Inheritance of certain economic and agronomic traits in burley tobacco

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Vererbung einiger wertbestimmender und agronomischer Merkmale in Burleytabak

1. Introduction

Selection of qualitative genetic material, that is, selection of parent pairs for crossing, is of vital importance for the success of breeding, since hybridization is the most commonly used method for obtaining new cultivars. Most traits of interest to breeders are of quantitative nature. The diallel cross technique is used as one of the basic procedures to study the problem of inheritance of quantitative traits. GRIFFING (1956) elaborated mathematically four methods for the analysis of diallel cross data, depending on the material available. In most papers dealing with tobacco, significant GCA for economic and agronomic traits was estimated by LEGG et al. (1970), LEGG and COLLINS (1971a, 1971b), MATZINGER et al. (1971), LEGG and COLLINS (1975), WILKINSON and RUFTY (1990). In some studies, however, along with significant GCA, also significant SCA was recorded for yield (LEGG et al., 1970; MATZINGER et al., 1971; GUDOY et al., 1987; WILKINSON and RUFTY, 1990), for plant height (GUDOY et al., 1987; WILKINSON and RUFTY, 1990), leaf number (GUDOY et al., 1987), and days to flowering (LEGG et al., 1970; LEGG and COLLINS, 1971a).

In addition to Griffing's method for estimating heritability and the manner of inheritance, the additive-dominant model after HAYMAN (1954) and JINKS (1954), as well as MATHER and JINKS (1971) is also used. Publication and application of the mentioned models was followed by appearance of numerous papers in which the authors tried to justify, restrict, compare or interpret the Hayman-Jinks and Griffing methods of diallel cross analysis (ARUNACHALAM, 1976; BAKER, 1978; POONI et al., 1984; SINGH and PARODA, 1984; WRIGHT, 1985; UKAI, 1991). The so far studies involving the use of the additive-dominant model of economic and agronomic traits in burley tobacco indicate significant additive variance (COLLINS et al., 1976; OKAMURA and NAKAHARA, 1983). Besides significant additive variance, however, significant nonadditive variance for plant height and internode lenght was also estimated in air-cured tobaccos by POVILAITIS (1966), AYUB et al. (1981) and OKAMURA and NAKAHARA (1983).

Zusammenfassung

Das Ziel der Untersuchung war die Schätzung der Vererbung von ökonomischen (Ernte und Qualität) und agronomischen (Kopfhöhen, Pflanzenhöhe, Internodienlänge, Blattzahl und Blühbeginn) Merkmalen, die für die Schätzung den genetischen Varianzkomponenten und der Kombinationsfähigkeit benutzt wurden. Für die Erfordernisse dieser Untersuchung wurden vier Elternsorten von Burley und sechs ihrer F_1 Hybriden ausgewählt und geprüft. Der vierjährige Feldversuch wurde als randomisierte Blockanlage (RCBD) in vier Wiederholungen geprüft. Die signifikante allgemeine und spezifische Kombinationsfähigkeit wurde für alle Merkmale beurteilt mit Ausnahme der allgemeinen und spezifischen Kombinationsfähigkeit des Blühbeginns und der allgemeinen Kombinationsfähigkeit der Pflanzenhöhe, die nicht beurteilt wurden. Die Sorte TN86 und Poseydon zeigten sich am besten hinsichtlich der allgemeinen Kombinationsfähigkeit, während die Hybriden Hy71 x BL1, Hy 71 x TN 86 und Poseydon x BL1 am besten hinsichtlich der spezifischen Kombinationsfähigkeit abschnitten. Die Analyse der genetischen Varianzkomponenten zeigte, dass die höhere nicht additive Varianz bei der Mehrzahl der untersuchten Merkmale zu finden war.

Schlagworte: *Nicotiana tabacum L.*, Burley, Kombinationsfähigkeit, genetische Varianzkomponenten, ökonomische und agronomische Merkmale.

Summary

The goal of the investigations was to estimate the manner of inheritance of economic (yield and grade index) and agronomic traits (topping height, plant height, internode length, leaf number and days to flowering) using the components of genetic variance and combining abilities. Four parent burley tobacco cultivars and their 6 F_1 hybrids were separated for the needs of this study. The 4-year trial was set up according to the RCBD in 4 replications. Significant GCA and SCA were estimated for all traits, except for days to flowering and GCA also for plant height. Cultivars TN 86 and Poseydon were the best general combiners while Hy 71xBL1, Hy 71xTN 86 and PoseydonxBL1 were the best specific combinations. According to the components of genetic variance, higher nonadditive variance was estimated for the most traits studied.

Key words: *Nicotiana tabacum L.*, burley, combining ability, components of genetic variance, economic and agronomic traits.

The goal of these investigations was to estimate on specific materials: 1. the manner of inheritance of economic traits (yield and grade index) and agronomic traits (topping height, plant height, internode length, leaf number, days to flowering) using the components of genetic variance, 2. the value of parent genotypes as combiners, and 3. the best specific cross combinations.

2. Material and methods

Four line cultivars were separated for the purposes of this trial: American line cultivar TN 86 (MILLER, 1987) and three burley lines, BL1, Hy 71 (DEVČIĆ and BOLSUNOV, 1975) and Poseydon (DEVČIĆ et al., 1984), developed in the Tobacco Institute Zagreb.

Four-year investigations started in 1992 at the experimental field of the Tobacco Institute Zagreb in Božjakovina. The trial was set up according to the RCBD in 4 replications. Standard agrotechnical practices for burley tobacco were applied.

In all four investigation years, the trial included 10 genotypes, viz. 4 line cultivars and their F_1 hybrids obtained a year earlier: Hy 71xTN 86, Hy 71xBL1, Hy 71xPoseydon, PoseydonxBL1, PoseydonxTN 86, and TN 86xBL1.

A number of agronomic traits were studied, while the only economic traits involved were leaf yield and grade index. Leaves were dried by the standard procedure for burley tobacco. Grade index was based on a 1 to 100 scale, with 100 representing the highest quality.

The following agronomic traits were studied: topping height, plant height, internode length, leaf number and days to flowering. Topping height was measured from the ground to topping level, and plant height to the inflorescence tip. Internode length was measured between the 12^{th} and 13^{th} leaves. Number of leaves was estimated at the end of the growing season. Days to flowering were estimated visually, the appearance of 25 % open flowers serving as the criterion. Data for all traits were taken on a sample of 80 plants.

The data were statistically analyzed by analysis of variance. Combining abilities for all traits and for all 4 investigation years were estimated according to Griffing's method 2, model l (GRIFFING, 1956). Components of genetic variance (D, H1, H2, F, E, $\sqrt{H1/D}$, H2/4H1 and Kd/Kr) were estimated using the methods of JINKS (1954), HAYMAN (1954), and MATHER and JINKS (1971).

3. Results

The average performance of all parents and F_1 hybrids for economic and agronomic traits from 1992 to 1995 are presented in Table 1. Results of F-test for genotypes and years according to agronomic and economic traits are in Table 2. Significant GCA and SCA were estimated for all traits, except for days to flowering and GCA also for plant height. The GCA mean squares were more than twice the SCA mean squares for yield, leaf number and days to flowering.

GCA effects of parent lines are presented in Table 3 for all the studied traits. Cultivar TN 86 was the best general combiner for yield and leaf number. The obtained values were significant. TN 86 would also significantly contribute to an increased topping height. Cultivar Poseydon was also among better cultivars, primarily for yield, grade index and internode length.

SCA effects are given in Table 4. All F_1 hybrids, except Hy 71xPoseydon were better specific combinations for yield,

Table 1: Means of parents and F_1 hybrids for economic and agronomic traits
Tabelle 1: Mittelwerte der Eltern und F_1 Hybriden für ökonomische und agronomische Merkmale

Trait	Genotype									
	TN 86	BL1	Hy 71	Poseydon	Hy 71x TN 86	Hy 71x BL1	Hy 71x Poseydon	Poseydon x BL1	Poseydon x TN 86	TN 86 x BL1
Yield (kg/ha)	2869	2003	1790	2508	2640	2741	2424	3198	3031	2899
Grade index	36,67	34,76	32,85	37,19	37,65	38,23	35,64	40,06	38,33	34,44
Topping height (cm)	139	127	123	137	140	146	137	142	151	140
Plant height (cm)	161	148	145	161	179	178	167	162	168	162
Internode lenght (cm)	3,83	3,55	3,71	4,03	4,34	4,27	4,06	4,25	4,48	4,01
Leaf number	26	25	23	25	26	26	25	27	27	27
Days to flowering	85	83	81	82	79	77	78	80	80	85

Table 2: Results of F-test for genotypes and years according to economic and agronomic traits
Tabelle 2: Ergebnisse des F-Testes für die Genotypen und Jahre nach wertbestimmenden und agronomischen Merkmalen

Source of variation	d.f.	Trait						
		Yield (kg/ha)	Grade index	Topping height (cm)	Plant height (cm)	Internode length (cm)	Leaf number	Days to flowering
genotype	9	7.52*	2.07N.S.	3.27*	9.21*	4.80*	3.29*	3.05*
year	3	8.38*	10.14*	2.83N.S.	24.24*	48.31*	4.31*	18.53*

* Significant at the 0.05 level of probability, respectively.

Table 3: GCA effects of parent lines for economic and agronomic traits
Tabelle 3: Wirkung der allgemeinen Kombinationsfähigkeit für wertbestimmende und agronomische Merkmale

Parents	Trait						
	Yield	Grade index	Topping height	Plant height	Internode length	Leaf number	Days to flowering
TN 86	209.39*	0,14	2.92*	2,56	0,04	0.58*	1,60
BL1	-34,68	-0,11	-1,50	-2,94	-0.11*	0,17	0,48
Hy 71	-277.77*	-0.95*	-3.58*	-0,23	-0,03	-0.87*	-1,69
Poseydon	103.06*	0.92*	2,17	0,60	0.09*	0,13	-0,39

* Estimate is significantly different from zero at the 0,05 level of probability, respectively.

Table 4: SCA effects for economic and agronomic traits
Tabelle 4: Wirkung der spezifischen Kombinationsfähigkeit für wertbestimmende und agronomische Merkmale

Crosses	Trait						
	Yield	Grade index	Topping height	Plant height	Internode length	Leaf number	Days to flowering
Hy 71 x TN 86	97.95*	1.87*	2,12	13.24*	0.27*	0,29	-2,29
Hy 71 x BL1	443.03*	2.70*	13.03*	17.99*	0.35*	0.96*	-3,17
Hy 71 x Poseydon	-11,71	-0,91	0,12	3,20	-0,06	-0,25	-1,04
Poseydon x BL1	519.20*	2.67*	3,03	1,16	0.21*	0.96*	-1,45
Poseydon x TN 86	108.11*	0,68	7.62*	1,91	0.29*	0,29	-1,83
TN 86 x BL1	113.86*	-2.17*	0,03	-0,55	0,03	0.75*	2,29

* Estimate is significantly different from zero at the 0,05 level of probability, respectively.

which achieved significant values. Hy 71xTN 86, Hy 71xBL1 and PoseydonxBL1 were also singled out as better specific combinations for grade index. These crosses are actually crosses of parents having poor GCA estimated, except cultivar Poseydon. Hy 71xBL1 would also significantly contribute to an increased topping height, plant height, internode length and leaf number while PoseydonxBL1 an increased internode length and leaf number. Hy 71xTN 86 can be singled out as a better specific combination for plant height and for internode length. Poseydon x TN 86 was also singled out as a better specific combinations for topping height and internode length and TN 86xBL1 for leaf number.

Components of genetic variance were estimated as well, in order to study the manner of inheritance of the seven chosen traits. Their values are given in Table 5. The statistics representing additive and dominance effects of genes were significant for yield, topping height, internode length and leaf number. Thus, it may be taken that additive and nonadditive variance participated to nearly the same extent in inheritance of these traits. However, grade index and plant height were nonadditively inherited. The sign of the component F indicates the relative frequencies of dominant and recessive allels. Positive values of F indicate an excess of dominant alleles and negative values an excess of recessive alleles. F for the studied traits is mainly of a positive sign and mostly marks dominant action, except for leaf number and days to flowering. A further ratio, Kd/Kr provides the estimate of the ratio between the total number of dominant to recessive genes in all the parents. Kd/Kr ratios are in line with the interpretation of values obtained for F values. The proportion H2/4H1, which provides an estimate of the average frequency (uv) of positive (u) versus negative (v) alleles in the parents, where u+v=1 attains a maximum value of 0.25 when these frequencies are equal (uv = 0.50 x 0.50 = 0.25). The estimated values for all traits deviated from 0.25, except for topping height and internode lenght. For the days to flowering, however H1<H2 and therefore the ratio has no particular meaning. Due to negative value D obtained for days to flowering, it was not possible to calculate the values for $\sqrt{H1/D}$ and Kd/Kr. According to the degree of dominance ($\sqrt{H1/D}$), overdominance in inheritance was estimated for all traits.

4. Discussion

Since most tobacco traits important for successful breeding are of quantitative nature, estimates of combining abilities and inheritance contribute to their better understanding, thereby enabling rational and targeted combining of desirable genes into future cultivars. Two good cultivars do not necessarily produce a progeny having some better traits or, even less frequently, an overall better progeny. We speak of good or poor combining abilities between certain parents. Unfortunately, knowing parent traits does not enable prediction of the combining abilities of these parents in hybrid combinations. Combining abilities should, therefore, be investigated in all the cases aimed at detecting the possibility of superior progenies. There are various mathematical models for the analysis of combining abilities, their use depending also on the genetic material available.

Quantitative traits are of major importance in all crops and so are also yield and quality in tobacco. Studies of yield and quality GCA and SCA (LEGG et al., 1970; LEGG and COLLINS, 1971a; 1971b; 1975; DEAN, 1974; OGILVIE and KOZUMPLIK, 1983; WILKINSON and RUFTY, 1990) and studies of yield components of genetic variance (COLLINS et

Table 5: Components of genetic variance, standard errors and significance for economic and agronomic traits
Tabelle 5: Genetische Varianzkomponenten, Standardfehler und Grenzwahrscheinlichkeit für ökonomische und agronomische Merkmale

Components of genetic variance	Trait						
	Yield	Grade index	Topping height	Plant height	Internode lenght	Leaf number	Days to flowering
D	226163.6+/-49731.4*	2.51+/-1.89N.S.	44.82+/-21.53*	35.01+/-59.48N.S.	2.79+/-1.04*	1.23+/-0.11*	-3,24+/-2.02N.S.
H_1	473535.3+/-144563.5*	15.42+/-5.51*	176.45+/-62.59*	437.05+/-172.89*	0.26+/-3.03*	2.39+/-0.31*	8.76+/-5.89N.S.
H_2	422436.5+/-133443.3*	14.93+/-5.09*	177.51+/-57.77*	375.98+/-159.59*	0.27+/-2.80*	2.11+/-0.29*	9.40+/-5.44N.S.
F	117926.9+/-127762.3N.S.	1.71+/-4.87N.S.	21.14+/-55.31N.S.	91.10+/-152.79N.S.	4.93+/-2.68N.S.	-0.14+/-0.27N.S	-11.60+/-5.21N.S.
E	12326.4+/-22240.6N.S.	1.38+/-0.85N.S.	13.44+/-9.62N.S.	34.91+/-26.59N.S.	1.35+/-4.67*	0.14+/-4.83*	6.37+/-0.91*
$H_2/4H_1$	0,22	0,24	0,25	0,22	0,25	0,22	0,27
H_1/D	1,45	2,47	1,98	3,53	3,10	1,39	-
Kd/Kr	1,43	1,31	1,27	2,17	1,06	0,92	-

al., 1976) point to preponderance of significant GCA over SCA and additive over nonadditive variance. Also in our own investigations, significant GCA values were obtained for yield. However, in our investigations and in some others (POVILAITIS, 1966; MATZINGER et al., 1971; PANDEYA et al., 1983; GUDOY et al., 1987), SCA was also significant along with GCA and additive component along with nonadditive component of genetic variance. So, inheritance of yield appears to be influenced by both additive and nonadditive variance. Our investigations, however, primarily point to a larger role of nonadditive variance for grade index.

Breeding programmes of recent years have been conceived so as to be aimed, among others, at reducing the height of tobacco plants and their internode length without decreasing the number of leaves. This should lead to a higher lodging resistance, whereby also to higher yields. According to the so far studies of GCA and SCA for topping height (LEGG et al., 1970; LEGG and COLLINS, 1971a; 1971b; MATZINGER et al., 1971) significant GCA prevails over SCA. In contrast to other studies, we have estimated, besides significant GCA, also significant SCA for topping height and for internode length. According to the results of AYCOCK Jr. (1980), ESPINO and GIL (1980), GUDOY et al. (1987), both combining abilities were significant for plant height and also additive and nonadditive components of genetic variance (POVILAITIS, 1966; OKAMURA and NAKAHARA, 1983) while internode length is inherited more dominantly (AYUB et al., 1981). Our results on topping and plant height point primarily to a greater role of the nonadditive component of variance. Moreover, only SCA were significant for plant height.

Leaf number is one of strongly genetically conditioned traits (BELJO, 1992). According to most studies of combining abilities and components of genetic variance, this trait is inherited additively (LEGG et al., 1970; LEGG and COLLINS, 1971a; 1971b; MATZINGER et al., 1971; COLLINS et al., 1976; OKAMURA and NAKAHARA, 1983). Based on our own research in combining abilities, however, significant GCA and SCA were estimated. Still, the GCA/SCA ratios obtained indicate a more pronounced effect of the additive component. However, the role of nonadditive variance is not negligible either. Components of genetic variance in our investigations manifest an equal role of additive and nonadditive variance in inheritance of this trait.

Another important plant trait is early ripeness, which is associated with the days to flowering. In inheritance of the days to flowering, important roles are played by dominance and epistasis, as well as their interaction, since some results of investigating combining abilities indicate significant SCA in addition to GCA (LEGG et al., 1970; LEGG and COLLINS, 1971a). In some studies, only SCA was estimated (GUDOY et al., 1987). Our own investigations also point to preponderance of nonadditive component of genetic variance.

The results obtained after application of different methods point to the conclusion that the additive/nonadditive variance ratio for the traits studied may vary in dependence on the genetic materials but also on the method applied. Based on the estimated results, which indicate a greater role of nonadditive genetic variance, a significant heterosis effect can be expected for the traits studied. Hence, breeding should be oriented towards development of hybrid cultivars.

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