ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 51, nr 3-4: 429-440
1982

The high mutagenic effectiveness of MNUA in inducing a diversity of dwarf and semidwarf forms of spring barley

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(Received: March 5, 1982)

Abstract

By the modified method of mutagenic MNUA treatment consisting in a short interincubation germination, a very high frequency of point mutations was obtained in many varieties and stocks of spring barley. In the obtained collection of dwarf and semidwarf mutants a rich variability of many traits not connected with the plant height was noted. Mutations concerned the productivity of the plants, their tillering, the length and width of leaves, the habitus, distribution of leaves on the stalk and the morphology of the ear. The diversity of forms described in the collection of dwarf and semidwarf mutants characterises MNUA as a mutagen inducing a very high frequency of mutations in initial cells.

INTRODUCTION

It has been repeatedly domonstrated that, among the numerous mutagenic agents, compounds with an alkylating action exhibit a high effectiveness (Müller 1965, Ehrenberg and Gichner 1967). In this group methyl and ethyl dervatives of nitrosourea are particularly capable of evoking a high frequency of point mutations. Rapoport et al. (1966) suggested for these compounds the name "supermutagens". A high effectiveness of mutagens is the condition of their usefulness in genetic and breeding work, and all possibilities of increasing the frequency of the evoked point mutations contribute to the acceleration of progress in this kind of research and their utilisation in plant breeding practice. Modification of the mutagenic action of MNUA by metal ions and EDTA has been described by Małuszyński (1973), the possibility, however, of increasing in this way the effectiveness of treatment is greatly limited, in contrast to treatment by interincubation germination (iig) (Małuszyńska 1978).

MATERIAL AND METHODS

The material for study consisted of 21 spring barley varieties and stocks (*Hordeum vulgare* L. convar. *distichon* (L.) Alef. (2n=14)). The mutagenic experiments were performed in the years 1972, 1974, 1976. Induction with MNUA both by the standard method and with interincubation germination was done as described in detail by Małuszyńska (1976). Treatment with a 2 mM sodium azide solution was done after 8-h preliminary soaking of the grain in distilled water at 24°C and 6-h interincubation germination at pH 3. Irradiation with fast neutrons (700 and 900 rad) was done in the Institute of Nuclear Physic in Cracow on a U 120 cyclotron. Field experiments were performed in collaboration with the Plant Breeding Station Polanowice-Łagiewniki.

RESULTS AND DISCUSSION

Under the experimental conditions with the application of the standard method of MNUA treatment (8-h preliminary soaking of the grain in distilled water at 24°C and 3-h soaking in mutagen solution) a 1 mM dose proved optimal (Table 1). Further increase of the MNUA concentration was unfavourable for germination and fertility of the plants. When a 0.5 mM dose was applied twice with 22-h interincubation germination (iig) an increased frequency of chlorophyll mutants (Msd) by more than 2 per cent as compared with the result of standard treatment with a 1 mM dose was noted. The increase in the sensitivity of the embryo cells due to the break in the mutagenic treatment was so large that an increase of mutagen concentration to 1 mM caused complete sterility of M_1 plants.

It was demonstrated in the successive experiments that this reaction was not specific only for the barley variety Damazy with which the experiments were performed since plants of the varieties Aramir and Menuette reacted similarly. It was found that for increasing the mutagenic effectiveness of MNUA even a 4-h period of interincubation germination is sufficient. In this way an almost 63 per cent increase of the frequency of chlorophyll mutants was obtained as compared with the standard method.

In 1976 a comparative experiment on the mutagenic effect of MNUA was performed with treatment by the modified method with the use of fast neutrons and sodium azide (each treatment separately) on 10 varieties and stocks of spring barley (Salka, Zita, Menuette, Rupal, Georgia, VD, Sundance, Q 448, Mg 3039-5, RPB 39473). The data in Table 2 are means for all the tested varieties in the particular experiments. The mean frequency of chlorophyll mutants obtained by treatment with MNUA according to the modified method was 5.3 per cent, whereas the maximum frequency after treatment with fast neutrons (900 rad dose) was 4.1 per cent. A further increase of the neutron dose was of no avail on account

Table 1

Mutagenic effect of MNUA when standard and modified treatment method was applied

Treatment	No. of M_1 plants	Reduced germination	Reduced height (I)	Sterility (S)	Frequency of chlorophyll mutations (Msd)	Efficiency $\frac{Msd}{I}$	Efficiency $\frac{Msd}{S}$
Control	1280	–	–	–	–	–	–
Variety Damazy:							
0.5 mM MNUA	1215	12.2 ± 2.9	4.5 ± 2.8	19.7 ± 5.3	2.1 ± 0.3	0.467	0.107
1.0 mM MNUA	1208	42.1 ± 3.4	24.2 ± 11.4	51.6 ± 10.3	4.1 ± 0.2	0.169	0.079
2 × 0.5 mM MNUA (22^h iig)	1215	17.3 ± 5.5	36.2 ± 6.1	67.2 ± 12.4	6.4 ± 0.4	0.177	0.095
2 × 1.0 mM MNUA (22^h iig)	264	91.7 ± 1.7	83.7 ± 4.1	100.0	–	–	–
2 × 0.7 mM MNUA (4^h iig)							
Variety Aramir	1380	6.1 ± 4.9	32.7 ± 2.8	80.0 ± 0.8	5.01 ± 1.8	0.153	0.062
Variety Menuette	1160	12.8 ± 6.1	17.0 ± 5.2	79.4 ± 7.4	6.7 ± 0.2	0.394	0.084

of the almost 100 per cent sterility of the M_1 plants. A similarly lower mutagenic effectiveness of 2 mM sodium azide than of MNUA was noted. The increase of the dose of this mutagen was limited by somatic damage appearing particularly as a considerable reduction of germination.

The conditions of mutagenic treatment, the environment of the field experiment and the genetic specificity of the varieties cause some difficulties for comparison of the effect of action of the same mutagen in various laboratories. Hence many varieties were tested of different origin and single control treatments were applied. This revealed that the frequency of chlorophhyll mutations is significantly higher than that of mutations obtained by other authors using the standard method of treatment with this mutagen (Gichner et al. 1968, Gaul et al. 1972, Konzak et al. 1972).

The usefulness of the chlorophyll mutations test for establishing the potential abilities of the mutagen to induce point mutations has been proved many a time. It was also confirmed by results of experiments. In investigations with the use of the modified method several thousand mutants have been selected, characterised by changed morphological and physiological traits. The high frequency of mutants made possible the establishment of a collection of dwarf and semidwarf forms and a collection of high--protein mutants of spring barley.

MNUA in the method of treatment applied proved to be a mutagen capable of inducing mutation in many loci conditioning dwarfism. For a long time only two genes responsible for dwarfism of the plant were localised: the gene *br* in chromosome 1 conditioning the phenotype "brachytic" and gene *uz* localized in chromosome 3 conditioning the phenotype "uzu". Takahashi et al. in 1975 reported the localisation of further five genes of barley dwarfism: genes *sld* and *lzd* in chromosome 3, gene *sid* in chromosome 4, gene *wnd* in chromosome 1 and gene *cud* in chromosome 7. Although many dwarfism mutants have been described in other laboratories, their genetical analysis concerned solely the way of inheritance of this trait. The described dwarfism mutants were mostly recessive, usually with a strongly pleiotropic character. As already mentioned, in the analysed collection of dwarf and semidwarf forms there occurred with a high frequency forms not exhibiting the pleiotropic effect. Over 20 forms were subjected to genetic analysis in which mutations of dominant characters were not found. Neither were allelic forms detected. Three from among the studied mutants showed the dwarfism trait polymerically conditioned and in one two not linkaged genes were responsible for the dwarf phenotype.

By utilising the translocation lines three genes conditioning the dwarf or semidwarf phenotype were localised (Małuszyński and Szarejko 1981). Two of them were localised in the short arm of chromosome 3 at a 34.5 per cent crossing-over distance from one another, the gene conditioning dwarfism showing linkage (20.5% crossing-over) with gene *uz* and a second one responsible for the semidwarfism trait exhibited independent inheritance.

Table 2

Mutagenic effect of MNUA, fast neutrons and sodium azide on some chosen cultivated spring barley varieties

Treatment	No. of M_1 plants	Reduced germination	Reduced height (I)	Sterility (S)	Frequency of chlorophyll mutations (Msd)	$\frac{Msd}{I}$	$\frac{Msd}{S}$
2×0.7 mM MNUA (4^h lig)	7875	7.4±4.0	19.3±3.3	83.4±5.0	5.1±0.3	0.264	0.061
700 rad (neutrons)	7420	10.8±3.5	16.4±2.2	85.3±3.8	3.3±1.0	0.201	0.039
900 rad (neutrons) (for 6 varieties)	7604	27.4±5.2	19.7±2.7	91.9±2.5	4.1±1.0	0.208	0.045
2×0.7 mM MNUA (6^h iig)	7501	12.9+10.3	27.7±6.6	85.6±17.5	5.6±1.5	0.202	0.065
2.0 mM NaN_3 (for 4 varieties)	7702	53.1±11.6	8.7±6.9	62.4± 9.3	3.0±1.0	0.345	0.048

The third gene was mapped in chromosome 1 and the test for allelism with the "brachytic" mutant confirmed the localisation in the same locus, although the mapped mutant was much lower than the typical "brachytic" form (Szarejko and Małuszyński 1983).

Among the forms with reduced height there occurred mutants exhibiting very high variability of many other morphological traits. It was observed that in the majority of these forms the reduction of the plant height was connected with a rather proportional shortening of the neck and the remaining internodes and the ear. The mutants then obtained, however, did not show these correlations (Table 3). Among the very low forms not exceeding 45 cm in height two lines have been described with neck identical as in the control form. A long neck was sometimes also found in the remaining dwarf forms (up to 55 cm height). Relatively more frequent were semidwarf forms (55-65 cm) with a greatly shortened neck. In this collection 21 dwarf and semidwarf lines are described with the ear equal to or longer than in the outset variety.

Table 3

Height of plants and length of neck in collection of dwarf and semidwarf forms of spring barley*

Height of plants, cm	No. of mutants		
	total	including mutants with neck length	
		above 18 cm %	below 12 cm %
36-40	53	0.0	94.3
41-45	31	6.4	64.5
46-50	38	10.8	57.9
51-55	73	20.8	21.9
56-60	88	46.6	5.7
61-65	62	67.7	1.6
Total	345	–	–

*—mean height of control forms 69.3 ± 3.4;
neck length 19.8 ± 5.9

In homozygotic lines of the sixth and seventh generation after MNUA treatment the diversity of morphological and physiological mutations is best illustrated by the yield as index of the general productiveness of the analysed forms. Randomly chosen 250 dwarf and semidwarf mutants from the collection were grouped in five classes as regards yield in relation to the outset form (Table 4). As many as 27 of the studied lines showed a yield, in terms of mean grain weight from one plant, higher by 10 per cent than the control form, whereas nine mutants gave a yield exceeding by 30 per cent that of the outset varieties. The high-yielding lines did

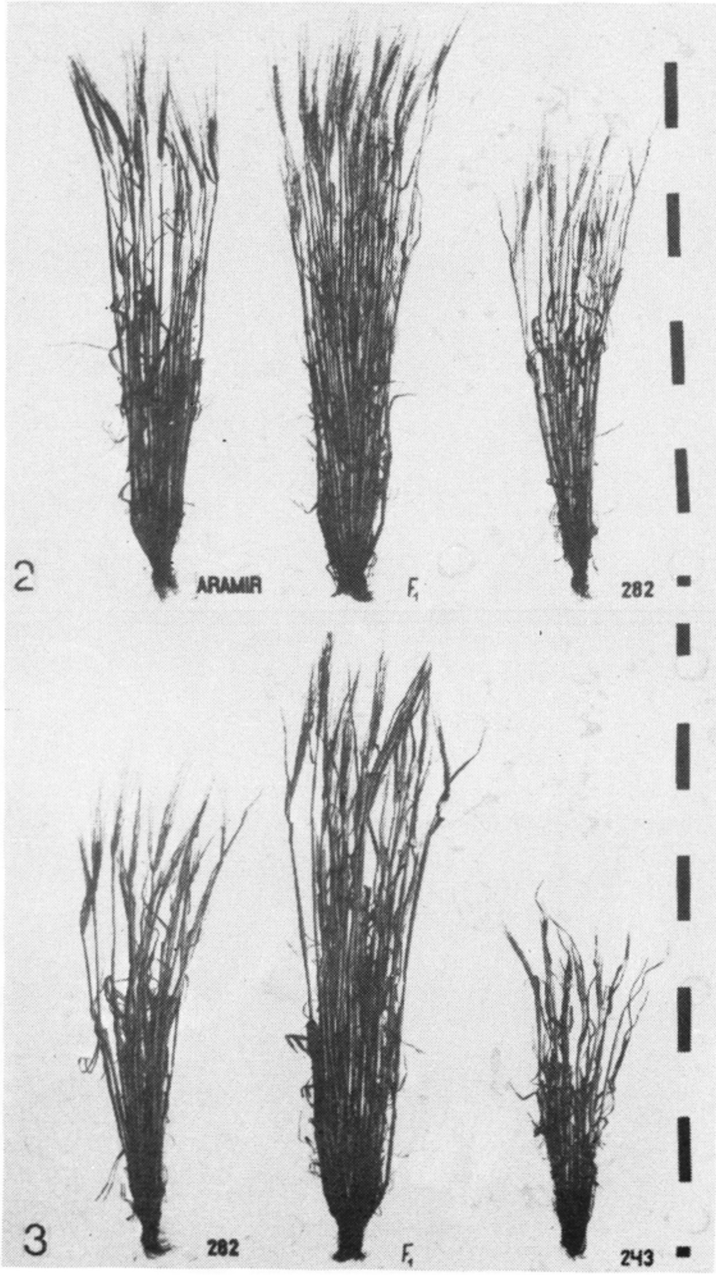

Fig. 2. Hybrid F_1 of variety Aramir and mutant 282 of the same variety (Photo. by A. Fuglewicz)

Fig. 3. F_1 hybrid mutants 282 and 243 obtained from variety Aramir (Photo. by A. Fuglewicz)

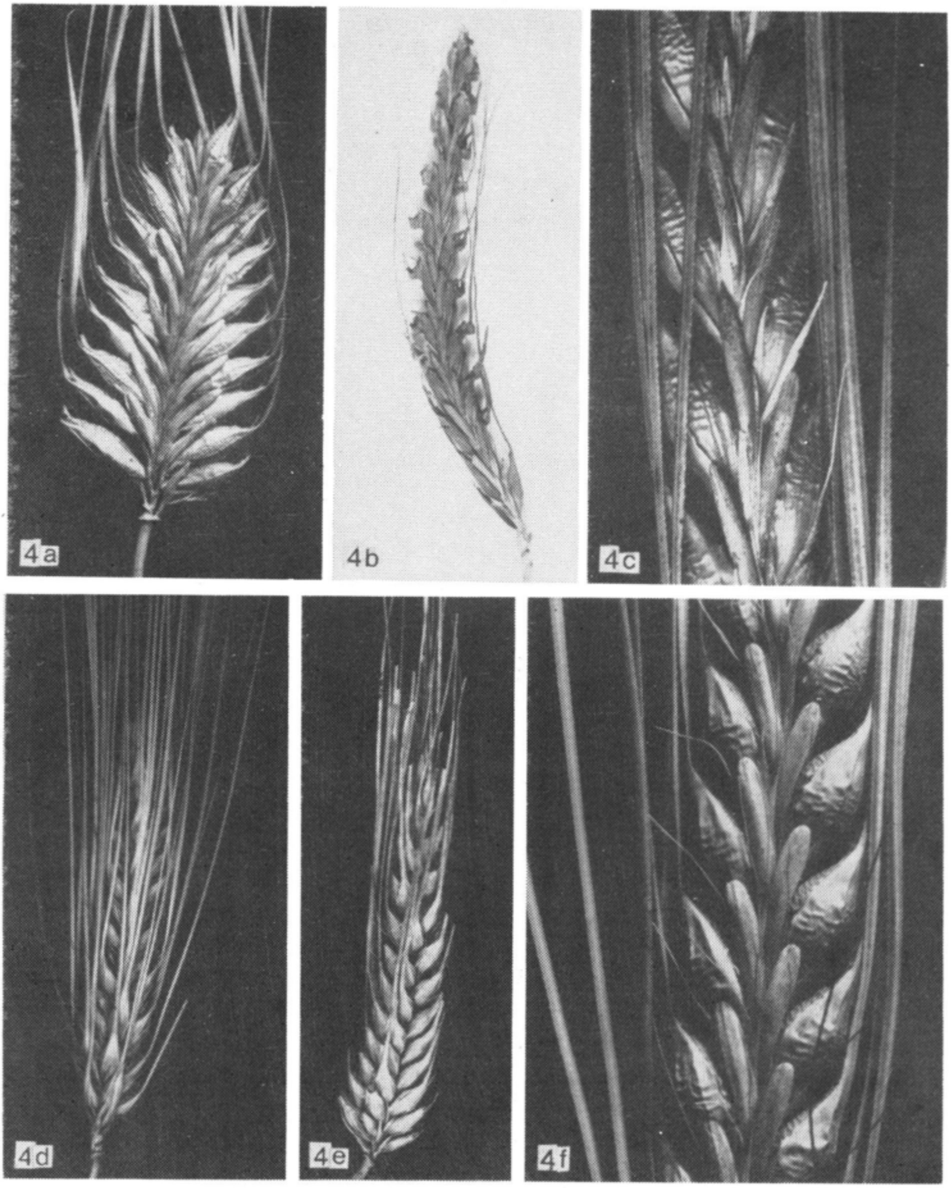

Fig. 4. Variability of ears in dwarf and semidwarf mutants: a—distichon type var. zeocrithon (Georgia mutan 27); b—distichon type var *calcaroides* (Georgia mutan 25); c—intermedium type (Aramir mutan 54); d—polystichon type var, tetrastichon (Aramir mutant 10); e—polystichon type var. hexastichon (Aramir mutan 22); f—distichon type var, erectum, barrel-shaped grains; (Georgia mutant 55) (Photo by M. Gaj)

not occur among highly dwarfed mutants, most of them were forms relatively but little reduced in size.

Table 4

Number of dwarf and semidwarf mutants classified according yield in relation to outset form. Yield terms of mean grain weight per plant

Mean height of plants, cm	Yield in relation to control, %				
	up to 50	51-90	91-110	111-130	above 130
36-40	11	9	1	–	–
41-45	2	4	3	–	–
46-50	9	8	2	1	1
51-55	8	35	8	2	–
56-60	10	44	13	7	3
61-65	8	32	16	8	5
Total number of mutants in class	48	132	43	18	9
%	19.2	52.8	17.2	7.2	3.6

Of the varieties chosen for this experiment the doubtlessly best yielding one was Aramir, however, among as many as 67 forms derived from this variety only one mutant was found yielding better than the control form (increase in yield 55%, plant height 60 cm). More numerous high-yielding mutants were obtained from the variety Trumph (18.2% of forms of this variety). In the remaining three varieties Diva, Mg 4170 and Hdm high-yielding mutants constituted 11 per cent of the studied lines from the collection of dwarf and semidwarf lines.

Only four among the selected 27 mutants showed a tillering similar to that of the control forms (Fig. 1). All the remaining ones had an increased number of ear-bearing stalks. This trait, however, was not decisive for the final productiveness of the plants. Mutations must have involved also other genes from the group of polymeric ones conditioning yield since among the selected mutants there were both very high-yielding forms (155% of control yield) with tillering somewhat more abundant than in the outset variety (117.6%) and forms tillering very abundantly with 15 to 18 stalks (211.8% of tillering), giving a yield only slightly higher than that of the variety from which they were derived. No significant influence of the genotype of the outset form on the above discussed relation could be noted. Beside that change in the number of ear-bearing stalks, mutation of other traits was observed such as length and width of leaves, habitus of the plant or distribution of leaves on the stalk. In this case too no direct correlation was observed of these traits with the yield.

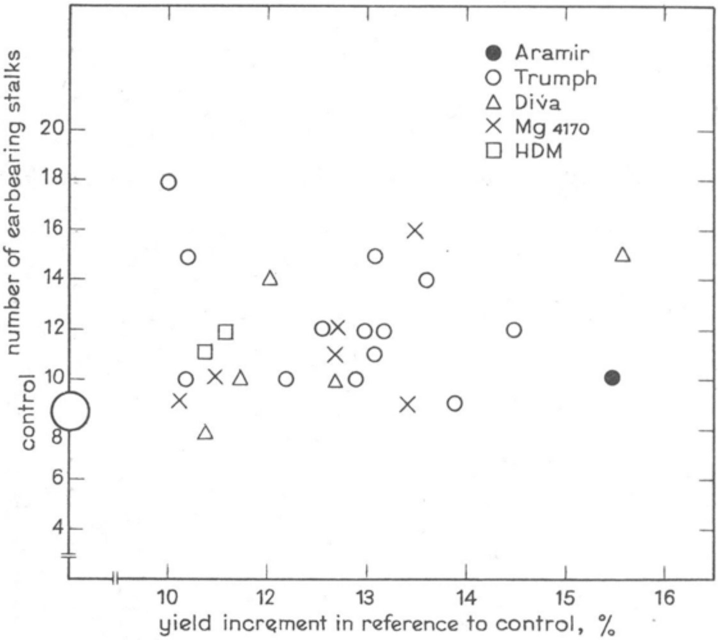

Fig. 1. Dependence of yield increment on number of ear-bearing stalks in 27 high-yielding lines from the collection of dwarf and semidwarf barley forms

The here presented results showing the rich variability in the polygenically conditioned productivity of the plants in dwarf and semidwarf forms may indicate, according to Hänsel's (1967) papers, that a much larger number of point mutations in the nuclei of initial cells of the embryo of the treated grains is induced by the mutagen than it would result from the frequency of chlorophyll mutations. This variability, however, may be explained by the pleiotropic effect of the gene conditioning the reduction of the height of the plants. Although the latter concept cannot be completely ruled out, particularly as regards greatly dwarfed forms where the pleiotropic character of the dwarfism gene action has been proved (Hoskins and Poelhman 1971, Takahashi et al. 1975), it is, however, difficult to explain by the pleiotropic effect the significant increase of the yield or its decrease in some semidwarf or dwarf forms. An immediate proof suggesting the simultaneous induction by MNUA of numerous mutations in cells lying on the generative pathway, are results of studies concerning analysis of the isoenzymatic spectrum in the described collection of dwarf and semidwarf mutants (Małuszyński and Kucharska 1981). A particularly rich variability was obtained in loci conditioning esterases in mutants from all the varieties studied. Variability of asparagine transaminase (GOT), although not so rich has also been described.

An indirect proof supporting the high frequency of mutations evoked by MNUA in one cell is no doubt the effect of heterosis observed in F_1 hybrids of dwarf and semidwarf mutants selected from the same outest variety. Notwithstanding the vigour of some morphological traits, the effect of heterosis appeared most distinctly in the yield of F_1 hybrids, measured both in terms of number and weight of grains per plant. In hybirds obtained from crossing of mutants derived from the variety Aramir the increase in yeild measured as weight of grain per plant ranged from about 11 to 217 per cent in relation to the highest yielding plant of the Aramir variety under the given conditions. A similar effect of heterosis appeared also in F_1 hybrids from crosses of the outset variety with mutants selected from it (Table 5). It should be stressed that in the F_1 generation obtained, both as the result of crossing mutants of various varieties and from crosses between the outset varieties only, a similar yield increment was noted. Simultaneously with yield increment in the hybrids a great richness of forms manifested generally by an increased number of ear-bearing stalks was observed, the height of the plants not exceeding that of the outset ones (Figs. 2 and 3).

A similar effect of heterosis in F_1 crosses of *Petunia axillaris* mutants selected from generation M_4 after treatment with MNUA of seeds from a selfpollinated plant has been described by Górny (1976). Gustafsson et al. (1973 a, b) demonstrated the effect of heterosis in crosses of mutants derived from various spring barley varieties after exposure to ionising radiation. In the analysed collection of dwarf and semidwarf mutants a considerable variability of protein and lysine contens in the grain has been reported (Table 6). Among the dwarf and semidwarf mutants forms are described with increased lysin content from a dozen or so to 120 per cent as compared to the outset variety. The observed diversity of forms in this respect was similar as in the collection of not dwarfed mutants selected for instance from the variety Julia. It should be stressed that mutants with an increased, in respect to the control form, protein or lysin content showed a high diversity of yield and grain filling. Among these forms, in spite of the increased lysine content mutants have been described characterised by a normal grain filling, manifested by an unchanged 1000-grain weight as compared with that of the outset variety.

Easiest for observation was the rich variability of morphological forms occurring in the collection of dwarf and semidwarf mutants. Forms with a changed leaf shape, habitatus and particularly with a changed ear morphology were numerous. Many-rowed mutants were obtained from two-rowed forms, intermediate forms with transformed glumes and bracts, mutants with changed length of rachis internodes, with changed rachilla or with mutation in the collar region. (Fig. 4 a-f). Genetic analysis demonstrated that only

Table 5

Yield increment of F_1 hybrids in relation to yield of Aramir variety

Hybrids of mutants of Aramir variety				Intervariety hybrids			
Cross	increment in tille-ring, %	increment in no. of grains, %	increment in grain weight, %	Cross	increment in tille-ring %	increment in no. of grains, %	increment in grain weight, %
Aramir × 282	61.0	92.9	113.7	Trumph × Diva	55.9	61.3	56.9
Aramir × 243	76.1	80.6	94.1	Diva x Aramir	46.8	3.5	15.4
Aramir × 233	66.0	104.5	86.3	239 × 125 (Aramir) (Diva)	144.6	50.9	56.9
Aramir × 275	4.4	13.0	19.6	233 × 125 (Aramir) (Diva)	16.1	35.7	60.8
282 × 275	27.0	41.5	58.8	243 × 125 (Aramir) (Diva)	−8.6	18.3	−23.1
243 × 233	58.5	91.7	60.8	275 × 125 (Aramir) (Diva)	−3.2	−2.9	3.9
282 × 243	71.1	7.3	11.8	243 × 188 (Aramir) (Trumph)	−45.9	45.5	58.8
282 × 239	25.8	130.4	152.9	282 × 188 (Aramir) (Trumph)	80.5	67.2	54.9
243 × 239	−8.2	45.2	35.3	275 × 188 (Aramir) (Trumph)	28.9	60.9	47.1
233 × 282	66.7	178.7	217.6	125 × 188 (Diva) (Trumph)	2.2	−38.3	−46.2
233 × 239	73.6	127.3	133.3	188 × 233 (Trumph) (Aramir)	50.9	86.8	82.4
275 × 233	72.9	74.5	56.9	188 × Diva (Trumph)	61.3	63.5	61.5
243 × 275	39.6	44.9	68.6	Aramir × 188 (Trumph)	33.9	63.5	1.9

Table 6

Protein and lysin contents in some chosen spring barley mutants

Mutant	Protein, %	Lysin, g/100 g protein	Lysin content in reference to control, %	1000-grains weight, g	Grain weight in reference to control, %	1000-grains weight in reference, to control %
Aramir	14.9	2.55	–	51.7	100.0	–
Mutant 239/2*	17.9	3.00	117.6	51.7	64.9	100.0
Mutant 217/4*	16.8	2.97	116.5	37.2	34.0	71.9
Mutant 281/4*	16.5	3.20	125.5	51.3	81.9	99.2
Delisa	13.6	2.01	–	29.5	100.0	–
Mutant 588	16.0	4.43	220.4	18.4	58.2	62.3
Julia	13.7	2.00	–	48.5	100.0	–
Mutant 257	16.0	4.81	240.5	40.0	70.5	82.5
Mutant 234	15.7	3.95	197.5	41.0	64.2	84.5
Mutant 239	14.8	4.74	237.0	48.5	64.2	100.0
Mutant 318	18.2	1.84	92.0	51.0	119.5	105.2

*—dwarf mutants

part of the selected mutations was allelic in respect to analogous ones described by other authors.

The here briefly presented results of selection work supported by genetic investigations qualify MNUA as a mutagen the effectiveness of which may be markedly increased by the application of the modified method of treatment, owing to which a high frequency of mutations in one initial cell may be obtained. The diversity of forms with physiological and morphological traits changed within a wide scope decides of the special usefulness of this mutagen in genetic and breeding work.

Acknowledgement

The author wishes to thank the collaborators from the Department of Genetics of the Silesian University for help in elaboration of the results.

This work was supported by the Polish Academy of Sciences under the project 09.3.1. and MR 2.2.B.

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Wysoka efektywność mutageniczna MNUA w indukowaniu różnorodności form karłowych i półkarłowych jęczmienia jarego

Streszczenie

Stosując zmodyfikowaną metodę mutagenicznego traktowania MNUA, polegającą na zastosowaniu krótkiego kiełkowania międzyinkubacyjnego, otrzymano bardzo wysoką częstotliwość mutacji punktowych u wielu odmian i rodów jęczmienia jarego. W uzyskanej kolekcji mutantów karłowych i półkarłowych stwierdzono bogatą zmienność wielu cech nie związanych z wysokością roślin. Mutacje dotyczyły produktywności roślin, krzewistości, długości i szerokości liści, pokroju rośliny, rozmieszczenia liści na źdźbie oraz morfologii kłosa. Różnorodność form opisana w kolekcji mutantów karłowych i półkarłowych charakteryzuje MNUA jako mutangen indukujący bardzo wysoką częstotliwość mutacji w komórkach inicjalnych.