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Original article

Studies of Inheritance and Heterosis for Quantitative Traits in Diallel F_1 Crosses in Tobacco

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Abstract

This paper studies the inheritance and heterotic effect in ten F1 crosses obtained by one-way diallel crossing between five parent genotypes: MV-1, P 76/86, Adiyaman, Basma-Cebel and P 66 9 7, for the following quantitative traits: number of leaves per stalk, length of leaves from the middle belt of the stalk and yield of green leaf mass per stalk and per hectare. The experiment was placed on the experimental field at the Scientific Institute for Tobacco - Prilep by random block system in 4 repetitions in the period from 2018 and 2019. During the vegetation period of the tobacco in the fields, all the usual agro-technical measures were applied. The aim of this work was to study the mode of inheritance of the quantitative traits, to detect heterosis in F1 generation and assess its economic viability. Analysis of variance revealed statistically significant differences between parents and their hybrids for traits in the two years of investigation. The most common way of inheritance of the traits is the partial-dominant, then the intermediate. Negative heterotic effect on the number of leaves per stalk has in P 76/86 x P 66 9 7. The hybrids MV-1 x Adiyaman, P 76/86 x Basma-Cebel, P 76/86 x P 66 9 7 and Basma-Cebel x P 66 9 7 have a positive heterotic effect on the length of the leaves. For the yield of green leaf mass per stalk and per hectare positive heterosis have Oriental hybrids where one of the parents is the variety P 66 9 7. Research provides very useful guidance for future successive selection activities.

Keywords: Tobacco, Quantitative Traits, Inheritance, Inthermediance, Partial Dominance, Dominance, Heterosis.

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INTRODUCTION

The mode of inheriting traits is an important factor for determining the directions and the duration in different selection programs. Heterotic effect or F_1 vigor is a phenomenon that occurs in the first generation where the offspring show higher (or lower) values for a particular trait from both parents. It is widely used in many crops where high yielding hybrids are developed. In tobacco F_1 hybrids with heterotic effect are poorly used due to their economic unviability, however there are opportunities for their use, such as resistance to economically significant diseases.

The topic of this paper is focused on how to inherit the most important quantitative traits in F_1 offspring of hybrids obtained by diallel crosses between varieties from different types of tobacco. In the last ten years, a number of authors – breeders have worked on this subject: Aleksoski (2010), in a two-year study of four parental genotypes and their six diallel F_1 hybrids, obtained a different way of inheriting of leaf length and a weak heterotic effect without economic justification. Gixhari & Sulovari (2010), performed three years of research at two locations in a genetically diverse population of eight oriental tobacco and their one-way diallel hybrids and obtained a dominant and partial-dominant mode of inheritance and heterosis for leaf size and yield. Aleksoski & Korubin – Aleksoska (2011), conducted three-year studies for green and dry mass yields in a one-way diallel of three oriental and one large-leaf variety and their six F_1 crosses and obtained positive and negative heterosis. Dimanov & Dyulgerski (2012), in ten F_1 crosses obtained from parent pairs of local and introduced Burley tobacco varieties found heterosis with varying strength for the number of leaves. Aleksoski et al. (2013), in a three-year study of four parent tobacco genotypes of different types and their six diallel F_1 hybrids found weak heterosis in inheritance of the leaf number. Imtiaz et al. (2014), in an experiment in Khan Gari, Mardan, Pakistan, with seven Virginia flue-cured genotypes and their 42 two-way diallel crosses found heterosis with high heterotic effect, with possibility of using it for leaf number per stalk, leaf length and weight of green leaf mass per plot. Dyulgerski & Radoukova (2015), studied the mode of inheritance, the coefficient of inheritance and the expression of heterosis and transgression in seven Burley-type crosses and seven Virginia-type crosses of local and introduced origin in F_1 and F_2 offspring and found a dominant and partial-dominant inheritance for the length of the leaves, always in the direction of the parent with longer leaves, and the resulting heterosis had no economic importance. Ramachandra et al. (2015), in genetic studies on the yield and quality of 62 genotypes (six lines of different types of tobacco, eight testers and their crosses), at the Agricultural Research Station, Nipaniat Belgaum, Karnataka - India, obtained hybrids superior to the control variety in number and length of leaves. Kinay & Yilmaz (2016), in the investigation with hybrids obtained with semidiallel hybridisations of Xanthi-2A, Nail, Gümüşhacıköy, Taşova, Katerini, Canik and Erbaa in Tokat Province, Turkey, found an average heterosis of 28.4%. The heterotic effect on dry leaf yield was 4%. Shah et al. (2017), In a two-year study of ten Virginia flue-cured hybrids in a field experiment set in agro-ecological conditions at Khan Gari

in Mardan, Pakistan, they found highly significant differences in the number of leaves per stalk. Aleksoski (2018), in four oriental varieties and their diallel F_1, F_2, BC_1 (P1) and BC_1 (P2) crosses for the number and length of leaves per stalk, and found low variability in F_1 generation, indicating uniformity of populations due to homozygosity of parent pairs. Dyulgerski & Docheva (2018), analyzed ten introduced Burley tobacco varieties for biological, economic, and chemical traits and found that Kentucky 908 and Banquet 102 could be used in selection programs as donors to increase leaf number, leaf length, and yield. Ganachari et al. (2018), examined six flue-cured tobaccos and their 30 crosses at ZAHRS (Zonal Agricultural and Horticultural Research Station), College of Agriculture - Shivamogga, Karnataka - India, to assess heterosis for dry leaf yield and its components. The authors discovered five hybrids that showed a highly significant heterotic effect. Ganachari et al. (2018), in their research on six flue-cured tobacco and their 30 diallel crosses in ZAHRS, Karnataka, India, for inheritance of leaf number per stalk, did not show significant differences between genotypes but received heterosis with a highly significant heterotic effect on leaf number and yield. Korubin – Aleksoska & Dojcinov (2018), in five parent varieties of which four oriental in the role of a mother and one large-leafed flue-cured variety in the role of a father and their four F_1 crosses to inherit the dimensions of the leaves from the middle belt and found intermediate and partial dominant mode of inheritance, without heterosis. Aleksoski (2019), in a one-way diallel of four small-leaf aromatic and one large-leaf flue-cured variety, and their 10 F_1 crosses, discovered partial dominance and negative heterosis for leaf number per stalk, all possible inheritance modalities and positive heterosis for leaf dimensions and yield. Dyulgerski (2019), in eight Burley newly created hybrid combinations from first-generation, for leaf number and yield has found that all of them are better than the standard variety Pliska 2002, which indicates the possibility of exploiting heterosis in Burley tobacco. Dyulgerski & Radoukova (2019), investigated the inheritance and manifestation of transgression and heterosis in seven Burley hybrids in the F_1 and F_2 generation and found dominance of the parents with more leaves, the existence of all modes of dominance in inheriting leaf dimensions in the direction of the stronger parent. Qaizar et al. (2019), did research on seven flue-cured varieties and lines and their complete diallel, in the Mardan and Mansehra regions of Pakistan, and found positive and negative heterosis in the inheritance of some agronomic and biochemical traits. The best hybrids with favorable significant heterotic effect for yield were: KHG24 x Spt G 28; KHG21 x NC606 and Spt G 126 x KHG24. Kinay et al. (2020), in a semi-diallel of seven genotypes and 21 F_1 hybrids, tested in two locations in the Black Sea region of Turkey, obtained positive heterosis for yield without economic justification. Dyulgerski (2021), in local and introduced varieties of Burley and seven hybrids of F_1 and F_2 generation, found a positive-dominant and partial-dominant way of inheriting for dimensions of the leaves, indicating effective selection in later hybrid generations. The resulting heterosis had no economic significance.

The aim of this investigations was to study the mode of inheritance and to detect possible heterosis for the number of leaves per stalk, the length of the leaves from the middle belt and the yield of green

leaf mass per stalk and per hectare. The F_1 generation obtained by diallel crosses of tobacco varieties from different types will give us an important guidance for future selection programs in tobacco breeding.

MATERIALS and METHODS

In order to investigate the quantitative traits of tobacco, with previous studies of the available assortment at the Scientific Tobacco Institute - Prilep, in 2016 five varieties of different types were selected: MV-1 is a large-leaf variety of the Virginia type, P 76/86 is an oriental variety of the Prilep type, Adiyaman is an oriental variety of the Kabukalak type, Basma-Cebel (Basma-Dzebel or Basma-Djebel) is an oriental variety of the type Basma, P 66 9 7 is an oriental variety of the Prilep type.

In 2017, in field conditions, by applying the diallel method of crossing, using hand castration and pollination method, ten one-way diallel crosses were made: MV-1 x P 76/86, MV-1 x Adiyaman, MV-1 x Basma-Cebel, MV-1 x P 66 9 7, P 76/86 x Adiyaman, P 76/86 x Basma-Cebel, P 76/86 x P 66 9 7, Adiyaman x Basma-Cebel, Adiyaman x P 66 9 7 and Basma-Cebel x P 66 9 7.

In 2018, at the Experimental Field at the S.T.I. - Prilep, an experiment was set with 15 genotypes (5 parents and 10 F_1 hybrids), according to a Randomized block system in four replications. That same year we collected seeds for the second generation and again made diallel crosses between the listed parents for the first generation.

In 2019, an experiment was set up using the same method, in which the same set of 15 genotypes was planted.

The total area of the experiment (working area - 405m^2 + area of paths - 477 m^2) was 882 m^2.

To fill the surface of one repetition were planted 826 plants (770 plants + 56 plants as protection). A total of 3304 plants (stalks) were planted in the experiment.

This paper places the analysis of: number of leaves per stalk, length of leaves from the middle belt and yield of green mass per stalk and hectare. Measurements of leaf number and length were taken during flowering, in late July and August, when the population is in lush growth. Due to the uniformity of the homozygous parent genotypes and the heterozygous F_1 offspring, 20 stalks of each variant were measured in one replication, meaning 80 plants in the four replications (1200 plants in total). The yield of green leaf mass was measured after each harvest, the weight of all harvests from each plot was collected, and was divided by the number of plants from which the tobacco was harvested, which gave us the weight of a green leaf per stalk. The yield of green leaf mass per hectare was obtained by multiplying the weight of the green leaf per stalk by the number of plants planted on the surface of one hectare.

Processing of results

Statistical processing was performed on the data from the measurements of the subject traits for each variant. The mode of inheritance of traits is determined on the basis of test-significance from the mean value of the F_1 generation in relation to the average of both parents, according to Borojevic (1981). Intermediate mode of inheritance (i) occurs when the mean value of a trait in the offspring is equal to the parent average. There is a partial-dominant mode (pd) when the mean value of the hybrid offspring approaches one of the parent varieties. Dominance in inheritance (d) - positive or negative, occurs when the mean value of the cross coincides with the mean value of one of the parents (+ d - when the parent with a higher mean value dominates, -d - when the parent with a lower mean value dominates). Positive heterosis (+ h) occurs in the hybrid with a significantly higher value than that of the parent with a higher mean value, while negative heterosis (-h) occurs in the hybrid with a significantly lower value than the one from the parent with a lower mean value.

Meteorological data

A more realistic vision for the inheritance of quantitative traits is obtained by displaying data on climatic conditions during the tobacco vegetation in 2018 and 2019.

In 2018: The average monthly air temperature from May to September was 22.12 0C (May 19.8 0C, June 22.4 0C, July 24.4 0C, August 23.9 0C, September 20.1 0C). The average monthly maximum air temperature from May to September was 25.82 0C (May – 22.3 0C, June – 25.9 0C, July – 27.5 0C, August – 29.8 0C, September – 23.6 0C). The average monthly minimum air temperature from May to September was 13.4 0C (May – 11 0C, June – 12.9 0C, July – 15.8 0C, August – 15.3 0C, September – 12 0C). The average monthly air humidity from May to September was 78.8 % (May – 81 %, June – 80 %, July – 78 %, August – 75 %, September – 80 %). The total rainfall from May to September was 169 mm (May – 18 mm, June – 20 mm, July – 21 mm, August – 20 mm, September – 90 mm).

In 2019: The average monthly air temperature from May to September was 22.43 0C (May 15.77 0C, June 22.77 0C, July 24.26 0C, August 27.39 0C, September 21.97 0C). The average monthly maximum air temperature from May to September was 27.2 0C (May – 20.0 0C, June – 28.0 0C, July – 29.0 0C, August – 32.0 0C, September – 27.0 0C). The average monthly minimum air temperature from May to September was 14.8 0C (May – 8.0 0C, June – 16.0 0C, July – 14.0 0C, August – 22.0 0C, September – 14.0 0C). The average monthly air humidity from May to September was 58.7 % (May – 71.30 %, June – 67.17 %, July – 59.42 %, August – 42.61 %, September – 53 %). The total rainfall from May to September was 404.8 mm (May – 124.1 mm, June – 139.9 mm, July – 91.8 mm, August – 9.5 mm, September – 39.5 mm).

The results for temperature and relative humidity are within the optimal limits for normal development of tobacco and obtaining quality tobacco raw material. In July and August, one irrigation was performed with a field norm of 300 m^3/ha of water.

Soil conditions: The soil with its mechanical composition and nutrient content is the substrate on which tobacco grows and develops. Our investigations were performed on the Experimental Field at the Scientific Tobacco Institute - Prilep on deluvial (colluvial) soil type. This soil is characterized by low humus content and total nitrogen, moderately acidic to neutral reaction, low to extremely low supply with readily available phosphorus and medium to good potassium supply. Throughout its depth, the soil is carbonate-free. Taking into account the stratigraphy of the profile and the agrochemical traits of the soil for the performance of the profile, it was properly prepared. One autumn and spring plowing were carried out along with basic tillage. The basic fertilization was performed with the spring plowing.

RESULTS and DISCUSSION

The number of leaves is a trait that is directly related to yield, which is why it is the most common subject of research in all selection programs for tobacco breeding.

The most common way of inheriting the number of leaves per stalk in the F_1 generation in 2018 is the partial-dominant. Intermediate is found only in Adiyaman x P 66 9 7. Intermediate inheritance occurs only in Adiyaman x P 66 9 7. The hybrid P 76/86 x P 66 9 7 has heterosis with a negative heterotic effect, which means that the offspring in the F_1 generation has less leaves than both parents (Table 1.).

In 2019 we found an identical scheme for this trait. This indicates the fact that these are stable homozygous parents whose offspring forms the first investigated generation , and the number of leaves is a highly inherited trait on which environmental factors have limited influence.

Table 2. Mode of inheritance for the number of leaves per stalk in diallel F_1 hybrids

Parents	Number of leaves per stalk				
	MV-1	**P 76/86**	**Adiyaman**	**Basma-Cebel**	**P 66 9 7**
2018					
MV-1	27.65	37.90 [pd]	28.09 [pd]	25.02 [pd]	32.75 [pd]
P 76/86		60.09	35.09 [pd]	28.60 [pd]	48.55 [-h]
Adiyaman			29.89	25.86 [pd]	44.62 [i]
Basma-Cebel				18.07	29.84 [pd]
P 66 9 7					54.81
2019					
MV-1	28.52	39.32 [pd]	28.88 [pd]	24.62 [pd]	33.93 [pd]
P 76/86		59.56	36.68 [pd]	27.54 [pd]	49.72 [-h]
Adiyaman			30.82	26.46 [pd]	46.08 [i]
Basma-Cebel				17.26	27.51 [pd]
P 66 9 7					56.44

In inheriting the length of the leaves from the middle belt of the F_1 offspring in 2018, all the modalities are met. There is intermediate inheritance in Adiyaman x P 66 9 7. There is a partial-dominant

way of inheritance in MV-1 x Basma-Cebel, MV-1 x P 66 9 7, P 76/86 x Adiyaman and Adiyaman x Basma-Cebel. Positive dominance occurs in MV-1 x P 76/86. Positive heterosis in inheritance of this trait occurs in MV-1 x Adiyaman, P 76/86 x Basma-Cebel, P 76/86 x P 66 9 7 and Basma-Cebel x P 66 9 7, which means that the F_1 generation has longer leaves than the leaves of the both parents (Table 2).

The same mode of inheriting thise crosses was obtained in 2019, which means that the trait is highly inherited and is a varietal characteristic.

Table 2. Mode of inheritance for the length of the leaves from the middle belt of the stalk in diallel F_1 hybrids

Parents	Length of the leaves from the middle belt (cm)				
	MV-1	**P 76/86**	**Adiyaman**	**Basma-Cebel**	**P 66 9 7**
2018					
MV-1	50	48.51 $^{+d}$	55.22 $^{+h}$	45.12 ^{pd}	46.23 ^{pd}
P 76/86		23.62	31.55 ^{pd}	25.04 $^{+h}$	24.47 $^{+h}$
Adiyaman			35.75	30.53 ^{pd}	30.26 ^{i}
Basma-Cebel				20.57	24.39 $^{+h}$
P 66 9 7					23.01
2019					
MV-1	52.57	51.86 $^{+d}$	56.57 $^{+h}$	43.78 ^{pd}	47.05 ^{pd}
P 76/86		23.44	35.22 ^{pd}	24.36 $^{+h}$	24.16 $^{+h}$
Adiyaman			37.29	32.05 ^{pd}	29.28 ^{i}
Basma-Cebel				20.74	23.73 $^{+h}$
P 66 9 7					22.49

The most common way of inheriting the yield of green leaf mass per stalk in 2018 in F_1 offspring is the partial-dominant in the direction of the parent with higher yield, followed by the positive-dominant. Intermediate mode is found only in MV-1 x Basma-Cebel. Crosses where one parent is P 66 9 7 have positive heterosis, which means that they are more productive than the parent with higher yield (with the exception of MV-1 x P 66 9 7 where there is partial dominance).

In 2019, the vision for complete identity is changed by the cross P 76/86 x Adiyaman (with positive dominance) and Adiyaman x Basma-Cebel (with partial dominance). If we take into account that the yield is a variable quantity that is greatly influenced by environmental factors, then the obtained values are very reliable and reflect the professional setting of the experiment and timely activities for its cultivation and analysis (Table 3.).

Table 3. Mode of inheritance for green mass yield per stalk in diallel F_1 hybrids

Parents	Green mass yield per stalk (g)				
	MV-1	**P 76/86**	**Adiyaman**	**Basma-Cebel**	**P 66 9 7**
2018					
MV-1	970.94	716.14 ^{pd}	742.64 ^{pd}	567.41 ^{i}	667.67 ^{pd}
P 76/86		168.95	165.25 ^{pd}	163.45 $^{+d}$	177.58 $^{+h}$
Adiyaman			153.81	144.79 $^{+d}$	168.07 $^{+h}$
Basma-Cebel				63.59	148.85 $^{+h}$
P 66 9 7					137.12
2019					
MV-1	990.42	751.47 ^{pd}	757.34 ^{pd}	581.72 ^{i}	683.86 ^{pd}
P 76/86		172.45	174.54 $^{+d}$	177.28 $^{+d}$	182.49 $^{+h}$
Adiyaman			150.38	135.15 ^{pd}	176.80 $^{+h}$
Basma-Cebel				69.84	153.35 $^{+h}$
P 66 9 7					129.39

The mode of inheritance for the yield of green leaf mass per hectare in 2018 in F_1 offspring is partially-dominant and positively dominant. Negative heterosis is present in crosses where one of the parents is MV-1 (with the exception of MV-1 x Basma-Cebel where there is partial dominance in the direction of the weaker parent). The occurrence of positive heterosis has the Oriental crosses where one of the parents is P 66 9 7 (Table 4.).

In 2019, there are changes in the way of inheriting the yield of green leaf mass per hectare at the same hybrids for yield of green leaf mass per stalk (P 76/86 x Adiyaman - positive dominance and Adiyaman x Basma-Cebel - partial dominance).

The analysis of the heredity of the yield of green leaf mass per stalk and the yield of green leaf mass per hectare indicates drastic differences and therefore it is necessary to indicate the reasons. From the shown heredity in the crosses where the parent pairs are of oriental type, the reliability of the results is confirmed as a reflection of the professional approach to the overall work. Namely, all oriental hybrids showed the same inheritance pattern in yield per stalk and yield per hectare. But this is not the case with hybrids where one parent is the large-leaf variety MV-1. Here, instead of partial dominance, negative heterosis occurs (with the exception of MV-1 x Basma-Cebel, where instead of intermediate, partial dominance occurs). The reason for this outcome lies in the different planting distance of the plants in the experiment. Oriental parents and oriental hybrids are planted with a row spacing of 45 cm and plant spacing of 15 cm, while the large-leaved MV-1 and its crosses are planted with a row spacing of 90 cm and plant spacing of 50 cm, which means that the calculation of yield per hectare is different, depending on the plant composition of the genotype.

Table 4. Mode of inheritance for the green mass yield per hectare in diallel F_1 hybrids

Parents	Green mass yield per hectare (t)				
	MV-1	**P 76/86**	**Adiyaman**	**Basma-Cebel**	**P 66 9 7**
2018					
MV-1	21.576	15.914 $^{-h}$	16.503 $^{-h}$	12.609 ^{pd}	14.837 $^{-h}$
P 76/86		25.030	24.482 ^{pd}	24.215 $^{+d}$	26.307 $^{+h}$
Adiyaman			22.786	21.450 $^{+d}$	24.899 $^{+h}$
Basma-Cebel				9.420	22.051 $^{+h}$
P 66 9 7					20.314
2019					
MV-1	22.009	16.699 $^{-h}$	16.830 $^{-h}$	12.927 ^{pd}	15.197 $^{-h}$
P 76/86		25.548	25.858 $^{+d}$	26.264 $^{+d}$	27.035 $^{+h}$
Adiyaman			22.278	20.022 ^{pd}	26.193 $^{+h}$
Basma-Cebel				10.347	22.718 $^{+h}$
P 66 9 7					19.170

CONCLUSION

The mode of inheritance for quantitative traits covers all modalities. Negative heterosis for the number of leaves per stalk in F_1 generation showed P 76/86 x P 66 9 7. Positive heterosis for the length of the leaves from the middle belt of the stalk occurs in: MV-1 x Adiyaman, P 76/86 x Basma-Cebel, P 76/86 x P 66 9 7 and Basma-Cebel x P 66 9 7. Positive heterosis for green mass yield per stalk and per hectare is present in all oriental hybrids where one of the parents is P 66 9 7. The inheritance of the traits for the hybrids in 2018 is identical to that in 2019, which indicates the fact that the parents in the diallel are stable and homozygous, and that these are highly inherited traits on which environmental factors have a limited impact. The results of this paper are a good original source material for further successive selection activity.

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