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INVESTIGATIONS OF HERITABILITY AS AN INDICATOR OF THE INHERITANCE OF QUANTITATIVE CHARACTERS IN TOBACCO

Jane Aleksoski, Miroslav Dimitrieski[1], Ana Korubin-Aleksoska[1]

[1]Un."St. Kliment Ohridski"-Bitola, Scientific Tobacco Institute-Prilep, Republic of Macedonia
e-mail: janealeksoski@yahoo.com, anakorubin@yahoo.com

ABSTRACT

Mode and level of inheritance of some major quantitative characters (stalk height, leaf number per stalk, middle belt leaf area, green and dry mass yield per stalk) was investigated in four parental genotypes (Burley - B 2/93, Suchum - S1, Suchum - S2 and Prilep - P-84) and their six diallel F1 hybrids. The trial was set up in 2007, 2008 and 2009 in the field of Tobacco Institute-Prilep in a randomized block design with four replications.
The aim of these investigations is to study the mode of inheritance and to determine heritability, i.e. degree of inheritance of major quantitative characters, which will allow us to give recommendations regarding the choice of parental genotypes and directions in creation of new cultivars, as our contribution to genetics of tobacco.
Mode of inheritance was estimated according to the test- significance of the mean value of F1 progeny compared to the parental average. Narrow-sense heritability was estimated after Allard (1960), while broad-sense heritability and genetic components after Mather and Jinks (1974).
The mode of inheritance in the hybrids was different. Positive heterosis for stalk height was recorded in S1 x S2 and S2 x P - 84, and for green and dry mass yields per stalk in S1 x S2. Negative heterosis occurs for leaf number and dry mass yield in S1 x P - 84 and S2 x P - 84 , while for dry mass yield in S1 x P - 84. Inheritance of the characters during the three years of investigation was identical. The highest narrow- and broad-sense heritability index during the three years of investigation was recorded for stalk height in 2007, and for dry mass yield in 2008 and 2009. The lowest values for both types of heritability were recorded for the character leaf number per stalk. In all investigated charcters, the values of broad-sense heritability were higher than those of narrow-sense heritability.

Keywords: tobacco (*Nicotiana tanacum* L.), heredity, intermediate, partial dominance, dominance, heterosis, narrow-sense and broad-sense heritability (h^2).

ПРОУЧУВАЊА ЗА ХЕРИТАБИЛНОСТА КАКО ПОКАЗАТЕЛ ЗА НАСЛЕДНОСТА НА КВАНТИТАТИВНИТЕ СВОЈСТВА КАЈ ТУТУНОТ

Испитувањата ги опфаќаат начинот и степенот на наследување на поважните квантитативни својства: висина на страк, број на листови по страк, површина на листовите од средниот појас, принос на зелена и принос на сува маса по страк, кај четири родителски генотипови (Берлеј – Б 2/93, Suhum – S1, , Suhum – S2 и Прилеп – П-84) и нивните шест дијалелни F1 хибриди. Опитот беше поставен во 2007, 2008 и 2009 година на опитното поле при Научниот институт за тутун – Прилеп по случаен блок – систем во четири повторувања.

Целта на овие истражувања е да го откриеме начинот на наследување и да ја одредиме херитабилноста т.е. степенот на наследување на поважните квантитативни својства, со што ќе дадеме напатствија за изборот на родителски генотипови и насоки во селекцијата за создавање на нови сорти, како и допринос во генетиката на тутунот.

Начинот на наследување се одреди врз база на тест сигнификантноста на средните вредности кај F1 потомството во однос на родителските просеци. Херитабилноста во потесна смисла се пресмета спрема Allard (1960), а херитабилноста во поширока смисла, како и генетските компоненти спрема Mather и Jinks (1974).

Наследувањето на својствата во трите години на истражување е идентично. Начинот на наследување кај крстоските е различен. Позитивен хетерозис се јавува за висина на стракот кај S1 x S2 и S2 x П-84, а за приносот на зелена маса и приносот на сува маса по страк кај S1 x S2. Негативен хетерозис се јави за бројот на листови и приносот на зелена маса по страк кај S1 x П-84 и S2 x П-84, додека за приносот на сува маса по страк кај S1 x П-84. Највисока процентуална вредност за херитабилноста во потесна и поширока смисла во 2007 година има својството висина на стракот, а во 2008 и 2009 година принос на сува маса по страк. Најниска процентуална вредност за двата типа на херитабилност во трите години на истражување има својството број на листови по страк. Кај сите проучувани својства вредностите за херитабилноста во поширока смисла се повисоки од оние за херитабилноста во потесна смисла.

Клучни зборови: тутун (Nicotiana tanacum L.), наследување, интермедијарност, парцијална доминантност, доминантност, хетерозис, херитабилност (h^2) во потесна и поширока смисла.

INTRODUCTION

Heritability is genetic index for prognosis of the selection results. Many authors made investigations on the inheritance of characters in various cultures, including tobacco. Povilaitis (1966) reported low heritability in a diallel set of eight flue-cured varieties for leaf number and yield per stalk, while for the character leaf area the highest heritability was recorded in top leaves. Espino and Capote (1976), in diallel of seven dark tobacco varieties, reported medium heritability for stalk height and leaf number and low heritability for yield per stalk. Ibrahim and Avratovscukova (1984), in five flue-cured varieties and ten diallel F1 hybrids, recorded high to moderate broad-sense heritability for stalk height and yield, and moderate heritability for leaf number per stalk. Dobhal (1987) reported high heritability for leaf number in 25 genotypes of cigar wrapper tobacco. Naumovski (1987) reported high heritability in a diallel of oriental tobacco for leaf number. In 55 genotypes of Nicotiana rustica (hookah and chewing tobacco) Dobhal and Nageswara Rao (1988) reported moderate heritability for stalk height and yield. Legg (1989), in seven homozygous genotypes of dark and flue-cured tobacco and 21 F1 hybrids, found heritability high enough to justify the process of selection. Chaubey et al. (1990) obtained high heritability for leaf number and yield per stalk in 72 genotypes of Nicotiana rustica. Butorac (1999) investigated four parental varieties of Burly tobacco and their diallel F1, F2, BC1 and BC2 progenies and reported that their broad-sense heritability was higher than the narrow-sense heritability. The highest heritability was estimated in inheritance of the leaf area and the sixth leaf weight. Korubin-Aleksoska and Aleksoski (2009) in three oriental and one semi-oriental variety and their F1 and F2 progenies obtained very high index for both types, with predominance of the broad-sense heritability.

The aim of the three-years investigation was to determine the mode and grade of inheritance of some major quantitative characters of F1 progeny in four varieties in order to improve our knowledge on the genetic nature and to give further directions in selection of tobacco.

MATERIAL AND METHODS

Four tobacco varieties were included in investigations: one large-leaf - Burley B2/93 (Photo 1) and three oriental - Suhum S1 and S2 (Photo 2 and Photo 3) and Prilep P-84 (Photo 4), together with their six diallel F1 hybrids (Aleksoski, 2009). The trial with parental genotypes and their F1 progenies was set up in 2007, 2008 and 2009 in the field of Scientific Tobacco Institute-Prilep in randomized blocks with four replications. The area of each replication was 150 m^2 and the area of the total trial was 600 m^2. All suitable cultural practices were applied during the growth period of tobacco.

In 2007, during tobacco growth in field (May-September), mean monthly temperature was 20.88 ^{0}C and the number of rainy days was 40, with 229.9 mm total amount of precipitation. In the same period in 2008, mean monthly temperature was 19.91^0 C, the number of rainy days 39 and the total amount of precipitations 235.4 mm. In 2009, mean monthly temperature was 19.89^0 C, the number of rainy days 42 and the total amount of precipitations 240.6 mm.

The following characters were investigated in this paper: stalk height without inflorescence, leaf number per stalk, middle belt leaf area, green mass yield per stalk and dry mass yield per stalk. Data obtained for each character were analysed using the analysis of variance.

Mode of inheritance of quantitative characters was determined by test-significance of the mean values in F1 progeny and their comparison with parental averages (Borojević, 1981).

Heritability (h^2) is the ratio between the components of genetic and phenotypic variance. It can be presented in two ways and is expressed in percentages.

Photo 1. Burley B 2/93

Photo 2. Suchum S1

Photo 3. Suchum S2

Photo 4. Prilep P - 84

Narrow-sense heritability in some combinations is the ratio of the additive component of genetic variance over the phenotypic variance and is calculated using the Allard's formula (1960) :

$$h^2_{NS} = VA / VP \text{ or } h^2 = \frac{\sigma^2 F_2 - \frac{\sigma^2 P_1 + \sigma^2 P_2 + \sigma^2 F_1}{3}}{\sigma^2 F_2} \cdot 100$$

Broad-sense heritability for all combinations of F1 progeny is the ratio of the total genetic variance (additive and dominant) over the phenotypic variance, and is calculated using the formula of Mather and Jinks (1974):

$$h^2_{BS} = (VA + VH) / VP \text{ or } h^2 = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}$$

Estimation of the genetic copmponents D, H1, H2 and F was made after Mather and Jinks (1974).

RESULTS AND DISCUSSION

Our three-year investigations revealed different modes of inheritance of the character stalk height without inflorescence (Table 1). In hybrids where one of the parents is the large-leaf B 2/93 this character is inherited intermediary, except for the hybrid B 2/93 x FO in 2009, where the mode of inheritance was partial dominance. Positive heterosis was observed in S1 x S2 and S2 x FO. No occurrence of negative heterotic effect was observed in the diallel.

Table 1. Mode of inheritance of the character stalk height without inflorescence in F1 progeny (cm)

Parents and F1 hybrids	2007 $\bar{x} \pm s_{\bar{x}}$		2008 $\bar{x} \pm s_{\bar{x}}$		2009 $\bar{x} \pm s_{\bar{x}}$		$\bar{x}$	
1. P1	147,09 ± 0,37		141,85 ± 0,36		149,88 ± 0,35		**146,27**	
2. P2	69,97 ± 0,29		67,83 ± 0,27		70,09 ± 0,26		**69,30**	
3. P3	69,53 ± 0,30		66,79 ± 0,28		70,01 ± 0,28		**68,78**	
4. P4	57,75 ± 0,25		57,29 ± 0,23		57,82 ± 0,21		**57,62**	
5. P1 x P2	104,85 ± 0,16	i	103,35 ± 0,18	i	108,20 ± 0,18	i	**105,47**	i
6. P1 x P3	102,50 ± 0,19	i	101,91 ± 0,19	i	102,65 ± 0,18	i	**102,35**	i
7. P1 x P4	100,50 ± 0,18	i	91,15 ± 0,19	i	99,89 ± 0,17	pd	**97,18**	i
8. P2x P3	**70,19 ± 0,9**	**+h**	**68,85 ± 0,10**	**+h**	**71,48 ± 0,10**	**+h**	**70,17**	**+h**
9. P2 x P4	70,98 ± 0,12	+d	68,97 ± 0,13	+d	71,08 ± 0,12	+d	**70,34**	+d
10. P3 x P4	**71,82 ±0,14**	**+h**	**69.86 ± 0,12**	**+h**	**72.53 ± 0,14**	**+h**	**71,40**	**+h**

Legend:

- P1 - Burley B - 2/93
- P2 - Suchum S1
- P3 - Suchum S2
- P4 - Prilep P - 84
- i - Intermediate
- pd - Partial dominance
- d - Dominance (positive and negative)
- h - Heterosis (positive and negative)

The inheritance of leaf number per stalk in hybrids where B 2/93 is one of the parents was negatively dominant in all three years of investigation. This indicates the dominance of the parent with lower number of leaves. In S1 x S2 partial and positive dominance were recorded, while in S1 x P-84 and S2 x P-84 there was occurrence of negative heterosis (Table 2).

Table 2. Mode of inheritance of the character number of leaves per stalk in F1 progeny

Parents and F1 hybrids	2007 $\bar{x} \pm s_{\bar{x}}$		2008 $\bar{x} \pm s_{\bar{x}}$		2009 $\bar{x} \pm s_{\bar{x}}$		$\bar{x}$	
1. P1	35,61 ± 0,12		34,19 ± 0,10		35,45 ± 0,11		**35.08**	
2. P2	46,70 ± 0,10		44,66 ± 0,10		46,81 ± 0,09		**46.06**	
3. P3	47,09 ± 0,10		44,87 ± 0,10		46,92 ± 0,10		**46.29**	
4. P4	53,47 ± 0,09		52,37 ± 0,11		53,33 ± 0,10		**53.06**	
5. P1 x P2	35,24 ± 0,07	-d	34,54 ± 0,06	-d	35,47 ± 0,06	-d	**35.08**	-d
6. P1 x P3	35,85 ± 0,06	-d	34,41 ± 0,05	-d	35,58 ± 0,06	-d	**35.28**	-d
7. P1 x P4	36.88 ± 0,07	-d	35,22 ± 0,05	-d	36,79 ± 0,07	-d	**36.30**	-d
8. P2x P3	46,95 ± 0,04	pd	44,90 ± 0,03	+d	46,93 ± 0,04	+d	**46.26**	+d
9. P2 x P4	43,26 ± 0,05	-h	42,25 ± 0,04	-h	42,07 ± 0,05	-h	**42.53**	-h
10. P3 x P4	44,65 ± 0,05	-h	42,88 ± 0,04	-h	43,26 ± 0,04	-h	**43.60**	-h

The character middle belt leaf area was inherited with partial dominance, except for S2 x P-84 where the inheritance was intermediate. In selection, this indicates fast stabilization of the character in future (Table 3).

Table 3. Mode of inheritance of the character middle belt leaf area in F1 progeny (cm²)

Parents and F1 hybrids	2007 $\bar{x} \pm s_{\bar{x}}$		2008 $\bar{x} \pm s_{\bar{x}}$		2009 $\bar{x} \pm s_{\bar{x}}$		$\bar{x}$	
1. P1	1263,88 ± 9,55		1138,31 ± 9,43		1304,21 ± 0,35		**1235.47**	
2. P2	230,22 ± 1,73		204,60 ± 1,77		234,74 ± 0,26		**223.19**	
3. P3	239,24 ± 1,71		220,46 ± 1,62		239,87 ± 0,28		**233.19**	
4. P4	146,24 ± 1,87		137,56 ± 1,75		148,63 ± 0,21		**144.14**	
5. P1 x P2	1063,44 ± 2,23	pd	1015,70 ± 2,53	pd	1063,17± 2,33	pd	**1047.44**	pd
6. P1 x P3	1074,49 ± 2,18	pd	988,24 ± 2,62	pd	1018,29 ± 2,25	pd	**1027.01**	pd
7. P1 x P4	903,39 ± 2,99	pd	832,39 ± 2,38	pd	942,43 ± 2,44	pd	**892.74**	pd
8. P2x P3	233,34 ± 1,73	pd	209,59 ± 1,44	pd	236,21 ± 1,53	pd	**226.11**	pd
9. P2 x P4	185,26 ± 1,73	i	173,40 ± 1,79	i	187,93 ±1,70	i	**182.20**	i
10. P3 x P4	174,53 ± 1,86	pd	158,22 ± 1,53	pd	176,28 ±1,67	pd	**169.68**	pd

The inheritance of green mass yield per stalk in progenies with B 2/93 as one of the parents was partially dominant. Positive heterosis ocurred in S1 x S2 and negative heterotic effect was recorded in the hybrids S1 x P-84 and S2 x P-84 (Table 4).

Table 4. Mode of inheritance of the character green mass yield per stalk in F1 progeny (g)

Parents and F1 hybrids	2007 $\bar{x}$		2008 $\bar{x}$		2009 $\bar{x}$		$\bar{x}$	
1. P1	1098,63		1016,90		1100,24		**1071,92**	
2. P2	267,27		209,64		283,18		**253,36**	
3. P3	260,45		207,65		275,41		**247,84**	
4. P4	159,73		157,88		169,35		**162,32**	
5. P1 x P2	812,77	pd	800,19	pd	812,93	pd	**808,63**	pd
6. P1 x P3	811,58	pd	808,36	pd	824,11	pd	**814,68**	pd
7. P1 x P4	795,45	pd	790,55	pd	832,39	pd	**806,13**	pd
8. P2x P3	**269,44**	**+h**	**210,50**	**+h**	**294,27**	**+h**	**258,07**	**+h**
9. P2 x P4	133,24	-h	130,26	-h	146,32	-h	**136,61**	-h
10. P3 x P4	135,11	-h	133,27	-h	148,24	-h	**138,87**	-h

Modes of inheritance and average values for the character dry mass yield per stalk in the investigating period are presented in Table 5. Positive heterosis was observed in S1 x S2 and negative heterosis in S1 x P-84.

Table 5. Mode of inheritance of the character dry mass yield per stalk in F1 progeny (g)

Parents and F1 hybrids	2007 $\bar{x}$		2008 $\bar{x}$		2009 $\bar{x}$		$\bar{x}$	
1. P1	185,43		177,85		190,55		**184.61**	
2. P2	25,99		24,73		26,04		**25.59**	
3. P3	26,03		25,03		26,17		**25.74**	
4. P4	24,01		23,68		24,49		**24.06**	
5. P1 x P2	132,15	pd	129,88	pd	130,42	pd	**130,82**	pd
6. P1 x P3	133,24	pd	130,04	pd	145,95	pd	**136,41**	pd
7. P1 x P4	122,15	i	117,33	i	116,31	i	**118,60**	i
8. P2x P3	**26,40**	**+h**	**25,29**	**+h**	**26,88**	**+h**	**26,19**	**+h**
9. P2 x P4	23,14	-h	22,74	-h	23,79	-h	**23,22**	-h
10. P3 x P4	24,05	-d	23,75	-d	24,29	-d	**24,03**	-d

Our investigations on the major quantitative characters of tobacco showed high values for both types of heritability, which indicates the presence of a very high genetic variability and insignificant environmental variability. For these reasons, the investigated characters appeared to be highly heritable, i.e. their manifestation can be easily predicted and their faster stabilization can be obtained.

The highest narrow- and broad- sense heritability in 2007 (Table 6) was recorded for the character stalk height without inflorescence (h^2_{NS} = 0,9776, h^2_{BS} = 0,9988), while in 2008 and 2009 for dry mass yield per stalk (2008 - h^2_{NS} = 0,9687, h^2_{BS} = 0,9988; 2009 - h^2_{NS} = 0,9788, h^2_{BS} = 0,9989). The lowest values for both heritability types in the three-year investigations was recorded for leaf number per stalk ((2007 - h^2_{NS} = 0,7447, h^2_{BS} = 0,9867; 2008 - h^2_{NS} = 0,7577, h^2_{BS} = 0,9879; 2009 - h^2_{NS} = 0,7563, h^2_{BS} = 0,9869).

High heritability values were also reported by the following authors: Ibrahim and Avratovscukova (1984) in five flue-cured varieties and ten F1 hybrids for stalk height and yield per stalk, Dobhal (1987) in 25 cigar wrapper genotypes, Naumovski (1987) in a diallel of oriental varieties for leaf number per stalk, Chaubey et al. (1990) in 72 genotypes of Nicotiana rustica for leaf number and yield per stalk and Korubin –Aleksoska анд Aleksoski (2009) in a diallel of three oriental and one semi-oriental variety for some more important quantitative characters in tobacco. Butorac (1990) reported higher broad-sense heritability compared to the narrow-sense heritability in a diallel of four Burley varieties, which coincides with the results of the above mentioned authors and with data presented in this paper.

Table 6. Heritability of the quantitative characters in F1 progeny

Heritability (%)	Stalk height without inflorescence	Leaf number per stalk	Middle belt leaf area	Green mass yield per stalk	Dry mass yield per stalk
		2007			
Narrow - sense	0.9776	0.7447	0.9335	0.9578	0.9714
Broad - sense	0.9988	0.9867	0.9983	0.9965	0.9954
		2008			
Narrow - sense	0.9676	0.7577	0.9184	0.9418	0.9687
Broad - sense	0.9973	0.9879	0.9948	0.9983	0.9988
		2009			
Narrow - sense	0.9753	0.7563	0.9245	0.9492	0.9788
Broad - sense	0.9983	0.9869	0.9978	0.9972	0.9989

CONCLUSIONS

On the basis of presented data and analysis, the following conclusions can be drawn:

- Parental genotypes B 2/93, S1, S2 and P-84 and their F1 progenies are uniform. Stalk height without inflorescence was most frequently inherited with intermediate mode, leaf number per stalk with negative dominance and middle belt leaf area, green mass yield and dry mass yield per stalk with partial dominance. Positive heterosis for stalk height was observed in S1 x S2 and S2 x P - 84, and for green mass yield in S1 x S2. Negative heterotic effect for leaf number and green mass yield was observed in S1 x P-84 and S2 x P-84, while for dry mass yield in S1 x P-84. The mode of inheritance of quantitative characters was identical in all three years of investigation (except for the characters stalk height in B 2/93 x P - 84 and leaf number per stalk in S1 x S2, in which insignificant differences provoked by non-genetic factors were observed).
- The highest value of narrow- and broad-sense heritability in 2007 was recorded for stalk height and in 2008/2009 for dry mass yield. The lowest value for both heritability types during the three years of investigation was observed in leaf number. In all characters investigated, the values for broad-sense heritability were higher than those for narrow-sense heritability.
- High genetic variance is manifested in investigated quantitative characters, which can be noted from the high percentual values for heritability. Therefore, it is about highly heritable characters which will be fixed and stabilized in a short period of time.

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