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Polygenic Inheritance of Bracts Number in Sunflower

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Abstract: Two inbreds of mutant origin, differing in the number of bracts, were crossed to obtain the F_1 hybrid. One mutant line had 24.5 ± 1.01 bracts, while the other, 78.6 ± 1.69 bracts. The F_1 hybrid had an average value between parents, which practically did not differ from the mean value in the F_2 population. The variability of the trait under study in the F_2 population was continuous, varying from 20 to 84 bracts. This indicated the probable participation of several genes with an additive effect in the control of the number of bracts. Assuming that the differences between the parental lines are due to two pairs of genes, the F_2 plant population, grown in 2016, was divided into 5 classes. In that population the observed classes ratio turned out to be close to the theoretically expected ratio of 1 : 4 : 6 : 4 : 1. Over the next two years F_2 populations were tested in a similar way. In all the cases, the calculated chi-square value did not exceed the critical value for 4 degrees of freedom and 5 % significance level. This gave reason to talk about the two-loci control of a such quantitative trait as the number of bracts. The participation of two non-allelic genes in the control of this trait is also proved by matching the actual number of plants in the parental classes to the theoretically expected number of plants. Thus, the number of bracts depends on the number of dominant alleles of two different genes in the genotype.

Keywords: sunflower, number of bracts, polygenic inheritance, two-loci control, additive effect

Introduction

Sunflower inflorescence is a multiflorous head. The inflorescence of this type is peculiar to the *Asteraceae* family, which from an evolutionary point of view is

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the most progressive group of plants. In the plants of this and some other families, the receptacle on the outside is surrounded by bracts consisting of more or less modified upper leaves. In these plants, the role of the calyx, which usualy serves to protect the inner parts of the developing flower, is lost. This function is performed by the bracts, which close the entire set of flowers in the head during their formation and development (Turnbull, 2005).

The protection provided by the bracts can be varied. On the one hand, their participation in protection from adverse weather conditions is undoubted. Thus, for example, it is shown that the function of the bracts in *Saussurea velutina* (*Asteraceae*) is to provide warmer temperatures for floral and seed development at high elevations in the Hengduan Mountains, Southwestern China (Yang and Sun, 2009). On the other hand, the bracts can take part in protection against diseases and harmful insects. In this regard, researchers note that, for example, sunflower bracts, which cover the front of the head very well, contribute to the accumulation of various harmful insects under them, and some fungal diseases. This leads to the damage of seeds and reducing their crop properties (Kirichenko *et al.*, 2007). In prey plants bracts can play a more active role in protecting plants from pests. Thus, in the *Passiflora* genus, the main function of the bracts is to minimize the predatory damage to the development of flowers and fruits. However, in addition to serving as traps for insects, the bracts also have a mechanism for digesting trapped insects in order to obtain free amino acids (Radhamani *et al.*, 1995).

The bracts surrounding the inflorescence also possess a photosynthetic mechanism. The example of sunflower shows a higher activity of enzymes participating in carbon fixation in bracts compared to the leaf, although the contribution of leaves is more significant because of their relatively larger surface area and net photosynthetic rates (Laxman and Srivastava, 2000). According to Vanderbrink *et al.* (2014), despite the fact that the photosynthetic contribution of bracts is much less than the contribution of leaves, it undoubtedly contributes to the successful growth and development of reproductive structures. In the study of Weighsheng (1991), the removal of bracts decreased the sunflower seed yield by 1.9–7.6 %. The active participation of the bracts in the process of photosynthesis is also evidenced by the better development of peripheral achenes compared to the central ones due to their more favorable position relative to nutrition.

Bract characteristics are also important for identifying sunflower genotypes. However, the genetics of various inflorescence traits, and, especially, of such part of it as the bracts, remains poorly understood. The aim of our research was to study the inheritance pattern for the number of bracts in sunflower.

Materials and methods

Two mutant sunflower lines with a contrast expression of “number of bracts” trait, F_1 reciprocal hybrids obtained from the crossing of these lines, and F_2 plant populations obtained from the self-pollination of the F_1 hybrids were used as the material. A mutant line with a reduced number of bracts was obtained as a result of mutagenic treatment of immature embryos of ZL809 line. It was characterized by a nearly halved reduction, compared to the original line, of the bracts number. This mutant was also distinguished by a reduced number of ray florets (Soroka and Lyakh, 2009). Another mutant line, significantly superior to the first one in the number of bracts and ray florets, was isolated as a result of treating the mature seeds of the ZL9 line with a chemical mutagen, ethyl methanesulphonate, and possesed a mutant trait of dihotomous (fan) venation of leaves (Lyakh *et al.*, 2005).

The seeds of both mutant lines, F_1 hybrids between the line with a large number of bracts and the line with a reduced number of bracts as well as their F_2 hybrid populations were simultaneously sown at the same density under the field conditions of 2016–2018. In the flowering period, the number of bracts was counted in each plant of the F_2 populations and in 10 plants of each parent and F_1 hybrids. In order to determine the correspondence between the actual segregations in the F_2 plant populations and the theoretically expected segregations according to the proposed model, the χ^2 method was used (Griffiths *et al.*, 2004).

Results and discussion

The use of a line with a large number of bracts and at the same time characterized by the trait of fan leaf venation type 1 (Soroka and Lyakh, 2015) as the maternal parent of the hybrids, made it possible to easily identify true hybrids of the first generation and remove plants derived from selfing.

The Figure 1 shows the inflorescences in the F_1 hybrid plant and its parents. Visually, both parents and the hybrid are contrasted in the bract number. It is interesting to note that in the line with the reduced number of bracts, those are arranged on the inflorescence in two rows, whereas in the hybrid and the second parent – in 4 and 6 rows, respectively. The mean values and ranges of variation in the bract number for both parents, the F_1 hybrid and the F_2 population are listed in Table 1.

Figure 1: Heads of the mutant parental lines and F_1 hybrid: a) line with large number of bracts (mutant of Zl9 line); b) F_1 hybrid (Zl9 mutant × Zl809 mutant); c) line with reduced number of bracts (mutant of Zl809 line).

Table 1: The number of bracts in two inbreds with the contrast value of this trait, and in F_1 and F_2 plants, pcs.

Genotype	Number of plants	Minimum	Maximum	Mean value
Mutant of Zl9 line	10	73	84	78.6 ± 1.69
Mutant of Zl809 line	10	20	30	24.5 ± 1.01
F_1	10	45	57	49.0 ± 1.23
F_2	308	20	84	45.3 ± 2.15

As can be seen from the Table 1, in the mutant of ZL9 line the number of bracts varied from 73 to 84 pieces and averaged 78.6 ± 1.69 pieces. The mutant of ZL809 line with a reduced bracts number had on average almost three times less bracts than the other parent. The F_1 was intermediate between the two parents with mean bract number of 49.0 ± 1.23 pcs. In the F_2 population, which consisted of more than 300 individuals, there were plants with different number of bract leaves, from 20 to 84. The F_2 mean was close to that of F_1 and intermediate between those of the parents. This is exactly as expected in the case of polygenic inheritance.

Quantitative variability results from the simultaneous action of several genes, each of which makes a small contribution to the value of the corresponding trait. We assumed that differences between parents in the number of bracts in our crossing are due to two pairs of genes. The number of genetic classes in the F_2 generation is one more than the number of alleles (Ayala, 1984; Griffiths *et al*., 2004). That is, in the case of two loci (pairs of genes), we will have five classes. The phenotype of each of these classes depends on the number of dominant alleles among these two pairs of genes.

The first conclusions about the inheritance of the bracts number in sunflower were made in 2016 after studying the structure of the F_2 population obtained from self-pollination of F_1 hybrids, whose parents contrasted according to the corresponding trait. We divided the F_2 population, consisting of 328 plants, into 5 classes, based on the number of bracts, namely 20–32, 33–45, 46–58, 59–71, and 72–84 bracts (Table 2). The number of bracts for both parents and F_1 hybrid was almost completely encompassed within the respective intervals. As a result, the observed ratio of plants was 14: 90: 134: 75: 15. If the trait "number of bracts" is controlled by two pairs of genes with an additive effect, this ratio should be 20.5 : 82 : 123 : 82 : 20.5. The calculated chi-square value (5.90) allowed to conclude that the observed ratio completely corresponds to the theoretically expected one. And, therefore, in this case, we can speak about the polygenic inheritance of the number of bracts.

Table 2: Inheritance of bracts number in sunflower.

Total F_2 plants	F_2 phenotypes, Number of bracts					Segregation ratio tested	χ^2 (P value)
	20–32	33–45	46–58	59–71	72–84		
			2016				
328	14	90	134	75	15	1:4:6:4:1	5.90 (0.21)
			2017				
208	10	67	74	46	11	1:4:6:4:1	6.22 (0.18)
			2018				
194	7	53	84	40	10	1:4:6:4:1	6.14 (0.19)

$\chi^2{}_{05}$ (df 4) = 9.49; $\chi^2{}_{01}$ (df 4) = 13.28

In 2017–2018 studies were continued and the structure of the newly obtained F_2 populations, consisting of 208 and 194 plants, was analyzed (Table 2). The calculated chi-square values turned out to be less than critical values for the corresponding number of degrees of freedom and level of significance. This confirms the hypothesis of controlling the number of leaves by two pairs of nonallelic genes that act additively.

The number of genes involved in the control of a quantitative trait can be also estimated by the proportion in the F_2 generation of individuals belonging to the parent classes (Ayala, 1984). If two loci govern the number of bracts trait, then in the F_2 generation the theoretically expected proportion of plants corresponding to each parent class should be $(1/2)^4$ or 1/16. As can be seen, in case of a population of 308 plants the number of plants with the bracts number corresponding to the mutants of ZL9 and ZL809 lines was 15 and 14 plants, respectively. This is consistent with the expected value – 20.5 plants or 1/16 for each parent class (chi-squares 1.57 and 2.20, respectively).

The inheritance pattern for the bract number is described in scientific literature neither for sunflower nor for any other crop. At the same time, analyzing half diallel crosses of four inbred sunflower lines for genetic components of variance, Jocić and Škorić (1996) came to the conclusion that the dominant components played a more important role than the additive ones.

In sunflower there are differences in such traits of the bracts as shape, tip length, pigmentation. As for the bract pigmentation it has been shown that the trait is controlled monogeneously with the codominant interaction of alleles (Vedmedeva, 2004). Even earlier, Tolmachev *et al.* (1998) revealed in sunflower a number of spontaneous mutations of the head traits including the traits of bracts shape. These authors have shown that the trait of slitted bracts is controlled by one recessive gene, whereas the trait of bulbous bracts does not fully dominate the norm.

Portis *et al.* (2015) studied the inheritance of two bract traits of the artichoke inflorescence variing in their pigmentation and the extent of fleshy thorn development. Both traits appeared to be simply inherited. The number of classes for the studied traits was limited to three for pigmentation and two for thorniness. In cotton germplasm in addition to normal broad bract exists narrow and twisting flower bract, named frego bract, with reduced bracteole. Due to the fact that this modified bract did not provide shelter for eggs and nymphs of insects, it granted greater resistance to them than the normal bract. It was found that frego bract is controlled by a single recessive gene and positively correlates with fibre strength (Sajid-ur-Rahman *et al.*, 2008).

Coming back to the present work, we have studied for the first time the inheritance of bract leaves number in sunflower, and demonstrated that this trait can be regarded as a quantitative one being under the control by at least two non-allelic genes that interact additively.

References

Ayala, F.J., 1984. Population and Evolutionary Genetics: A Primer, Mir, Moscow, pp. 232. (In Russian).

Griffiths, A.J.F., Wessler, S.R., Levontin, R.C., Gelbart, W.M., Suzuki, D.T., 2004. An Introduction to Genetic Analysis, 8th ed., WH Freeman and Company, New York, pp. 800.

Jocić, S., Škorić, D., 1996. The components of genetic variability for bract length, width and number in sunflower (Helianthus annuus L.) In: Proceedings of the 14th International Sunflower Conference, Beijing/Shenyang, China. Vol. 1, pp. 168–173.

Kirichenko, V.V., Petrenkova, V.P., Krivosheeva, O.V., Ryabchun, V.K., Markova, T.Y.U., 2007. Identification of Morphological Characteristics of Sunflower (Helianthus L.). Handbook, Institute of Plant Science named after. V. Ya. Yuriev UAAS, Kharkiv, pp. 78. (In Ukrainian).

Laxman, R.H., Srivastava, G.C., 2000. Photosynthetic characteristics of sunflower (Helianthus annuus L.) leaves and bracts. Indian Journal of Plant Physiology 5(2): 150–153.

Lyakh, V.A., Soroka, A.I., Vasin, V.A., 2005. Influence of mature and immature sunflower seed treatment with ethylmethanesulphonate on mutation spectrum and frequency. Helia 28(43): 87–98.

Portis, E., Mauro, R.P., Acquadro, A., Moglia, A., Mauromicale, G., Lanteri, S., 2015. Inheritance of bract pigmentation and fleshy thorns on the globe artichoke capitulum. Euphytica 206 (2): 523–531.

Radhamani, T.R., Sudarshana, L., Krishnan, R., 1995. Defense and carnivory: Dual role of bracts in Passiflora foetida. Plant Science 20(5): 657–664.

Sajid-ur-Rahman, T.A., Ashraf, M., Malik, S., 2008. Inheritance of frego bract and its linkage with fibre and seed traits in cotton. Pakistan Journal of Botany 40(4): 1621–1626.

Soroka, A.I., Lyakh, V.A., 2009. Genetic variability in sunflower after mutagen treatment of immature embryos of different age. Helia 32(51): 33–46.

Soroka, A.I., Lyakh, V.A., 2015. Inheritance of two types of modified leaf venation in sunflower (Helianthus annuus L.). Indian Journal of Genetics 75(1): 75–78.

Tolmachev, V.V., Lebed, Z.I., Bochkarev, N.I., Tolmacheva, N.N., 1998. New Spontaneous Mutations of Sunflower Head Traits and Their Inheritance. Scientific and Technical Bulletin of the Institute of Oilseed Crops NAAS 3: 82–91. (In Russian).

Turnbull, C.G.N., 2005. Plant Architecture and Its Manipulation. Annual Plant Reviews, Wiley and Blackwell Publishing, United Kingdom, pp. 322.

Vandenbrink, J.P., Brown, E.A., Harmerb, S.L., Blackman, B.K., 2014. Turning heads: The biology of solar tracking in sunflower. Plant Science 224: 1621–1626.

Vedmedeva, K.V., 2004. Creation of a Collection of Sources of Morphological Marker Traits in Sunflower and Studying Their Genetic Control: Thesis for Research Degree of Doctor of Sciences in Biology on Speciality 03.00.15 – Genetics, Plant Breeding and Genetics Institute – National Center of Seed and Cultivar Investigation, Odesa, p. 16 (In Ukrainian).

Weisheng, D., 1991. Effect of the bracteal leaf on yield of grain in sunflower. Helia 14: 73–78.

Yang, Y., Sun, H., 2009. The bracts of Saussurea velutina (Asteraceae) protect inflorescences from fluctuating weather at high elevations of the Hengduan Mountains, Southwestern China. Arctic, Antarctic, and Alpine Research 41(4): 515–521.

Résumé

Héritage polygénique de nombre de bractees dans le tournesol

Deux lignées d’origine mutante, différant par le nombre de bractées, ont été croisées pour obtenir l’hybride F_1. Une lignée mutante avait 24,5 ± 1,01 bractées, tandis que l’autre - 78,6 ± 1,69 bractées. L’hybride F_1 avait une valeur moyenne entre les parents, ce qui pratiquement ne différait pas de la valeur moyenne dans la population F_2. La variabilité du trait étudié dans la population F_2 était continue, allant de 20 à 84 bractées. Cela indiquait la participation probable de plusieurs gènes ayant un effet additif dans le contrôle du nombre de bractées. En supposant que les différences entre les lignées parentales soient dues à deux paires de gènes, la population de plantes F_2, augmentée en 2016, a été divisée en 5 classes. Dans cette population, le ratio des classes observées s'est avéré être proche du ratio théoriquement attendu de 1: 4: 6: 4: 1. Au cours des deux prochaines années, les populations F_2 ont été testées de manière similaire. Dans tous les cas, la valeur du khi-deux calculée ne dépassait pas la valeur critique pour 4 degrés de liberté et 5 % du seuil de signification. Cela a donné des raisons de parler du contrôle par deux loci d'un trait quantitatif tel que le nombre de bractées. La participation de deux gènes non alléliques au contrôle de ce caractère est également démontrée en faisant correspondre le nombre réel de plantes des classes parentales au nombre de plantes théoriquement attendu. Ainsi, le nombre de bractées dépend du nombre d'allèles dominants de deux gènes différents dans le génotype.

Resumen

Herencia poligénica de números de bracteas en girasol

Se cruzaron dos líneas de origen mutante, que diferían en el número de brácteas, para obtener el híbrido F_1. Una línea mutante tenía 24.5 ± 1.01 brácteas, mientras que la otra - 78.6 ± 1.69 brácteas. El híbrido F_1 tuvo un valor promedio entre los padres, que prácticamente no difirió del valor medio en la población F_2. La variabilidad del rasgo en estudio en la población F_2 fue continua, variando de 20 a 84 brácteas. Esto indicó la probable participación de varios genes con un efecto aditivo en el control del número de brácteas. Suponiendo que las diferencias entre las líneas parentales se deben a dos pares de genes, la población de plantas F_2, crecida en 2016, se dividió en 5 clases. En esa población, la proporción de clases observada resultó ser cercana a la proporción esperada teóricamente de 1 : 4 : 6 : 4 : 1. Durante los dos años siguientes, las poblaciones de F_2 se analizaron de manera similar. En todos los casos, el valor chi-cuadrado calculado no excedió el valor crítico para 4 grados de libertad y 5 % de nivel de significación. Esto dio razones para hablar sobre el control de dos loci de un rasgo cuantitativo como el número de brácteas. La participación de dos genes no alélicos en el control de este rasgo también se demuestra al hacer coincidir el número real de plantas en las clases parentales con el número teóricamente esperado de plantas. Por lo tanto, el número de brácteas depende del número de alelos dominantes de dos genes diferentes en el genotipo.