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Inheritance of Individual Traits in Millet (*Panicum mileaceum* L.)

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Aim. To determine the inheritance of the millet morphological traits: seed color, size, anthocyan coloring of its parts, race specified resistance to smut and genetic linkage relationships between these features, which are a reliable basis for the breeding of a new generation of varieties. **Methods**. Genetic analysis of the F1, F2 and F3 hybrids. **Results.** The interrelations between the seed size, its color and shape, and especially race specified resistance to smut have been determined. **Conclusions.** The degree of linkage between the loci of genes that control the expression of the relevant characteristics in experimental combinations interbreeding has been stated.

Keywords: millet, genetic linkage, inheritance, morphological traits.

INTRODUCTION

Due to insufficient explorations of the millet's specific genetics, the dedicated literature has no well matched and sufficiently deep scientific ideas about the special features of the inheritance of such clearly visible morphological traits as seed color, size, anthocyan coloring of its parts, race specified resistance to smut (RaceSRS), and also the genetic linkage between these traits, which could become a reliable basis for the breeding of the millet's varieties of the new generation.

The current state of the scientific ideas concerning the issue is caused by the technological complexity of the explorations of the kind [1]. However, team of scientists under the guidance of Professor I. V. Yashovskyi some successes has been achieved by the in the Institute of Agriculture NAAS (now NRC "Institute of Agriculture NAAS") [2].

They paid the significant attention to study of the special inheritance features of the millet's separate signs and, in particular, to the genetic linkage between them. The literature provides very limited and insufficiently coordinated information about these subjects.

MATERIALS AND METHODS

The explorations of the defined traits inheritance was accomplished using the genetic analysis of F1, F2 and F3 hybrids by the comparison of the actual relationship of the plant phenotypes number with the various manifestation of the examined traits with those theoretically expected, which mostly corresponded to one or another type of action and interaction defined as classical ones, according to the contemporary genetics of the self-pollinated plants; the millet is among them.

The selective varieties and lines of the elder generations of the hybrids (F6–F12) isolated from the previous crossings have been used as the parental plants in the majority of the crossing combinations. As of their phenotypes, all these varieties and lines are homozygous enough and characterized by the combination of economic valuable traits or properties.

RESULTS AND DISCUSSIONS

The principal attention in course of explorations was focused on the study of the special features of the seed color, size and form inheritance and their genetic linkage with other traits.

The experimental results will be demonstrated based on the example of the genetic analysis of the hybrids obtained from two crossing combinations. In combination # 1 the hybrids are obtained from the crossing of the line # 823 (*coccineum* variant, typical brick red seed color and resistance to the smut of races # 1, 2) with line # 481-97 (*subaureum* variant, typical golden yellow seed color and resistance to the smut of races # 1-3). In F_1 of these hybrids the golden yellow color of seed prevailed, while in F_2 the splitting occurred (Table 1), which statistically reliably corresponded to the monogenic ratio of presence-absence features of anthocyan painting ($\chi^2 = 2.59$), and also the ratio of the golden yellow seed color to the red one ($\chi^2 = 1.33$), and finally, independent digenic relationship 9: 3: 3: 1 according to both traits simultaneously ($\chi^2 = 3.23$).

Among the total number of 122 F2 plants obtained from this crossing combination 38 descendants (a quarter from each of four groups of phenotypes) were evaluated concerning the resistance to the smut of race #3, since the parental forms differed in the resistance to this race.

According to the results of estimation, nine of 38 tested descendants demonstrated the receptivity to race # 3 (approximately, a quarter of their total amount). That gives evidences on the monogenic nature of the inheritance of resistance to the indicated race of smut in hybrids from this crossing combination ($\chi^2 = 0.60$). However, the amount of the genotypes susceptible to the race #3 among the descendants of four studied F2 phenotypes comprised: in the anthocyan golden yellow group – 6; in the of brick red group – 1; in the golden yellow group without the anthocyan – 0; in the brick-red group without anthocyan – 2 pcs.

The discovered ratio of resistant and susceptible genotypes to race # 3 in the above mentioned phenotype groups of the hybrids' descendants testifies about the independence of the genes of resistance to the smut of race # 3 from the genes controlling the presence of anthocyan coloring of millet, and also genes controlling either golden yellow, or brick red coloring.

Table 1. **Phenotypes Parameters of F_2 Millet Plants (Line 823//Line 481-97), Plot 1206-99**

Plants Amount in Phenotypes Groups, pcs				
With Anthocyan		Without Anthocyan		Total
Golden Yellow	Brick Red	Golden Yellow	Brick Red	
67	17	30	8	122

For the hybrids from crossing combination # 2 line # 832 (taken apart by the individual selection from the Ilinovske variety, *sanquineum* variant) served as a maternal form. It is characterized with the reddish brown seed color, and simultaneously, resistance to the smut of races # 5 and 2 (the genes' conditional block of *Sph2* [3, 4]). The pollinator was line 612-97 (*subaureum* variant) noted by the specific golden yellow seed coloring and also resistance to the smut of races # 1 (1, 5, 4, 6) and # 3. The features of the anthocyan presence and the golden red seed coloring prevailed among the F1 ones.

The results of the genetic analysis of the F2 plants from this crossing combination give enough evidences on the fact that the parental forms of hybrids differ in the alleles of only one of two known genes – *Pr1* or *Pr2* (*purpl*) critical for presence or absence of anthocyan coloring of millet ($\chi^2 = 1, 32$).

Concerning the seed coloring, three phenotypes groups are discovered: golden red – 62 (both with anthocyan and without it), golden yellow – 47 and typically reddish brown – 27 plants. The specific features of this inheritance are not mentioned in the dedicated sources.

The actual ratio of the kind as for the indicated groups of the plants corresponds with high probability to the theoretically expected trihybrid independent ratio 27: 21:16 ($\chi^2 = 1.92$). It is necessary to note that the ratios of the kind were observed for the groups of plants either with the anthocyan coloring, or without it ($\chi^2 = = 1.64$ and 1.68 respectively). That indicates the absence of the genetic linkage of the genes controlling seed coloring and presence of anthocyan. This assumption is also coordinated with the actual ratio between the first and the second of three groups of mentioned phenotypes ($\chi^2 = 0.09$) and also actual ratio of the first two groups of plants together to the third one as a monohybrid one ($\chi^2 = 0.92$).

Thus, the foregoing data outlined make it possible to draw the grounded conclusion that the parental forms of combination # 2 differs in the alleles of two complementary (inhibiting) genes, whose dominant alleles are together capable of enlightening or "gold coloring" the conditionally reddish brown seed to the golden red one. Due to the presence of dominant alleles of only one among these genes, which possess a half-epistatic nature of action, i.e. without the presence of dominant alleles complementary to it epistatic component only yellow, slightly golden seed coloring is manifested, which is typical for the parental form *i. e.*, pollinator.

Since in the dedicated sources such genes are not identified, it is justifiable to introduce the symbol of the revealed genes. For one of these genes, which dominant alleles are capable of gold-coloring the yellow coloring to the yellow-gold one by themselves, the symbol of *Gld1* is introduced, and for another gene, complementary to it, which conjointly weakens the intensity of gold-coloring of reddish brown pigmentation to the golden-red – the symbol of *Gld2* is introduced.

For the sake of the given epistatic-hypostatic model of action and interaction between the identified genes corresponding to the data obtained experimentally, it is necessary to assume the presence of the dominant alleles of only one of two complementary genes – *Gld1*, which even in case of absence of *Gld2* complementary component's dominant alleles ensure the yellow-gold painting of seeds in the genotype of pollinators. However, in the maternal line of 832 alleles of *Gld1* gene are recessive, but dominant alleles of another gene – *Gld2* are noted, which in the absence of the basic "partner" either does not work, or its expression is little noticeable.

Concerning the F3 hybrids of the discussed crossing combination on the background of artificial infection separately with races # 1, 5, 4, 6, 2 and 3, 41 descendants of F2 plants selected with the observance of the corresponding relationship according to the types of coloring have been tested for race-specified resistance.

While estimating, the following amount of descendants susceptible to appropriate races of smut was revealed: # 1 – 7, # 5 – 0, # 4 – 7, # 6 – 6, # 2 – 8, # 3 – 10. No susceptible families have been stated on the background of race # 5 only, but as for the rest – the rate of the susceptible descendants in F2 genotype was about 1/4 part of their total number. This indicates that the F2 hybrids' splitting in crossing combination # 2 as of the resistance to races # 1, 4, 6, 2 and 3 occurred in the monohybrid rates (approximately 3:1) and only as of the resistance to race # 5 no splittings were observed. Thus, the parental forms of the explored hybrids differ in the alleles of the genes controlling resistance to races # 1, 4, 6, 2 and 3, and are resistant to race # 5. The data of the kind are well in line with the evaluations of the race-specified resistance to smut of the parental forms. Line # 832 is resistant simultaneously to races # 5, 2 and susceptible to races # 1, 4, 6 and 3, while line 612-97 is simultaneously resistant to races # 1, 5, 4, 6 and 3 and susceptible to race # 2.

No genetic linkage has been revealed between the traits of seed coloring and presence of anthocyan with the race-specified resistance to smut in these hybrids.

Due to absences of the data on the connections between the seed size and other its features in the dedicated sources, the search for the possible connections between the seed size, its coloring and form and, especially, with the race-specified resistance to smut has been carried out.

For that end, the genetic and genetics-immunological analysis of hybrids from a number of the specially selected crossings combinations has been accomplished and the following results have been obtained.

In hybrids obtained from the crossing of big-seed line 843 (red brown, *coccineum* variant, 1000 grains mass – 8.0-8.2 g, resistant to the smut of races # 1, 4, 5 and 6) with the small-seed sample of cat. BIP 1456 (strip yellow, *tephrum* variant, 1000 grains mass – 6.0 g, re-

Table 2. Millet Plants Phenotypes Distribution in F2 (Line 843//Catalogue Sample 1456), As For Seed Coloring and Size, Plot 324

Plants Amount in Phenotypes Groups, pcs								
Striped				No Stripes				Total
Yellow		Red Brown		Yellow		Red Brown		
Small	Big	Small	Big	Small	Big	Small	Big	
56	0	16	10	15	1	8	13	119
56		26		16		21		
82				37				

sistant to races # 1 and 2) in F1 the following features dominated: a sprawling plume, small size and strip yellow coloring of seed, while in F2 the splitting was observed for all features with the appearance of their new combinations in various ratios (Table 2).

Relying on the revealing of the specific inheritance features of such traits as quantity of the genes controlling each of them, nature of their action and interaction, and also presence of linkage between these genes, the analysis of the F2 hybrids obtained from the experimental crossing combination with the group of phenotypes on three corresponding pairs of the investigated features (Tables 3-5) has been accomplished.

Comparing the actual number of plants in the groups with different phenotypes with the theoretically estimated one, peculiar for various types of splitting, indicated in Table 4-6, it is possible to distinguish ratios determining the special features of explored features inheritance: the monogenic rate of phenotypes with the dark longitudinal strips in seed coloring (82 pcs) to ones without stripes (37 pcs, $\chi^2 = 2.18$) (Table 3).

The clear digenic ratio between the groups of yellow seed phenotypes (72 pcs) and red seed ones (47 pcs) as 9:7 ($\chi^2 = 0.86$), and also the monogenic ratio of the small-size phenotypes (95 pcs) to big-size (24 pcs) as 3:1 ($\chi^2 = 1.48$) (Table 4).

The low indices of the fitting criteria (0.86–2.18) give evidences on the high probability of the given actual rates to the theoretically estimated ones according to the indicated features (0.15–0.60).

The results of analysis confirm that the parental forms of these hybrids differ only in alleles of one among two known *Str* genes controlling the presence of strips on a millet seed. Likewise, the parental forms also differ in the alleles of only one among the genes controlling the seed size. In this case it has been revealed that the dominant alleles of this gene cause small seeds, while the recessive alleles – the big ones.

The distinct digenic relationship (9:7; $\chi^2 = 0.86$) between yellow seed (72 pcs) and red seed (47 pcs) phenotypes proves the fact that the parental forms of hybrids differ in the alleles of two known complementary genes of *Y1* and *Y2*, whose dominant alleles cause yellow coloring of a seed only subject to conjugated action, whereas the recessive ones of any of the genes – red coloring.

Thus, the clearly dependent nature of experimental hybrids' splitting as for the pairs of the features has been revealed: stripes and yellow or red coloring of a seed (Table 3); coloring and size of a seed (Table 4); stripes and seed size (Table 5).

That is confirmed with the high indices of the statistical fitting criterion – χ^2 (for the first pair of features – 23.24, for the second – 36.97 and for the third – 21.33).

On the ground of the exploration applying the χ^2 criterion it is reasonable to draw the conclusion that a locus of one among two complementary genes of yellow seed coloring (*Y1* or *Y2*) is genetically tightly linked with the locus of the gene of stripes (*Str*). They are lo-

Table 3. **Results of the Genetic Analysis for F2 Hybrids (Line 843//Catalogue Sample 1456) Due to Phenotype Grouping as for Seed Coloring and Stripes Presence**

Phenotype Group	Actual Number of Plants in Group, pcs				Splitting Estimated Rate			Fitting Criterion, χ^2	Splitting Nature
	Yellow Seed		Red Seed		As for One Feature		Coincidently		
	Striped	Without Stripes	Striped	Without Stripes	Coloring	Stripes			
Coincident	56 * 50 **	16/38 3:1	26/17	21/13 2.18	9:7	3 : 1	27 : 21 : 9 : 7	23.24	Trigenic Obviously Dependent
As for Coloring	72 67		47 52					0.86	Digenic Independent
As for Stripes	Striped – 82/89 Without Stripes – 37/30							2.18	Monogenic

Note. * – actual number; ** – estimated number; *n* = 119.

Table 4. **Results of the Genetic Analysis for F2 Hybrids (Line 843//Catalogue Sample 1456) Due to Phenotype Grouping as for Seed Coloring and Size**

Phenotype Group	Actual Number of Plants in Group, pcs				Splitting Estimated Rate			Fitting Criterion, χ^2	Splitting Nature
	Yellow Seed		Red Seed		As for One Feature		Coincidently		
	Small	Big	Small	Big	Coloring	Size			
Coincident	71 * 50 **	1 16	24 40	23 13	9:7	3 : 1	27 : 21 : 9 : 7	36.97	Trigenic Obviously Dependent
As for Coloring	72 67		47 52					0.86	Monohybrid
As for Size	Small seed – 95/90 Big seed – 24/30							1.48	Monogenic

Note. * – actual number; ** – estimated number; n = 119.

cated within one and the same chromosome (Table 3) in parental forms in the phase of connection.

The data of Table 4 also testify about the high level of genetic linkage of one of the complementary genes of yellow seed coloring (*Y1* or *Y2*) with one of the genes of small seed size in the phase of connection as well. The obtained values of χ^2 for the mentioned rates prove that the authenticity of conclusions about the presence of the noted connections exceeds 99.99 per cent (standard deviation is 0.01 per cent). However, the degree of the revealed linkage remains undetermined still yet.

The determination of the linkage degree between the loci of the genes controlling the manifestation of the relevant features in the experimental crossing combination has been accomplished according to Immer's formulas and tables [5].

The actual number ratio between the phenotypic groups according to the presence of yellow, red seed coloring and presence of strips, and also as for the seed size was estimated applying the formula for the case of linkage in the phase of connection or – for the case in the phase of separation. According to these indices

Table 4. **Results of the Genetic Analysis for F2 Hybrids (Line 843//Catalogue Sample 1456) Due to Phenotype Grouping as for Seed Size and Stripes Presence**

Phenotype Group	Actual Number of Plants in Group, pcs				Splitting Estimated Rate			Fitting Criterion, χ^2	Splitting Nature
	Striped		Without Stripes		As for One Feature		Coincidently		
	Small	Big	Small	Big	Stripes	Size			
Coincident	72 * 87 **	10 22	14 8	23 13	3 : 1	3 : 1	9 : 3 : 3 : 1	21.33	Digenic Complementary, Obviously Dependent
As for Stripes	82 90		37 30					2.35	Digenic Independent
As for Size	Small seed – 86 90 Big seed – 23 30							2.31	Monogenic

Note. * – actual number; ** – estimated number; *n* = 119.

with the aid of the appropriate tables the indices of the distance between the coupled loci V_{cr} (value of crossing-over) and their deviations in the units of crossing-over or per cent were calculated.

It has been revealed for the first time that the linkage degree (V_{cr}) between the genes of yellow seed coloring (*Y*) and stripes (*Str*) in combination #3 works out: $V_{cr} = 4.7 \pm 2.0$ per cent. This testifies about the very close linkage between the indicated traits .

The data given in Table 4 also confirm a very close genetic linkage between one of the genes of yellow seed coloring and one of the genes of small seed size in the phase of connection. The value of this linkage works out 3.3 ± 1.8 per cent of crossing-over units.

The results represented in Table 5 are obtained with the use of a formula with other than in Table 4, rate of number in the phenotypes groups () intended for the linkage in the phase of separation. The sufficiently close genetic linkage between the genes of stripes and seed size has been also revealed. The degree of this linkage according to the V_{cr} index composes 11.6 ± 1.1per cent.

It is important to note that the comparison of the results of the paired connections analysis as for the features between themselves according to the data of Tables 3–5 reveals on some disagreement of the obtained data at first glance. If there is a close linkage between the genes of yellow seed coloring with the genes of small seed size and stripes presence, then what can explain the absence of linkage between the genes of stripes presence and small seed size determined according to the same results of analysis? As a possible explanation that can completely match the results of analysis as for all paired genetic interrelations of the investigated traits , can be the fact that the discovered genetic linkage of one of the independent complementary genes of yellow seed coloring (for example, *Y1*) exist only with one of another independent pair of the complementary genes of stripes presence (for example, *Str1*). The similar idea is obviously correct in respect of the genetic connections between the features of yellow-red seed coloring and small-big seed size.

Quite possible, that the similar nature of genetic linkage exists also in the manifestation of other traits in the millet. This is coherent with the fact that, despite the discovered close linkage between the genes controlling seed color and size, stripes presence etc., the considerable amount of phenotypes is observed, in which the recombination of these trait occurs. Considering the frequency of its manifestation, it cannot be caused only due to the crossing-over.

CONCLUSIONS

The results obtained from the accomplished explorations have proven to satisfaction the epistatic-hypostatic nature of interaction of different genes controlling yellow, red seed coloring and stripes presence in the millet, and also the epistatic alleles of small seed size over the dominant alleles of the genes of big seed size. All the aforementioned gives evidences on the fact that the denoted traits are controlled with epistatic-hypostatic nature of interaction between different genes, though never – by either dominant, or recessive alleles within the limits of only one gene, as this is interpreted in the dedicated publications [6–8].

Особливості успадкування окремих ознак проса (*Panicum mileaceum* L.)

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Мета. Визначення особливостей успадкування морфологічних ознак проса: забарвлення зернівки, її величина, наявність антоціанового забарвлення її частин, расоспецифічна стійкість до сажки, а також генетичних зв'язків між цими ознаками, які є надійною основою для селекції нового покоління сортів цієї культури. **Методи**. Генетичний аналіз гібридів F1, F2 та F3. **Результати**. Встановлено зв'язки між величиною зернівки, її забарвленням і формою та особливо, расоспецифічною стійкістю до сажки. **Висновки**. Визначено ступінь зчеплення між локусами генів, що контролюють прояв відповідних ознак у піддослідній комбінації схрещування.

Ключові слова: просо посівне, генетичне зчеплення, успадкування, морфологічні ознаки.

Особенности наследования отдельных признаков проса *(Panicum mileaceum L.)*

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Цель. Определение особенностей наследования морфологических признаков проса: окраска зерновки, ее величина, наличие антоциановой окраски ее частей, расоспецифическая устойчивость к головне, а также генетических связей между этими признаками, которые являются надежной основой для селекции нового поколения сортов этой культуры. **Методы**. Генетический анализ гибридов F1, F2 и F3. **Результаты.** Установлена связь между величиной зерновки, ее окраской и формой и, особенно, с расоспецифической устойчивостью к головне. **Выводы.** Определена степень сцепления между локусами генов, контролирующих проявление соответствующих признаков в подопытной комбинации скрещивания.

Ключевые слова: просо посевное, генетическое сцепление, наследование, морфологические признаки.

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