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# INHERITANCE OF DWARFISM TRAIT BY WINTER WHEAT MUTANTS INDUCED IN THE CHORNOBYL NPP EXCLUSION ZONE

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**Background.** The development of short-stem cultivars is an effective way to increase the productivity of winter wheat grown under the intensive cultivation technology. Dwarf mutants, induced in the exclusion zone of ChNPP, can preserve a productive potential of an initial cultivar and be of a breeding value. The knowledge of the inheritance regularities of stem length by dwarf winter wheat mutants makes it possible to choose the pairs for crossing better and predict a final result in hybrid generations earlier.

**Materials and methods.** Hybrids  $F_1$  i  $F_2$  of *Triticum aestivum* L. were received by crossing medium-grown cultivar Sonechko with dwarf mutant lines UK 1145/10, UK 1147/10, and UK 1148/10, induced by the effect of the radionuclide contamination of the exclusion zone of ChNNP on the plants of 'Albatros odeskyi' cultivar. The nature of the trait inheritance in  $F_1$  was determined by the degree of phenotype dominance, the variability of plant height was determined by a variation coefficient. The segregation frequency of dwarf, low-, medium- and high-grown forms was accounted in the population of  $F_2$  plants.

**Results.** By stem length, plants  $F_1$  exceeded the genotypes involved in hybridization, or were closer to parental forms with a greater manifestation of the trait. The real heterosis in the plant height decrease was shown in the  $F_1$  hybrid 'Sonechko' × UK 1147/10. The hybrid productivity elements are inherited by the type of a partial positive dominance and over-dominance. From 2.2 % to 3.6 % of high-grown forms, atypical for parents, were recorded in the population of  $F_2$ .

**Conclusions.** When the crossing combination includes a medium-grown cultivar of winter wheat and dwarf mutants, induced in the exclusion zone of ChNPP, a stem length in  $F_1$  is inherited by an intermediate type and partial positive dominance. Dwarf mutant UK 1147/10 can be valuable for breeding short stem winter bread wheat. A significant



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variation of such indicator as a degree of phenotype dominance by all studied features confirms a complicated nature of genetic determination of a plant height and the productivity elements of winter wheat, in the formation of which various types of gene interaction take part.

**Keywords:** dwarf mutants, productivity elements, domination degree, *Triticum aestivum* L.

### INTRODUCTION

Cereal crops occupy half of the arable lands in the world, winter wheat being one of the main cereals of the planet that plays a leading role in food supply of mankind. In the world, the areas which are annually sown under this cereal crop amount to 217 million ha, and gross grain yield is over 700 mln t; 32.1 mln t of which are harvested in Ukraine (Cheremisina et al., 2022; Erenstein et al., 2022). Wheat is mostly grown for foodstuffs, which comprises 66 % of the world production; it is included in the diet of the population of 173 countries in the world. This food crop satisfies 18 % of man's needs in calories and is an important source of proteins and vitamins (Erenstein et al., 2022). Which is why, the issue of the wheat yield increase, grain quality, ecological plasticity and resistance to abiotic and biotic stress factors of the environment is of great relevance. A successful solution of these problems depends on the efficiency of the genetic improvement of wheat cultivars (Morgun & Topchii, 2018; Liu et al., 2021). The potential reserve for the increase of grain production is, through breeding, based on updated genetic techniques, the creation of new high yielding cultivars adapted to certain cultivation conditions (Krishnappa et al., 2022). In this connection, a great significance is given to the intensification of breeding through the expansion of a genetic diversity and the introduction of the following into a breeding process: the latest achievements of genomics, proteomics and metabolomics, genetically modified technologies, TILLINGtechnologies of target-oriented mutations, CRISPR/Cas-systems of genome editing, DArT-systems of molecular markers, induced mutagenesis (Yakymchuk, 2019).

Plant lodging is one of the factors limiting the realization of a genetic yield potential – the most important property of a cultivar (Lozinskyi, 2016; Mondal, 2020). The development of short-stem cultivars is the efficient way to avoid lodging and to increase winter wheat productivity when the intensive cultivation technology is applied (Morgun et al., 2014; Voloshchuk, & Yurchenko, 2015). The use of the forms with genetically determined reduction of a plant height in the program of breeding work initiated by so-called green revolution – one of the most significant achievements of the 20th century. This has resulted in a significant increase in the world yields of wheat grain (Morgun et al., 2014; Dash, & Rai, 2022). However, in most world donors of wheat dwarfism, this property is linked genetically with a decreased drought- and frost-resistance, which limits their use in the development of short-stem cultivars in Ukraine. Nowadays, more than 20 specific genes (*Rht1–Rht20*) that provide a significant diversity of bread wheat by this feature were found in the genetic plasma of genus *Triticum* L. 14 of them are of mutant origin (Lozinskyi, 2016; Ford et al., 2018; Xiong et al., 2018), which is a vivid proof of the efficiency of induced mutagenesis in the creation of short-stem forms.

The scientists of the department of the genetic plant improvement of the Institute of plant physiology and genetics (IPPG) of Ukraine's NAS have been conducting the research of the genetic consequences of the Chornobyl NPP accident. It was found

that under the chronic effect of low radiation doses in the radionuclide exclusion zone, dwarf and semi-dwarf plant mutants were induced in winter wheat with a high frequency (Morgun & Yakymchuk, 2021).

The received forms can preserve a productive potential of an initial cultivar, and they are of breeding value as donors of dwarfism when winter wheat cultivars of an intensive type are developed. Certainly, the information about the contribution of certain short stem trait genes to the determination of a plant height and the nature of their non-allele interaction presents interest for breeding practice. The knowledge of the inheritance regularities of a stem length by dwarf winter wheat makes it possible to choose the pairs for crossing better and to predict a possible final result from different hybrid generations earlier.

The purpose of the research was to study the inheritance nature of the dwarfism trait and the productivity elements by hybrids  $F_1$  of winter bread wheat, which resulted from the crossing of dwarf mutants with a medium-grown cultivar, and to identify the segregation peculiarities by a long-stem feature in generation  $F_2$ .

## **MATERIALS AND METHODS**

The present study was conducted on simple  $F_1$  and  $F_2$  hybrids of winter bread wheat (*Triticum aestivum* L.) obtained through the crosses between a medium-grown cultivar 'Sonechko' and dwarf mutant lines UK 1145/10, UK 1147/10, UK 1148/10 induced by the chronic effect of the radionuclide contamination in the exclusion zone of Chornobyl NPP on growing plants of cultivar 'Albatros odeskyi'. The hybrid plants were grown in the fields of the experimental agricultural production of the Institute of Plant Physiology and Genetics (IPPG) of the NAS of Ukraine in the village of Hlevakha, Fastiv district, Kyiv region. The samples were sown at optimal terms according to the farm practices which are generally accepted for the Forest-Steppe zone. The studies of the mentioned cultivar and mutant lines in the primary seedling nurseries showed their stability in the main morphological characteristics. Hybrids  $F_1$  were sown on single-row 1.5 m long plots using a wide-row method. The planting scheme was as follows: maternal form –  $F_4$  – paternal form, parental forms being the standards.

A structural analysis based on the morphological indicators and the plant productivity elements of hybrids and parental forms was conducted in a triple replication. To determine the inheritance pattern of a stem length trait and the plant productivity elements in  $F_1$ , the degree of phenotype dominance (hp) was calculated by B. Griffing (1950) formula:

$$hp = \frac{\left(F_1 - Mp\right)}{\left(P_{max} - Mp\right)},$$

where hp is the degree of dominance,  $F_1$  is the value of the hybrid trait, Mp is the mean value of the trait of both parents;  $P_{max}$  is the highest value of the trait in one of the parents. The grouping of the obtained data was carried out according to the classification of G. M. Beil and R. E. Atkins (1965): numerical values of hp > +1 – heterosis (overdominance); +0.5 < hp  $\leq$  +1 – partial positive dominance; -0.5  $\leq$  hp  $\leq$  +0.5 – intermediate inheritance; -1  $\leq$  hp < -0.5 – a partial negative dominance; hp < -1 – depression. The coefficient of heterosis (Hbt – true heterosis and Ht – hypothetical heterosis) was calculated using D. F. Matzinger, T. J. Mannand, and C. C. Cockerham (1962) as well as S. Fonseca and F. L. Patterson (1968) formulas:

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$$Hbt(\%) = \frac{(F_1 - BP)}{BP \cdot 100} - \text{true heterosis},$$

$$Ht(\%) = \frac{(F_1 - MP)}{MP \cdot 100} - \text{hypotherical heterosis},$$

where  $F_1$  is the arithmetic mean value of the trait in the hybrid, MP is the arithmetic mean value of the indicator in both parental forms, and BP is the highest trait manifestation of one of the parents. The modification variability of a plant height was determined by the coefficient of variation (CV, %), and the distribution groups were used: <10 % – weak; 11–25 % – moderate; >25 % – strong (Atramentova & Utevska, 2007). The distribution of the parental forms and hybrids by a plant height was carried out according to the classification of S. F. Lyfenko (1987).

Hybrids  $F_2$  were sown in a selection nursery with sparse planting on plots of 10 m<sup>2</sup>. After the vegetation period was over, hybrid  $F_2$  populations were examined for dwarf, low-, medium-, and tall-grown forms.

The obtained data was statistically analyzed using the method of analysis of variance, and the sample mean, a standard deviation, a coefficient of variation, and a standard error of the mean were determined (Atramentova & Utevska, 2007).

#### **RESULTS AND DISCUSSION**

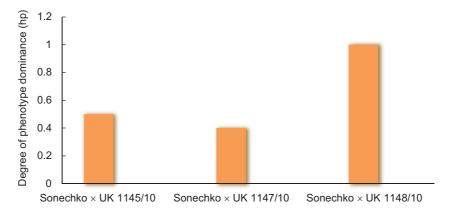
The long-term phenological observations and the studies of the data concerning the structural analysis, included into the scheme of dwarf hybridization, have shown that dwarf mutant wheat forms induced by the radionuclide contamination of the exclusion zone of ChNPP, inherit the short-stem rait regularly. Parental wheat samples, involved in the hybridization scheme, belong to various groups by a plant height: medium-grown – cultivar 'Sonechko' 79.0 cm high and dwarfs – mutant lines UK 1145/10, UK 1147/10, UK 1148/10 – 51.2, 55.0 and 52.7 cm high, respectively, which is significantly lower (p  $\leq$ 0.05) than a plant height of an initial cultivar 'Albatros odeskyi' – 82.3 cm. Plants F<sub>1</sub> exceeded the genotypes involved in the hybridization by a stem length or they were closer to a parental form with a more vivid manifestation of this trait. Only in the combination of 'Sonechko' × UK1147/10 stem length of the hybrids was significantly smaller than that of a parent form and amounted to 75.6 cm (p  $\leq$ 0.05) (**Table 1**). In the crossing combinations of 'Sonechko' × UK 1145/10 and 'Sonechko' × UK 1147/10 stem lengths in hybrids F<sub>1</sub> were inherited by an intermediate type (they were hp 0.5 and 0.4, respectively) (**Fig. 1**).

Table 1. Stem length inheritance by hybrids F<sub>1</sub> in the crossing combinations of dwarf mutants with a medium-grown cultivar

Crossing combination	Р	lant height,	cm	C\/ in F 0/	Hbt, %	Ht, %
	2	8	F <sub>1</sub>	CV III F <sub>1</sub> , %		
'Sonechko' × UK 1145/10	79.0±1.0	51.2±0.9	78.7±0.9 <sup>#</sup>	5.6	-0.4	20.9
'Sonechko' × UK 1147/10	79.0±1.0	55.0±1.1	75.6±1.2*#	7.5	-4.3	12.8
'Sonechko' × UK 1148/10	79.0±1.0	52.7±1.0	79.2±1.1#	6.8	0.3	20.3

Note: M ± SD, n = 30; \*, # – a difference in comparison with a parent and parental forms, respectively, is significant at p ≤0.05

In the crossing combination of 'Sonechko'  $\times$  UK 1148/10 a partial positive dominance was recorded (hp = 1.0). Stem length in the studied generations  $F_1$  varied slightly (CV was equal to 5.6–7.5 %). By the level of real and hypothetic heterosis in  $F_1$ , the combination of 'Sonechko'  $\times$  UK 1147/10 appeared to be more valuable for breeding, as by stem length heterosis towards lessening of the trait manifestation of hybrids was recorded as compared with parental samples with more intensive manifestation of the trait (Hbt = -4.3 %); the coefficient of hypothetical heterosis, as compared with other crossing combinations under study, turned out to be the smallest (Ht = 12.8 %).



**Fig. 1.** Degree of phenotype dominance of the stem length trait in hybrids F<sub>1</sub> in the crossing combinations of dwarf mutant lines with a medium-grown cultivar

In the crossing combinations of 'Sonechko'  $\times$  UK 1145/10 and 'Sonechko'  $\times$  UK 1148/10 the coefficient of real heterosis in hybrids varied both towards the decrease (Hbt = -0.4 %) and towards the increase (Hbt = 0.3 %) of the manifestation of the stem height trait. The hypothetical heterosis effects of their hybrid combinations were high, 20.9 % ('Sonechko'  $\times$  UK 1145/10) and 20.3 % ('Sonechko'  $\times$  UK 1148/10).

The comparison of the productivity elements of dwarf mutants with the initial cultivar 'Albatros odeskyi' makes it possible to identify the breeding value of the received mutant samples while developing the winter wheat cultivars of highly intensive and intensive types. A potentially high productivity of dwarf mutants is confirmed by the indicators of general and productive tillering which exceed those of the initial cultivar by 0.6–1.6 pcs. and 0.8–1.0 pcs., respectively (**Table 2**). When the number of grains in a spike is small, their mass (1.7–1.8 g) and the mass of the grains from a plant (6.3–6.8 g) are at the same level as those of the cultivar 'Albatros odeskyi'. Among the studied dwarf mutants, lines UK 1145/10 and UK 1148/10 preserve the weight of 1000 grains as one of the most important indicators of the wheat yield formation at the level of an initial cultivar (40.7 and 39.3 g, respectively).

As the result of the analysis of the experimental material a significant difference in the hybrids of the first generation by the elements of productivity structure from parental forms was recorded. In the crossing combinations of 'Sonechko'  $\times$  UK 1145/10 and 'Sonechko'  $\times$  UK 1147/10 a spike length of plants  $F_1$  appeared to be much smaller as compared with a similar indicator of a parental form, and it showed a partial negative dominance (hp was -0.8 and -1.0, respectively). In the combination of 'Sonechko'  $\times$ 

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UK 1148/10 the spike length trait indicator was smaller as compared with that of a parent form; it exceeded this feature in the maternal form and it was characterized by an intermediate inheritance.

Table 2. Analysis of the productivity elements of hybrids F1 and the degree of their dominance

			Biometric indicators							
Cultivar/line		Spike length, cm	Total tillering, pcs.	Productive tillering, pcs.	Number of ears in a spike, pcs.	Number of grains in a spike, pcs.	Grain weight from a spike, g	Grain weight from a plant, g	Weight of 1000 grains, g	
"	Sonechko'	9.2±0.1	4.9±0.2	4.3±0.2	19.0±0.3	34.6±1.5	2.0±0.1	8.2±0.3	44.5±0.9	
U	IK 1145/10	10.1±0.2	5.6±0.3°	4.9±0.2°	17.2±0.1°	39.4±1.4°	1.8±0.3	6.7±0.2	40.7±1.2	
U	IK 1147/10	10.6±0.3	5.4±0.3°	4.9±0.3°	17.4±0.3 <sup>^</sup>	36.2±1.3°	1.7±0.2	6.3±0.3	35.6±0.8°	
U	IK 1148/10	10.3±0.2	5.1±0.2°	4.7±0.2°	17.7±0.2 <sup>^</sup>	38.6±1.3°	1.8±0.2	6.8±0.2	39.3±1.4	
'Alba	atros odeskyi'	10.2±0.1	4.5±0.2	3.9±0.2	20.3±0.3	44.2±1.5	2.0±0.1	6.6±0.4	40.9±0.6	
×	UK 1145/10	9.3±0.2 <sup>#</sup> -0.8	5.0±0.3 -0.7	4.5±0.3 -0.33	18.8±0.2 <sup>#</sup>	37.7±1.6 0.3	2.3±0.1 4.0	9.1±0.4 <sup>#</sup> 2.2	37.6±0.8** -2.6	
Sonechko' ×	UK 1147/10	9.2±0.2 <sup>#</sup> -1.0	5.0±0.4 -0.6	4.8±0.2 0.7	18.9±0.2 <sup>#</sup>	36.4±1.3 1.3	2.1±0.3 1.7	8.4±0.3 <sup>#</sup>	42.1±1.3 <sup>#</sup> 0.5	
loS,	UK 1148/10	9.7±0.3 -0.1	4.7±0.2 -3.0	4.4±0.2 -0.5	18.3±0.1* <sup>#</sup> -0.1	39.1±1.5* 1.3	2.0±0.2 1.0	8.8±0.3 <sup>#</sup> 1.9	40.3±1.1* -0.6	

Note: above the dash – absolute meanings, under the dash – degree of phenotype dominance (hp); ^ difference with cultivar 'Albatros odeskyi' is significant at p ≤0.05; \*, # – a difference in comparison with a parent and parental forms, respectively, is significant at p ≤0.05

No significant differences between hybrids and parental forms by the indicators of total and productive tillering were found. The degree of phenotype dominance ranges within -3.0–+0.67, which corresponds to the inheritance of the trait from a partial positive dominance ('Sonechko'  $\times$  UK 1147/10) to depression ('Sonechko'  $\times$  UK 1148/10).

The hybrid material of the first generation by the trait of the number of ears in a spike, which is 18.3-18.8 pcs., exceeds statistically (p  $\leq$ 0,05) a parent form by 1.6 pcs. (p  $\leq$ 0.05) – 'Sonechko'  $\times$  UK 1145/10 (hp = 0.8), 1.5 pcs. – 'Sonechko'  $\times$  UK 1147/10 (hp = 0.9), which is inherited by the type of a partial positive dominance. The generation of a hybrid combination of 'Sonechko'  $\times$  UK 1148/10, as compared with the maternal form, is characterized by a significantly lower manifestation of the number of ears in a spike trait, which is inherited by an intermediate type (hp = -0.1), and exceeds its number in the parent form by 0.6 pcs.

Hybrids  $F_1$  exceed the maternal form – cultivar 'Sonechko' – by the indicator of the number of ears in a spike. A significant increase of this trait indicator (39.1 pcs.), as compared with both maternal and parent forms, was found in the plants which resulted from the crossing of 'Sonechko'  $\times$  UK 1148/10. The degree of a phenotype dominance amounts to 0.3 and 1.3, which corresponds to an intermediate inheritance and overdominance (heterosis).

In the hybrids of the first generation from the crossing of a medium-grown cultivar with dwarf mutants of wheat such trait as the grain weight from a spike corresponds to the best parent form and it is equal to 2.3, 2.1 and 2.0 g, provided mutant lines UK 1145/10, 1147/10 and UK 1148/10 are involved in the crossing combination. The degree of phenotype dominance amounts to 1.0–4.0, which is typical for overdominance. Over-dominance (heterosis) in plants  $F_1$  was also recorded by the grain weight trait in the plants (hp = 1.2–2.2), which ranges within 8.4–9.1 g; this considerably exceeds the indicators of both parental forms.

By the weight of 1000 grains hybrids were not equal to the maternal form. The nature of phenotype inheritance of the trait refers to an intermediate type (hp = 0.5) ('Sonechko'  $\times$  UK 1147/10), to a partial negative dominance (hp = -0.5) ('Sonechko'  $\times$  UK 1148/10) and depression (hp = 2.6) ('Sonechko'  $\times$  UK 1145/10).

In the population of plants  $F_2$  a segregation by the plant height trait with the change of phenotypes from dwarf to high-grown ones takes place; this is indicative of an important formation process (**Table 3**).

Table 3. Plant distribution of hybrids F <sub>2</sub> by plant height in the crossing combinations of	f
dwarf mutant lines with a medium-grown cultivar	

	Number of studied plants in F <sub>2</sub>	Intra-family variability of F <sub>2</sub> plants by height						
Crossing combination		dwarfs		low- and medium-grown		high-grown		
		pcs.	%	pcs.	%	pcs.	%	
'Sonechko' × UK 1145/10	828	24	2.9±0.58	786	94.9±0.76	18	2.2±0.51	
'Sonechko' × UK 1147/10	640	25	3.9±0.76	592	92.5±1.04	23	3.6±0.73	
'Sonechko' × UK 1148/10	780	28	3.6±0,66	729	93.5±0.88	23	2.9±0.60	

The most frequent forms (92.5–94.9 %) were low-grown and medium-grown ones. The appearance of dwarf forms in the populations of  $F_2$  plants was typical for all crossing combinations; their share amounted to 2.9–3.9 %. They were most frequently found among  $F_2$  hybrids, which was the result of the crossing of cultivar 'Sonechko' with mutant UK 1147/10. The appearance of high-grown plants with the frequency equal to 2.2–3.6 %, which are typical neither of the parent generation nor of  $F_1$  hybrids indicates the adaptive effect of the interaction of non-allele genes and confirms numerous data about a polygenic control nature of such a trait as stem length of winter bread wheat. The highest frequency of their segregation in the second hybrid generation was also recorded as a result of the crossing of 'Sonechko' × UK 1147/10.

#### CONCLUSIONS

The crossing combination of a medium-grown cultivar with dwarf mutants of winter wheat, induced by the action of the radionuclide contamination in the exclusion zone of ChNPP, results in the inheritance of stem length in  $F_1$  plants through an intermediate type and a partial positive dominance. Considering the inheritance pattern of stem length and negative heterosis for this feature, as well as the preservation of the productivity elements at the level of the best parental forms in the combination with high 1000 grain weight and an increased proportion of dwarf forms in the population of  $F_2$  hybrids, the combinations involving the dwarf mutant UK 1147/10 may be valuable for

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breeding of short-stem winter bread wheat. The significant variation in the degree of phenotype dominance for all studied traits suggests a complex genetic nature of the determination of a plant height and the productivity elements in winter wheat, various types of gene interactions being involved.

#### **COMPLIANCE WITH ETHICAL STANDARDS**

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Human Rights:** This article does not contain any studies with human subjects performed by any of the authors.

**Animal Studies:** This article does not include animal studies.

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# УСПАДКУВАННЯ ОЗНАКИ КАРЛИКОВОСТІ МУТАНТАМИ ОЗИМОЇ ПШЕНИЦІ, ІНДУКОВАНИМИ У ЗОНІ ВІДЧУЖЕННЯ ЧОРНОБИЛЬСЬКОЇ АЕС

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**Обґрунтування.** Створення короткостеблових сортів — ефективний спосіб підвищення продуктивності озимої пшениці за інтенсивної технології вирощування. Карликові мутанти, індуковані в зоні відчуження ЧАЕС, можуть зберігати продуктивний потенціал вихідного сорту і становити селекційну цінність. Знання

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закономірностей успадкування довжини стебла карликовими мутантами пшениці дає змогу ефективніше добирати пари для схрещування й завчасно передбачати кінцевий результат у ранніх гібридних поколіннях.

**Матеріали та методи.** Гібриди  $F_1$  і  $F_2$  *Triticum aestivum* L., отримані від схрещування середньорослого сорту Сонечко з карликовими мутантними лініями УК 1145/10, УК 1147/10, УК 1148/10, індукованими дією радіонуклідного забруднення зони відчуження ЧАЕС на рослини сорту Альбатрос одеський. Характер успадкування ознак у  $F_1$  визначали за ступенем фенотипового домінування, модифікаційну мінливість висоти рослин — за коефіцієнтом варіації. У популяціях рослин  $F_2$  обліковували частоту вищеплення карликових, низько- та середньорослих і високорослих форм.

**Результати.** Рослини  $F_1$  за довжиною стебла перевищували залучені до гібридизації генотипи або наближалися до батьківської форми з більшим виявом ознаки. За комбінації схрещування Сонечко  $\times$  УК 1147/10 у гібридів  $F_1$  спостерігали істинний гетерозис у бік зменшення висоти рослин. Елементи продуктивності гібридів успадковуються за типом часткового позитивного домінування і наддомінування. У популяціях рослин  $F_2$  виявлено 2,2—3,6 % високорослих форм, які не були характерними для батьківського покоління.

**Висновки.** За комбінації схрещування середньорослого сорту озимої пшениці з карликовими мутантами, індукованими в зоні відчуження ЧАЕС, довжина стебла в  $F_1$  успадковується за проміжним типом і частковим позитивним домінуванням. Карликовий мутант УК 1147/10 може становити цінність у селекції озимої м'якої пшениці на короткостебловість. Значне варіювання показника ступеня фенотипового домінування за усіма вивченими ознаками підтверджує складний характер генетичної детермінації висоти рослини й елементів продуктивності пшениці озимої, у формуванні яких беруть участь різні типи взаємодії генів.

**Ключові слова:** карликові мутанти, елементи продуктивності, ступінь домінування, *Triticum aestivum* L.