

••• ГЕНЕТИКА ••• GENETICS •••

DOI: 10.26565/2075-5457-2022-39-1
UDC: 575.116:58.018+633.113.1**Inheritance of spike color in einkorn wheat (*Triticum monococcum* L.)**

Hao Fu

Aim: specify the spike color inheritance in einkorn wheat (*Triticum monococcum* L.) hybrids. Methods: reciprocal hybrids between the black-spikeed UA0300282 and white-spikeed UA0300311 cultivated einkorn accessions were created with the use of the “single cross” method. Four generations were analyzed using the segregation analysis method: P₁, P₂, F₁, and F₂ at autumn and spring sowing. Results: it was found that for the combination UA0300311 × UA0300282 at autumn sowing, the most suitable inheritance model is MX2-EA-AD, which implies the presence of two main genes with an equal additive effect plus polygene systems with an additive-dominant effect. In the plants of spring sowing, spike color is described by the MX2-CD-AD model, which suggests the presence of two major genes with full dominant effect plus polygenes with additive-dominant effect. In the reciprocal combination UA0300282 × UA0300311, the optimal model that describes best the spike color dispersion in plants of autumn sowing is MX2-ADI-AD, which suggests the presence of two main genes with an additive-dominant-epistatic effect plus polygenes with the additive-dominant effect. Distribution of the spring-sowing plants in terms of the spike color is well described by the MX2-ADI-ADI model – two main genes with an additive-dominant-epistatic effect plus a system of polygenes also with an additive-dominant-epistatic effect. The genes manifest themselves differently in the trait control depending on the weather conditions determined by the sowing time. In the group of direct combination plants (UA0300311 × UA0300282) of autumn sowing, heritability determined by the main gene is 97%, while that determined by polygenes is 2.7%; at spring sowing, these values are 67% and 32% respectively. In the reciprocal combination (UA0300282 × UA0300311) of autumn sowing, the main genes heritability effect is 99%, and the polygenic system accounts for 1%; in plants of spring sowing, respectively, 72%, and 28%. Conclusions: on the basis of the spike color expressiveness in the crossing combination of the einkorn kinds of wheat UA0300311 × UA0300282, the parental forms differ in two main genes and polygenes. The ratio of spike color heritability components depends on the growing conditions: at autumn sowing, 97–99 % of heritability is determined by the main genes, the polygenes account for 1–3 % of phenotypic variability; at spring sowing, the heritability component increases to 28–33 % due to the polygenic complex.

Key words: einkorn wheat, spike color, gene, segregation analysis.

Cite this article: Hao Fu. Inheritance of spike color in einkorn wheat (*Triticum monococcum* L.). The Journal of V. N. Karazin Kharkiv National University. Series “Biology”, 2022, 39, 6–11. <https://doi.org/10.26565/2075-5457-2022-39-1>

About the author:

Hao Fu – V.N. Karazin Kharkiv National University, Svobody Square, 4, Kharkiv, Ukraine, 61022, fuhaoinua@gmail.com, <https://orcid.org/0000-0003-3791-7958>

Received: 03.11.2022 / Revised: 18.11.2022 / Accepted: 07.12.2022

Introduction

Triticum monococcum L. is one of the first domesticated cereal crops whose cultivation has almost ceased until recently (Brandolini, Heun, 2019). In recent decades, interest in einkorn wheat has been revived among scientists, farmers, nutritionists, and ordinary consumers. This is explained by the fact that einkorn wheat has a higher content of gluten and protein (Geisslitz et al., 2019), antioxidants and vitamins (Pehlivan et al., 2021), microelements (Cakmak et al., 2000) than other wheat species which determines its value as a crop for healthy nutrition. Products of the einkorn wheat can be consumed by some categories of people with wheat gluten intolerance (Di Stasio et al., 2020; Rotondi Aufiero et al., 2022).

Comprehensive knowledge of the of wheat plant traits complex and the nature of their inheritance contributes to its purposeful improvement for cultivation. The color of the wheat spike determined by the color of the spike scales, has an adaptive value (Börner et al., 2005). This trait is widely used in taxonomy and for certification of wheat varieties and forms, and it is also a convenient model for genetic and molecular genetic studies (Khlestkina, 2013). Using spike color, agronomists calculate spikes number per unit area to predict yield (Zhao et al., 2014), and assess Fusarium wilt (Song et al., 2022).

It is known that the colored spike is dominant over the uncolored one (Khlestkina, 2013). In wheat and Aeglops, the genes determining the colored spike (red, brown, black, gray-smoky) are localized on the

distal sections of the short arms of the first homeologous group chromosomes: *Rg-A1*, *Rg-B1*, *Rg-D1*, respectively, in chromosomes *1A*, *1B*, *1D* (Khlestkina, 2013). In particular, the genes localized in the *A* genome derived from the einkorn wheat are of interest. Four alleles (*a-d*) are known for the *Rg-A1* gene, located on the short arm of chromosome *1A*. The *Rg-A1b* allele determines the red color of spikelet scales. The *Rg-A1c* and *Rg-A1d* alleles control black color of the scales (<http://www.shigen.nig.ac.jp/wheat/komugi/genes/download.jspMacGene>). Kozub et al. (2016) on *T. spelta* L. showed linkage of the *Rg-A1* allele which determines black spike color with the *Gli-A1j** allele which encodes the corresponding block of gliadin and can serve as a marker for the *Rg-A1* allele.

To determine nature of traits inheritance in hybrids, the method of segregation analysis "Mixed major genes plus polygenes inheritance analysis" was developed (Gai et al., 2003), which can be used to determine the number of major genes and polygenes controlling quantitative traits. This method has been used to study a number of traits in tetra- and hexaploid wheats, such as productivity (Xie et al., 2020) and grain characteristics (Yang et al., 2013) in common wheat (*Triticum aestivum* L.), plant height in durum wheat (*T. durum* Desf.) (Gong et al., 2021). The aim of this study was to determine the nature of spike color inheritance when crossing forms of einkorn wheat with an alternative manifestation of this trait.

Materials and methods

Object of study

The accessions from the National Plant Genetic Resources Bank of Ukraine were used to create reciprocal hybrids: UA0300282 var. *nigricultum* originating from Hungary, UA0300311 var. *monococcum* from Syria. The accession UA0300282 has a black spike, winter growth habit, the average spike length is of 6.25 cm, the 1000 kernels weight is of 25.0 g. The accession UA0300311 has a white spike, spring growth habit, the average spike length is of 6.95 cm, the 1000 kernels weight is of 22,8 g (Fig. 1).



Figure 1. Samples UA0300282 (right) and UA0300311 (left)

Field tests

The research was conducted on the experimental field of the Plant Production Institute named after V.Ya. Yuryev of the National Academy of Agrarian Sciences of Ukraine. The soil type is chernozem. The F_1 hybrids were created in 2019, the seeds were used to obtain F_2 . Re-crossing to obtain F_1 was carried out in 2020 on the plots sown in the autumn of 2019.

All the generations (P_1 , P_2 , F_1 , F_2) were grown at two sowing terms. Vegetation of autumn sowing plants began in October 2020 and ended in July 2021 (option E_1). Spring sowing was carried out in March 2021, ripening occurred in July 2021 (option E_2).

The plots were placed according to the block scheme: P_1 , P_2 , F_{1dir} , F_{2dir} , P_1 , P_2 , F_{1rec} , F_{2rec} , P_1 , P_2 . (F_{1dir} and F_{2dir} – accordingly F_1 and F_2 from direct cross; F_{1rec} and F_{2rec} – accordingly F_1 and F_2 from reciprocal cross). The row length is 1 m, the width between the rows is 15 cm. 30 seeds were sown in each row. By 20 plants each were analyzed from the plots P_1 , P_2 , F_1 ; by 180 plants at least in F_2 . The spike color was

evaluated after the plants ripened according to a nine-score scale: black (9), dark gray (8), gray (7), red (6), gray on a red background (5), light gray (4), pink on a red background (3), pink (2), white (1).

Statistical analysis

Segregation analysis was performed using R SEA v2.0 software developed by Wang et al. (2022a). Maximum likelihood indices and the Akaike information criterion of the genetic model were calculated. Three models were selected as candidates. The fit of the candidate model was checked using the χ^2 (U_1^2 , U_2^2 , U_3^2), Smirnov (nW^2), and Kolmogorov (D_n) criteria.

Results and discussion

Selection of a candidate model

The selection of the optimal genetic model was based on the AIC values obtained from the spike color data in the P₁, P₂, F₁ and F₂ generations. Models with the smallest AIC values were selected as candidates. The table 1 shows that in the combination UA0300311 × UA0300282 at autumn sowing, among the 24 calculated models, MX2-A-AD, 2MG-A and MX2-EA-AD have relatively low AIC values, which are 379, 383, 378, respectively. For spring sowing, three models were selected for testing: MX2-EA-AD, MX1-AD-AD, and MX2-CD-AD, with AIC values of 362, 392, and 346, respectively. In the reciprocal combination UA0300282 × UA0300311 for plants of autumn sowing, this condition is satisfied by the MX2-ADI-AD, MX2-CD-AD and 2MG-EAD models, the AIC values are 487, 492, and 500, respectively; for spring sowing – models MX1-A-AD, MX1-NCD-AD and MX2-ADI-ADI with the corresponding AIC values: 522, 489 and 482. The values of the maximum likelihood function (MLV) are also presented in the table 1.

Table 1. Maximum likelihood functions and Akaike criteria

E	Crossing combinations	Model	MLV	AIC
E ₁	UA0300311 × UA0300282	MX2-A-AD	-186	379
		2MG-A	-911	383
		MX2-EA-AD	-187	378
	UA0300282 × UA0300311	MX2-ADI-AD	-235	487
		MX2-CD-AD	-378	422
		2MG-EAD	-201	500
E ₂	UA0300311 × UA0300282	MX2-EA-AD	263	362
		MX1-AD-AD	289	392
		MX2-CD-AD	-378	346
	UA0300282 × UA0300311	MX1-A-AD	-235	522
		MX1-NCD-AD	239	489
		MX2-ADI-ADI	-279	482

Note: E is sowing time, E₁ is autumn sowing, E₂ is spring sowing, MLV is maximum likelihood function, AIC is Akaike's criterion, 2MG is two major genes, MX is mixed model of major gene and polygene system, A is additive effect, AD – additive-dominant effect, ADI – additive-dominant-epistatic effect, EA – equal additive effect, CD – complete dominant effect. For example: MX2-A-AD means a mixed model of two major genes with an additive effect plus a polygene system with an additive-dominant effect.

Test of spike color inheritance genetic models suitability

The suitability of the selected candidate models was tested according to the homogeneity (U_1^2 , U_2^2 , U_3^2), Smirnov (nW^2) and Kolmogorov (D_n) criteria. The genetic model with the lowest AIC value and the minimum number of statistically significant indicators is considered optimal (Akaike, 1977).

It was concluded that for the combination UA0300311 × UA0300282 at autumn sowing, the most suitable inheritance model is MX2-EA-AD, which assumes the presence of two main genes with an equal additive effect plus a system of polygenes with an additive-dominant effect. In spring-sown plants, spike color is described by the MX2-CD-AD model which assumes the presence of two main genes with a full dominant effect plus polygenes with an additive-dominant effect.

In the reciprocal combination – UA0300282 × UA0300311, the optimal model that best describes the dispersion of spike color in plants of autumn sowing is MX2-ADI-AD, which assumes the presence of two main genes with an additive-dominant-epistatic effect plus polygenes with an additive-dominant effect. The plant of spring sowing distribution by spike color is well described by the MX2-ADI-ADI model – two main genes with an additive-dominant-epistatic effect plus a system of polygenes with an additive-dominant-epistatic effect.

Parameters of the optimal genetic model based on spike color

The genes manifest themselves differently in a trait depending on the weather conditions determined by the sowing timing. In the combination UA0300311 × UA0300282 at winter sowing, the additive effect of the first pair of main genes is positive and equal to 1.96. The additive effect of polygene ([d]) is negative and is represented by the number –1.41, the dominant effect of polygene ([h]) is 2.52. In the plants of spring sowing, the additive effect of the first and second pairs of main genes is negative and expressed weaker and at the same level, amounting to –0.08. The additive effect of polygenes is –2.35, and the dominant effect of polygenes is estimated at 2.69. In the reciprocal combination UA0300282 × UA0300311, the additive effect of the first pair is much greater than that of the second pair of main genes in terms of absolute value: respectively –2.98 and –0.01 for winter sowing, –3.25 and –0.25 for spring sowing. The dominant effect of the first pair of main genes is also much greater than that of the second pair: respectively, 1.86 and 0.04 for winter sowing, 1.75 and 0.25 for spring sowing.

In the plants of direct combination (UA0300311 × UA0300282) of autumn sowing, heritability determined by the main gene is 97%; and that determined by polygenes is estimated at 2.7%; in spring sowing, these values are equal to 67% and 32%, respectively. In the reverse combination (UA0300282 × UA0300311) from autumn sowing, the heritability is 99%, the polygenic system accounts for 1%; in plants from spring sowing, respectively, 72% and 28%. In the reverse combination (UA0300282 × UA0300311) of autumn sowing, the heritability is 99%, the polygenic system accounts for 1%; in plants of spring sowing, respectively, 72% and 28%. This means that the growing conditions and the environment strongly influence the spike color (Wei et al., 2017), it depends on the growing conditions, in particular on the light intensity (Zeven, 1983).

The results of the study on the plants quantitative traits inheritance obtained by the method of Mixed major genes plus polygenes inheritance analysis and the methods of molecular genetics, evaluate the genetic effect in various aspects. Studies show that the numbers predicted by these two methods and the QTL positioning results of major genes controlling plant quantitative traits are in agreement (Zhang et al., 2007; Wang et al., 2022b).

Conclusions

1. The difference in spike color between the black-spikeed and white-spikeed forms of einkorn wheat is under the control of two main genes and a polygene system.
2. The ratio of heritability components of spike color in einkorn wheat depends on the vegetation conditions: at autumn sowing, 97–99 % of the heritability is caused by the main genes and 1–3 % of the phenotypic variability is accounted by polygenes; at spring sowing, the heredity component due to the polygenic complex increases to 28–33 %.

Acknowledgments

The research was supported by the China Scholarship Council (201906300105).

I would like to express my sincere gratitude to Professor L.O. Atramentova and leading researcher R.L. Boguslavskiy for their constant help in conducting the research, valuable advice and discussion of the results.

References

- Akaike H. (1977). On entropy maximization principle. In: Proceedings of the symposium on applications of statistics. *Applications of Statistics*, Amsterdam: North-Holland, 27–41.
- Börner A., Schäfer M., Schmidt F. et al. (2005). Associations between geographical origin and morphological characters in bread wheat (*Triticum aestivum* L.). *Plant Genetic Resources*, 3(3), 360–372. <https://doi.org/10.1079/PGR200589>
- Brandolini A., Heun M. (2019). Genetics of brittleness in wild, domesticated and feral einkorn wheat

- (*Triticum monococcum* L.) and the place of origin of feral einkorn. *Genetic Resources and Crop Evolution*, 66(2), 429–439. <https://doi.org/10.1007/s10722-018-0721-7>
- Cakmak I., Ozkan H., Braun H.J. et al. (2000). Zinc and iron concentrations in seeds of wild, primitive and modern wheats. *Food and Nutrition Bulletin*, 21(4), 401–403. <https://doi.org/10.1177/156482650002100411>
- Di Stasio L., Picascia S., Auricchio R. et al. (2020). Comparative analysis of *in vitro* digestibility and immunogenicity of gliadin proteins from durum and einkorn wheat. *Frontiers in Nutrition*, 7, 1–7. <https://doi.org/10.3389/fnut.2020.00056>
- Gai J.Y., Zhang Y.M., Wang J.K. (2003). *Genetic system of quantitative traits in plants*. Science Press, Beijing. 380 p. (in Chinese)
- Geisslitz S., Longin C.F.H., Scherf K.A. et al. (2019). Comparative study on gluten protein composition of ancient (einkorn, emmer and spelt) and modern wheat species (durum and common wheat). *Foods*, 8(9), 1–14. <https://doi.org/10.3390/foods8090409>
- Gong Y.S., Wei S.H., Peng Z.S. et al. (2021). Genetic study on plant height and its components, partial yield traits in durum wheat ANW16F. *Southwest China Journal of Agricultural Sciences*, 34(2), 229–235. <https://doi.org/10.16213/j.cnki.scjas.2021.2.001> (in Chinese with English abstract)
- Khlestkina E.K. (2013). Genes determining the coloration of different organs in wheat. *Russ. J. Genet. Appl. Res.*, 3(1), 54–65. <https://doi.org/10.1134/S2079059713010085> (in Russian)
- Kozub N.A., Sozinov I.A., Niniyeva A.K. et al. (2016). Genetic marking of glume color in *Triticum spelta* L. var. *caeruleum* using gliadins. *Cytology and Genetics*, 50(3), 168–172. <https://doi.org/10.3103/S0095452716030075>
- Pehlivan K.F., Keskin C.N., Agil F. et al. (2021). Profiles of vitamin B and E in wheat grass and grain of einkorn (*Triticum monococcum* ssp. *monococcum*), emmer (*Triticum dicoccum* ssp. *dicoccum* Schrank.), durum (*Triticum durum* Desf.), and bread wheat (*Triticum aestivum* L.) cultivars by LC-ESI-MS/MS analysis. *Journal of Cereal Science*, 98, 1–10. <https://doi.org/10.1016/j.jcs.2021.103177>
- Rotondi Aufiero V., Sapone A., Mazzarella G. (2022). Diploid wheats: are they less immunogenic for non-celiac wheat sensitive consumers? *Cells*, 11(15), 1–11. <https://doi.org/10.3390/cells11152389>
- Song Y., Chen Y., Yang J. et al. (2022). Identification wheat scab by color feature index of digital image. *Jiangsu Agricultural Sciences*, 50(2), 186–191. <https://doi.org/10.15889/j.issn.1002-1302.2022.02.031> (in Chinese)
- Wang J.T., Zhang Y.W., Du Y.W. et al. (2022a). SEA v2.0: an R software package for mixed major genes plus polygenes inheritance analysis of quantitative traits. *Acta Agronomica Sinica*, 48(6), 1416–1424. <https://doi.org/10.3724/SP.J.1006.2022.14088> (In Chinese with English abstract)
- Wang L.M., Dang Z., Zhao W. et al. (2022b). Genetic analysis of plant height in flax using segregating generations and recombination inbred line populations. *Journal of Plant Genetic Resources*, 23(5), 1446–1457. <https://doi.org/10.13430/j.cnki.jpgr.20220305001> (in Chinese with English abstract)
- Wei Y., Hu F., Zheng X. et al. (2017). The molecular mechanism of the impacts of illumination on litchi fruit coloration and anthocyanin biosynthesis. *Acta Horticultural Science*, 44(7), 1363–1370. <https://doi.org/10.16420/j.issn.0513-353x.2016-0717> (in Chinese with English abstract)
- Xie S.F., Ji W.Q., Zhang Y.Y. et al. (2020). Genetic effects of important yield traits analyzed by mixture model of major gene plus polygene in wheat. *Acta Agronomica Sinica*, 46(3), 365–384. <https://doi.org/10.3724/SP.J.1006.2020.91044> (in Chinese with English abstract)
- Yang X.S., Liang Z.Y., Li H. et al. (2013). Analysis on genetic model of grain characteristics in common wheat by mixed inheritance model of major genes plus polygenes. *Journal of Triticeae Crops*, 33(6), 1119–1127. <https://doi.org/10.7606/j.issn.1009-1041.2013.06.009> (in Chinese with English abstract)
- Zeven A.C. (1983). The character brown spike of bread wheat: A review. *Euphytica*, 32, 299–310.
- Zhang J.F., Qi C.K., Pu H.M. et al. (2007). Inheritance and QTL identification of oil content in rapeseed (*Brassica napus* L.). *Acta Agronomica Sinica*, 33(9), 1495–1501.
- Zhao F., Wang K., Yuan Y. (2014). Study on wheat spike identification based on color features and AdaBoost algorithm. *Crop Journal*, 1, 141–144. <https://doi.org/10.16035/j.issn.1001-7283.2014.01.042> (in Chinese with English abstract)

Успадкування забарвлення колосу у пшениці однозернянки (*Triticum monosocum* L.) Хао Фу

Ціль: встановити характер успадкування забарвлення колосу у гібридів пшениці однозернянки (*Triticum monosocum* L.). Методи: реципрокні гібриди двох зразків культурної однозернянки, чорноколосого UA0300282 та білоколосого UA0300311, були створені за допомогою методу single cross. З використанням методу сегрегаційного аналізу проаналізовано чотири генерації: P1, P2, F1 та F2 при осінньому та весняному посіві. Результати: встановлено, що для комбінації UA0300311 × UA0300282 при осінньому посіві найбільш сприятливою моделлю успадкування є MX2-EA-AD, яка передбачає наявність двох головних генів з рівним адитивним ефектом плюс системи полігенів з адитивно-домінантним ефектом. У рослин від весняного посіву забарвлення колосу описується моделлю MX2-CD-AD, яка передбачає присутність двох головних генів з повним домінантним ефектом плюс полігенів з адитивно-домінантним ефектом. У реципрокній комбінації – UA0300282 × UA0300311 оптимальна модель, яка найкраще описує дисперсію кольору колосу у рослин від осіннього посіву, – це MX2-ADI-AD, яка передбачає наявність двох головних генів з адитивно-домінантно-епістатичним ефектом плюс полігенів з адитивно-домінантним ефектом. Розподіл рослин від весняного посіву за кольором колосу добре описує модель MX2-ADI-ADI – з двома головними генами з адитивно-домінантно-епістатичним ефектом плюс системою полігенів з адитивно-домінантно-епістатичним ефектом. Гени по-різному проявляють себе у контролі ознаки залежно від погодних умов, що визначаються термінами посіву. У групі рослин прямої комбінації (UA0300311 × UA0300282) від осіннього посіву успадкованість, що визначається головним геном, становить 97%, а та, що визначається полігенами, оцінюється числом 2,7%; при весняному посіві ці значення дорівнюють відповідно 67% і 32%. У зворотній комбінації (UA0300282 × UA0300311) від осіннього посіву успадкованість ефекту головних генів становить 99%, на полігенну систему припадає 1%; у рослин від весняного посіву відповідно 72% і 28%. Висновки: за ознакою виразності забарвлення колосу в комбінації схрещування пшениць однозернянок UA0300311 × UA0300282 батьківські форми розрізняються двома головними генами та полігенами. Співвідношення компонент успадкованості забарвлення колосу у пшениці однозернянки залежить від умов вегетації: при осінньому посіві 97–99 % успадкованості зумовлюють головні гени, а на частку полігенів припадає 1–3 % фенотипічної мінливості; при весняному посіві компонента успадкованості, зумовлена полігенним комплексом, збільшується до 28–33 %.

Ключові слова: пшениця однозернянка, забарвлення колосу, ген, сегрегаційний аналіз.

Цитування: Хао Фу. Inheritance of spike color in einkorn wheat (*Triticum monosocum* L.). Вісник Харківського національного університету імені В.Н. Каразіна. Серія «Біологія», 2022, 39, 6–11. <https://doi.org/10.26565/2075-5457-2022-39-1>

Про авторів:

Хао Фу – Харківський національний університет імені В.Н. Каразіна, майдан Свободи, 4, Харків, Україна, 61022, fuhaoinua@gmail.com, <https://orcid.org/0000-0003-3791-7958>

Подано до редакції: 03.11.2022 / Прорецензовано: 18.11.2022 / Прийнято до друку: 07.12.2022