more dominant genes for all characters except flowering time in the second season and plant height in both seasons, as indicated by the positive value of $\hat{F}$ component. This can also be seen from the ratios of K_D/K_R. These results are in agreement with those obtained by POVILAITIS (1966) who found that the average frequency of positive and negative genes in the parents were asymmetrically distributed with an excess of dominant genes.

The parameter $\hat{F}$ is an indicator of the relative frequencies of the recessive and dominant alleles in the parents. $\hat{F}$ is positive when there are more dominant than recessive alleles. If the $\hat{h}^2$ effects of the individual genes are unequal, the value of $\hat{F}$ will be in favor of the genes with the largest $\hat{h}^2$ values. An excess of recessive alleles will cause $\hat{F}$ to be negative. None of the $\hat{F}$ components was significant for all characters, suggesting that gene symmetry existed between the *loci* controlling these attributes. The parameter $\hat{F}$ was found to be negative in cases of flowering time in 1981 and plant height in both seasons, indicating an excess of recessive genes in the parents for these traits. For plant height and flowering time in the 1981 season and yield in both seasons, where dominance existed, the obtained insignificant $\hat{F}$ values might indicate that dominant and recessive alleles of *loci* exhibiting dominance were equally distributed among the parents. This finding again confirms the results reached above for $\hat{H}_2/4\hat{H}_1$.

The ratio of dominant to recessive genes, K_D/K_R, showed an excess of dominant alleles in the parents for all traits except flowering time in the 1982 season and plant height in both seasons.

The overall dominance effects of heterozygous *loci* ($\hat{h}^2$) were found to be significant for flowering time and plant height in both seasons, and the number of leaves per plant and leaf length in the season 1981. This indicates that dominance was unidirectional in these attributes. However, insignificant $\hat{h}^2$ estimates were obtained for the remaining traits, suggesting a considerable cancelling of dominant effects in the parental material.

The fraction $\hat{h}^2/\hat{H}_2$ symbolized as K indicates the number of groups of genes in the parents showing dominance for the characters under study. With the exception of plant height, where one to two groups of genes were distinguished, low K values were obtained for yield and yield components. For most of the studied attributes, quite low values were logically expected as non-appreciable estimates were obtained for dominance components indicating little or no dominance effects of the genes controlling these attributes. Relative low estimates were computed for flowering time and leaf length in the 1981 season and the number of leaves in both seasons, suggesting that among the genes governing each of these traits there were one or more whose high dominance led to disproportionate effects on the K estimate (CRUMPACKER and ALLARD 1962). These values will be underestimated unless the

dominance effects of all the genotypes are equal in size and sign, and the distribution of the genes is independent. Two to three groups of genes were found to control the leaf number, plant height, flowering time and leaf shape in flue-cured tobacco (OKA 1959).

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