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Dnipro State Agrarian
and Economic University,
Serhii Efremov St., 25,
Dnipro, 49600, Ukraine.
Tel.: +38-095-848-53-86.
E-mail: nik_nazarenko@ukr.net

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Advantageous of chemical high genetic active mutagens action on well local-adapted bread wheat germplasm

V. Didenko, M. Nazarenko
Dnipro State Agrarian and Economic University, Dnipro, Ukraine

Abstract. Creating new sources of diversity in winter wheat is essential both for cultivation of new varieties and strengthening parental pools in crossing schemes. In this study, we assessed two classical mutagens, ethyl methanesulfonate (EMS at 0.025%, 0.05%, 0.1%) and sodium azide (SA at 0.01%, 0.025%, 0.05%, 0.1%), to identify operational dose windows that shift phenotype and grain quality without unacceptable vitality harm. Seeds of two contrasting cultivars, Vezha and Ihrysta, were soaked for 24 h according to standard protocols and were analyzed for agronomic and technological traits. Responses were both dose-responsive and genotype-dependent. The best results were produced by the intermediate, average-low doses: SA 0.025–0.05% and EMS 0.05% (with EMS 0.1% being useful for a few target traits). Elevating SA concentration to 0.1% increased the raw mutation count, but lowered the efficiency, as fewer positive or perspective lines were obtained, while the incidence of undesirable changes was higher. Vezha was the variety that converted induced variability into perspective material most effectively and reacted positively to both mutagen. The best variant was SA 0.05% (the highest rate of positive changes and promising lines), followed by SA 0.025% and EMS 0.05%. Vezha was the preferred donor for early ripening (SA 0.025%), for long-spike architecture (SA 0.025–0.05%), and for balanced quality gains (SA 0.05%). Ihrysta leaned toward quality improvement: SA 0.05% reliably increased protein, enriched HMW glutenins, and improved micronutrient profiles; stature reduction was produced by EMS 0.1% and SA 0.1%, although the latter is not recommended due to efficiency loss. We recommend using SA 0.05% as default for a balanced complex of architecture and bread-making quality in both the varieties; using SA 0.025% for conservative programs aiming at early ripening (especially for Vezha); applying EMS 0.05–0.1% for height reduction, wax, and microelements, coupled with fitness screening. SA 0.1% should be avoided in standard practice. The screening yielded several candidate lines combining high yield with favorable baking traits, which now entering pre-registration evaluation. The ongoing work will characterize adaptive physiology, including drought performance and winter survival.

Keywords: winter wheat; chemical mutagenesis; supermutagen; positive changes; nutrients; proteins; variability.

Introduction

Genetic change originates with mutation, every novel allele that eventually spreads through a population's gene pool first appears as a mutational event, spontaneous or induced. Without this continual occurrence of new variations, neither natural selection nor deliberate human selection could shift trait distributions. In plant breeding, this foundational truth becomes a practical lever: By provoking heritable changes, breeders expand the palette of phenotypes available for improvement, including combinations that regular crossing rarely produces. Extensive practice of cultivating cereals, legumes, and industrial crops has shown that carefully managed chemical mutagenesis can generate stable, transmissible alterations that are immediately usable for selection focusing on yield, stress adaptation, and product quality. Strikingly, even brief exposures to modest doses can lead to long-lived developmental and heritable shifts, providing breeders with extensive raw material for progress (Stearns et al., 2025).

Within the toolbox of mutational methods, a set of agents often referred to as chemical supermutagens occupies a prominent niche. These compounds are appreciated for achieving a productive balance: they elicit mutations at useful frequencies while suppressing extreme collateral damage, lethality, gross malformations, or reproductive collapse. Because of that balance, supermutagens are deployed both in routine improvement pipelines and in basic genetic studies designed to clarify how mutagenesis acts at the molecular and chromatin levels. In a considerable share of contemporary cultivars, key alleles can be traced to mutation-derived ancestry, underscoring the method's lasting impact on agriculture. In modern programs, chemical mutagenesis plays two complementary roles. First, it creates parents carrying desirable point changes or small rearrangements that can be recombined and accumulated over the process of crossing. Second, it exposes or perturbs gene networks controlling complex traits, such as biochemical pathways that shape baking quality, thereby enabling targeted selection and hypothesis-driven gene discovery (Didenko & Nazarenko, 2025; Monika et al., 2025).

When paired with disciplined selection, induced mutagenesis provides a relatively straight and cost-effective route to gaining both quantitative and qualitative traits. Seed or tissue treatment is technically straightforward; the costs are modest; and measurable advantages can appear within a few generations. These properties are especially valuable for traits for which natural variation is limited or polygenic (disease resistance, tolerance to heat or drought and performance in marginal soils). The literature shows that intermediate, well-controlled doses usually yield the most useful balance of change and viability, producing selectable phenotypes while avoiding the heavy burdens of pleiotropy that often accompany excessive DNA damage (Fradgley et al., 2024).

Dosage, nevertheless, remains a topic of ongoing debate. Those advocating for higher concentrations emphasize the wider mutation spectrum: More mutations can mean a higher probability of complex, multigenic outcomes within a single genetic background. Meta-analyses document successes at elevated doses for some species and trait suites (Monika et al., 2025). Yet, a parallel body of work shows that mid-low levels frequently suffice to produce lines with strong abiotic/biotic stress performance and promising agronomic profiles, without the fitness losses that often emerge following excessive treatments. Novel morphotypes emerge under exposure to moderate doses: altered architecture, shifts in spike morphology, larger kernels, and improved compositional traits directly associated with nutritional and technological quality (Bharathi et al., 2025).

It is also important to recognize the dual character of mutagenic outcomes: Chemical treatments regularly produce highly visible variants that are easy to consider in the field (dwarfs, semi-dwarfs, waxy plants, long-spike forms) and subtler biochemical and regulatory changes detectable only through laboratory studies. Although some physical methods can produce higher general mutation rate, chemical treatment of seeds re-

mains exceptionally effective for generating selection-ready variability that can be carried through a breeding pipeline. By contrast, simply chasing maximal mutation rates through alternative means can encounter practical constraints: poor fertility, unstable inheritance, and impaired performance that negate any initial gains (Horshchar & Nazarenko, 2023; Rodge et al., 2025).

The agricultural footprint of induced mutagenesis is already vast, thousands of registered varieties, food staples and industrial crops, contain mutation-derived alleles that underpin yield, resilience, and end-use quality. Cereal crops such as wheat, rice, and barley, together with fiber crops such as cotton, figure prominently in these achievements, illustrating that mutagenesis is a mature, dependable instrument for genetic improvement (Bayhan et al., 2024).

From a methodological standpoint, mutagens are often grouped into two broad classes. Chemical agents include alkylators such as ethyl methanesulfonate (EMS), which primarily generates point substitutions; sodium azide (SA), which after metabolic activation induces base changes; and diepoxybutane (DEB), which can produce both point mutations and small deletions. Physical agents comprise ionizing and non-ionizing radiation (X-rays, gamma rays, fast neutrons, and ultraviolet) each with characteristic mutation spectra (Arumingtyas et al., 2023). While both families have contributed substantially, chemical agents frequently stand out for their genotype-contingent, sequence-biased interaction with chromosomal DNA. This relative site-specificity can be exploited to direct variation toward pathways of interest, enabling more predictable shifts in trait distributions compared with those that are typical for broadly damaging radiation (Bharathi et al., 2025; Kryshyn & Nazarenko, 2025).

These capabilities are particularly relevant for winter wheat, a cornerstone cereal in regions experiencing intensifying climatic variability, including most of Ukraine. As climate warming nudges thermal zones poleward, breeding targets must reconcile robust overwintering with flexibility during erratic springs characterized by dry spells, heat pulses, and late frosts. The need for tools that accelerate adaptation, while maintaining or improving grain functionality, has never been greater (Nazarenko & Okselenko, 2025).

Against this backdrop, our program examined heritable variability generated in a panel of local and introduced winter wheat genotypes, with attention to the breadth and usefulness of induced changes spanning morphology, physiology, and biochemistry. We focused on classical chemical supermutagens (SA and EMS), evaluating their capacity to create heritable, potentially site-biased modifications that elevate breeding value. Because mutagenic outcomes depend jointly on dose, exposure conditions, and recipient genotype, we explicitly interrogated genotype × mutagen interactions: how does each background respond not only in frequency of change but in trait spectrum (Phadungsawat et al., 2025).

The evidence we assembled supports two complementary breeding pathways. The first is direct advancement: identifying mutants that meet or exceed thresholds for yield, stability, and quality, and moving them toward candidate-variety testing. The second is parental deployment: using mutation-derived lines as donors in recombination schemes to introgress favorable alleles or epialleles into elite backgrounds, thereby accumulating gains while diluting undesirable linkages. The capacity to steer biochemical quality, such as shifting the glutenin profile toward a higher proportion of high-molecular-weight (HMW) subunits without inflating low-molecular-weight fractions, or elevating micronutrients that are commonly deficient in wheat grain, represents a tangible step beyond the largely stochastic outcomes of older mutagenesis practice (Khare et al., 2025).

Our study objectives were as follows: quantifying response rates by estimating the frequency of favorable variants under a range of treatment levels, and determining how efficiently those variants convert into perspective lines suitable for further breeding; mapping the mutation spectrum, identifying which traits (architectural shifts (dwarfism, long spike), physiological adjustments (earliness, tillering) and biochemical endpoints (protein content, glutenin subunit balance, micronutrient enrichment)) are most amenable to change under each agent and concentration; probing site-bias and genotype dependence, evaluating whether SA and EMS display patterns consistent with preferential action in certain genomic or chromatin contexts, thereby permitting more directed manipulation of quality traits than is typical of classical physical mutagens.

Materials and methods

Field estimation was performed during three seasons (2023–2025; generations M_2–M_4) on the grounds of the Educational–Scientific Center of the Dnipro State Agrarian and Economic University (Dniprovskyi District, Dnipropetrovsk Oblast, Ukraine; 48°50′98″ N, 35°25′64″ E). The site belongs to a warm northern, moderately dry agroclimatic belt (hydrothermal coefficient > 0.9). During the experiments, growing-season rainfall generally reached 250–280 mm, with 450–490 mm annually, and the sum of effective temperatures above 10 °C approached 2900 °C. Soils were spatially uniform and classified as regular leached medium-loam chernozems of low humus content formed on loam. Routine soil tests reported 3–5 mg mineral N per 100 g dry soil (Tiurin), 20–30 mg mobile P per 100 g and 20 – 35 mg exchangeable K per 100 g (both by Chyrykov).

Two bread wheat (*Triticum aestivum* L.) cultivars Vezha and Ihrysta were used as initial material. Batches of 1,000 seeds per treatment were primed for 24 h in aqueous solutions of two mutagens (Sigma-Aldrich): ethyl methanesulfonate (EMS) at 0.025%, 0.05%, and 0.1% concentrations, and sodium azide (SA) at 0.01%, 0.025%, 0.05%, and 0.1% concentrations. Water-soaked seeds served as control. The priming procedure was performed following standard chemical mutagenesis guidelines (Monika et al., 2025).

In generations M_2 and M_3, putative mutants were identified visually and traced across generations to verify inheritance. Families were hand-planted in short rows (1–3 rows per family; 0.15 m between rows; 1.5 m row length). Mutation frequency was calculated as the percentage of mutant families among all evaluated families.

Selection for performance was carried in M_4. Depending on the season, plots ranged from 2 to 10 m² with one or two repetitions; the control varieties were planted after every 20 plots. Grain quality was characterized by total protein (Spektra RT), glutenin/gliadin fractions (HMW (high molecular weight glutenins), and LMW (low molecular weight glutenins), determined using reverse-phase HPLC, and also by concentrations of key microelements (Mg, Mn, Zn, Mo, Co, Cu), quantified on an Agilent 5110 ICP-AES spectometer, calibrated against Agilent multi-element standards.

Statistical processing was performed in Statistica 10.0 (TIBCO). A factorial ANOVA tested the effects of mutagen type, dose, and genotype; multivariate structure was examined via cluster analysis (Euclidean distance, single linkage) and discriminant analysis. When ANOVA effects were significant ($P < 0.05$), mean separation was carried out with Tukey's HSD.

Results

In total, 3,000 EMS families were examined in M_2 – M_3. From the families, 213 showed clear phenotypic deviation and were retained, 82 expressed traits with direct agronomic value and 27 satisfied elite criteria (beneficial changes without linked negatives) suitable for breeding deployment. Each EMS dose comprised 500 families. Across 3,950 SA families examined in M_2–M_3, 397 displayed recognizable alterations, 120 lines had unambiguous agronomic merit and 49 met elite standards. Most SA treatments also used 500-family cohorts, with one exception Ihrysta at 0.1% SA contained 450 families due to partial viability loss at the upper dose (see Tables 1 and 2).

Early-generation assessment emphasized readily scorable architectural and developmental traits: thicker culms, reduced height (short-stem, semi-dwarf, dwarf), greater epicuticular wax, extended or bulked spikes, larger kernels, earliness, visible disease tolerance, improved tillering, and preliminary signs of higher productivity (the latter verified in M_3 – M_4). By M_4, selection pivoted to technological quality: increased total protein, a remodeled gluten network (higher HMW-glutenin signal with restrained LMW fractions and calibrated shifts in gliadins), and enrichment of key micronutrients (Mg, Mn, Zn, Mo, Co, Cu). This combined set of criteria functioned as a practical marker suite to identify lines with genuine breeding utility.

Both mutagens proved efficient. EMS produced 2.7% actionable lines (82 of 3.000), while SA yielded 3.0% (120 of 3.950). Multi-generation checks confirmed that target phenotypes were inherited, implying fixation, either as genuine genomic mutations or as epigenetic alterations coupled to genetic mutations that transmit reliably.

For the variety Vezha (Table 1), the rate of changes varied from 7.0% to 12.1% (monotonic rise with higher concentration) under EMS action and 6.4% to 15.6% under SA action (steeper rise than EMS) across concentrations. As a result, SA generated the largest overall mutation load, peaking at 0.10% (15.60%), whereas EMS showed a lower peak (12.1%). The rate of positive changes varied from 2.8 to 4.4 under EMS action with concentration increase, and 2.8% to 6.0% under SA action

The maximum by SA was produced at 0.05% concentration, and then the parameter declined, to 4.4% at SA 0.1%. According to rate of positive mutations, the best result was achieved by SA 0.05% (6.0%). At SA 0.10%, it decreased to 4.4%, indicating efficiency loss.

The share of positive changes in the general rate varied from 0.36 to 0.43under EMS action, and 0.44–0.48 (peak) after SA treatment, then declining to 0.28. Thus, SA 0.05% produced the highest efficiency (0.48). High concentrations (0.1%) markedly diminish the usefulness of both agents. Number of lines varied from 15 to 17 under EMS action, declining to 12 at 0.10%, and 17 to 22 (max), then declining to 15 and 12 lines.

Number of promising lines (those without negative traits and that could be used as future varieties or components in hybridization programs) varied from 7 to 5 under EMS action (best at 0.025%) and from 8 to 9 (max) under SA, then declining from 5 to 4. SA 0.025% yielded the highest number of elite lines (9).

Table 1

Parameters of mutation action for supermutagens: Variety Vezha (x ± SD, n = 500)

Variant	RC, %	RPC, %	PGR	NL, pcs	NPL, pcs	RPL, %
Vezha	0.40 ± 0.07^{a}	0.00 ± 0.00^{a}	0.00	12	4	0.00 ± 0.00^{a}
Vezha, EMS 0.025%	7.00 ± 0.16^{b}	2.80 ± 0.14^{b}	0.40	15	7	0.80 ± 0.14^{b}
Vezha, EMS 0.05%	8.80 ± 0.20^{c}	3.80 ± 0.24^{c}	0.43	17	5	1.40 ± 0.12^{c}
Vezha, EMS 0.1%	12.10 ± 0.28^{d}	4.40 ± 0.17^{d}	0.36	12	5	1.00 ± 0.12^{b}
Vezha, SA 0.01%	6.40 ± 0.17^{b}	2.80 ± 0.17^{b}	0.44	17	8	1.00 ± 0.20^{b}
Vezha, SA 0.025%	9.40 ± 0.21^{c}	4.40 ± 0.14^{d}	0.47	22	9	1.60 ± 0.14^{c}
Vezha, SA 0.05%	12.60 ± 0.44^{d}	6.00 ± 0.28^{e}	0.48	15	5	1.80 ± 0.19^{cd}
Vezha, SA 0.1%	15.60 ± 0.53^{e}	4.40 ± 0.17^{d}	0.28	12	4	1.00 ± 0.12^{b}

Note: RC – rate of changes; RPC – rate of positive changes; PGR – proportion from general rate; NL – number of lines; NPL – number of promising lines; RPL – rate of promising lines; significant differences at $P < 0.05$ according to Tukey HSD test with Bonferroni amendment.

Best overall concentration was SA 0.05%, which produced the highest rate of positive changes (6.0%), proportion of beneficial mutations from the general (0.48), and rate of perspective lines (1.8%). Safest high-throughput variant was SA 0.025%, which produced the largest number of lines (22) and number of perspective lines (9) with strong efficiency (0.47 proportion of beneficial mutations from the general rate, 1.6% rate of perspective lines). Best EMS concentration was 0.05%. (3.8% rate of positive changes, 0.43 proportion of beneficial mutations from the general rate, 1.4% rate of perspective lines). For the variety Vezha, it is more preffable to use SA 0.05%, but when the goal is maximum conversion to elite lines, SA 0.025% could be used for a broader, efficient screening pool, meanwhile EMS 0.05% can be a reliable alternative.

Thus, for Vezha, an optimum concentration for protein level, protein profile, and microelements was SA 0.025–0.05% (demonstrating the strongest, most consistent effect), and EMS 0.05% was only slightly less effective with regards to microelements and protein components, but not in terms of total protein. For long and large spike, the optimum variant was SA 0.05% (0.8% and 0.4% respectively). Semi-dwarf and dwarf mutations were induced at a highest rate by SA 0.1%; however, negative complex changes in plant health. Safer variants were SA and EMS at 0.05% concentration. For short-stem plants, the best result was produced by SA 0.01%. Stress tolerance and surface traits, such as epicuticular wax, and disease tolerance were improved by EMS 0.05–0.1% (SA was ineffective).

As for the variety Ihrysta (Table 2), the rate of changes varied from 5.0% to 9.8% under EMS action, increasing with concentration. It also increased under SA, from 4.4% to 13.8%. Both mutagens demonstrated growth in the raw mutation count with increasing concentrations. However, SA generated the highest number of mutations at high doses. Rate of beneficial mutation varied from 2.4% to 5.0% under EMS action and from 2.2–5.2% under SA action, decreasing to 4.6% (peaks at SA 0.05%, and then decrease at SA 0.1%). The richest pool of useful forms appeared at SA 0.05%, and EMS produced steady positive effects with increasing concentration.

Table 2

Parameters of mutation action for supermutagens: Variety Ihrysta (x ± SD, n = 350–500)

Variant	RC, %	RPC, %	PGR	NL, pcs	NPL, pcs	RPL, %
Ihrysta	0.20 ± 0.07^{a}	0.00 ± 0.00^{a}	0.00	0	0	0.00 ± 0.00^{a}
Ihrysta, EMS 0.025%	5.00 ± 0.21^{b}	2.40 ± 0.14^{b}	0.48	9	2	0.40 ± 0.07^{b}
Ihrysta, EMS 0.05%	7.00 ± 0.16^{c}	3.80 ± 0.14^{c}	0.54	12	3	0.60 ± 0.11^{b}
Ihrysta, EMS 0.1%	9.80 ± 0.24^{d}	5.00 ± 0.21^{d}	0.51	17	3	0.60 ± 0.14^{b}
Ihrysta, SA 0.01%	4.40 ± 0.37^{b}	2.20 ± 0.14^{b}	0.50	9	4	0.80 ± 0.11^{bc}
Ihrysta, SA 0.025%	6.40 ± 0.17^{c}	3.40 ± 0.24^{c}	0.53	13	6	1.20 ± 0.24^{d}
Ihrysta, SA 0.05%	10.20 ± 0.37^{d}	5.20 ± 0.21^{d}	0.51	21	8	1.60 ± 0.14^{e}
Ihrysta, SA 0.1%	13.78 ± 0.33^{e}	4.60 ± 0.14^{e}	0.33	11	4	0.89 ± 0.16^{c}

Note: see Table 1.

The proportion of beneficial changes varied from 0.48 to 0.54 under EMS action, then 0.51 (best proportional quality at EMS 0.05%), and 0.50 to 0.53 under SA action, decreasing to 0.33 at 0.1%. SA 0.1% was inefficient, producing many mutations, but with only a small proportion of beneficial ones. The number of lines and number of perspective lines varied from 9 to 17 under EMS action, at the level of 2–3, respectively, and from 9 to 21 under SA, and then to 11, with 4 to 8 promising lines, and then 4 lines at SA 0.1%. SA 0.05% yielded the largest absolute number of promising lines (8 forms). The number of perspective lines varied from 0.40% to 0.60% under EMS action (flat above 0.05), from 0.80 to 1.60 under SA action, then to 0.89%. SA 0.05% provided the best conversion to elite candidates (1.60%), and 0.025% had the second best effect (1.20%).

In general, for the variety Ihrysta, the best concentration was SA 0.05%, which maximized both the number and proportion of perspective lines (the highest result), while maintaining good proportional efficiency (0.51 from the general rate). Conservative option was SA 0.025%, which produced slightly fewer positive changes than SA 0.05%, but still provided a high number of positive lines (1.20%) and good efficiency (0.53 from general rate). EMS produced optimum results at 0.05% (0.54, highest proportion from general rate), with 0.60% rate of positive lines; EMS 0.1% increased the scale of mutations, but did not improve conversion to perspective lines. At 0.1%, SA should be avoided or significantly limited: Despite the highest rate of changes, the number of promising lines was low (0.89%), as well as the number of psotive changes (0.33) and rate of positive lines.

In general, for the variety Ihrysta, SA 0.05% should be prioritized as a working dose, and SA 0.025% should be used when it is important to reduce risk and vitality concerns. EMS 0.05% can be used as a reliable alternative, especially when SA is unavailable or restricted. SA 0.1% should be avoided and EMS should be used with caution in high doses, because they produced lower conversion of mutations into elite, breeding-ready lines. For breeding purpose, the working range of SA should be 0.025–0.05%, and that of EMS 0.05%.

Overall, the best working concentration of SA for Ihrysta was 0.05%, which maximized the proportion of promising lines, provided long and large spikes and large-spike architecture and microelement enrichment. EMS 0.1% or SA 0.05% were best for plant stature reduction (short and semi-dwarf); the latter should be preferred for better overall efficiency. For earliness and disease tolerance, the best result was produced by SA 0.01–0.05%; SA 0.05% was clearly the best at enhancing grain quality (protein and HMW content, micronutrients); and SA 0.05% was the most

effective at producing long and large spikes. SA 0.1% should be avoided: It caused many changes, but only few were beneficial. For Ihrysta, the default option should be mid-low SA (0.05%); SA 0.025% can be used for enhancing earliness/tolerance; and EMS 0.1% can be adopted for stronger height reduction or wax traits, with fitness validation before before advancement.

Vezha yielded more perspective lines per treatment and responded well to both SA (0.025–0.05%) and EMS 0.05%; Ihrysta had better quality improvement and long-spike architecture under SA 0.05%, with stature reduction strongest at SA 0.1%/EMS 0.1%, but with higher risk. Factor analysis showed a strong effect of dose on the induction of beneficial changes, with higher concentrations increasing the rate of positive traits ($F = 20.99$; $F_{0.05} = 3.86$; $P = 3.01 \times 10^{-3}$). Varietal background was also a factor ($F = 7.77$; $F_{0.05} = 4.11$; $P = 0.009$), and a significant genotype × mutagen interaction was detected ($F = 5.34$; $F_{0.05} = 4.55$; $P = 0.03$).

Across both winter wheat varieties, induced variability was dose-dependent and genotype-conditioned. Mid-low concentrations delivered the most useful spectra: SA 0.025–0.05% and EMS 0.05% (occasionally 0.1% for specific traits).

Vezha showed the best conversion to promising material, with a broad response to both mutagens; the most effective variant was SA 0.05% (high positive-change rate and top rate of proising lines), followed by SA 0.025% and EMS 0.05%. SA 0.025% was effective for earliness, SA 0.025–0.05% produced long spikes, and SA 0.05% provided a balanced quality gains. Ihrysta was more quality-oriented, showing the strongest response to SA 0.05%, which consistently increased protein, improved the glutenin profile (higher HMW content), and enhanced micronutrients; stature reduction was greatest at EMS 0.1% or SA 0.1%, but the latter should not be recommended operationally due to efficiency loss. Practically, SA 0.05% should be prioritized as default for both varieties when targeting balanced architecture and grain quality; SA 0.025% can be adopted in safer, earliness-leaning programs (especially for Vezha); and EMS 0.05–0.1% should be used for stature, wax, and microelements, with fitness checks.

To elucidate genotype-specific, locus-targeted responses to EMS, we used linear discriminant analysis with a pooled multi-trait, multi-dose dataset (Fig. 1). Instead of analyzing each trait separately, the classifier captured each cultivar's aggregate reaction to EMS, consistent with the known genotype- and site-dependent nature of chemical mutagens. The model drew on a curated set of morphological descriptors, grain-quality biochemical indices, and cytogenetic features, combined across all EMS concentrations. This multivariate framing separated varieties by their composite EMS-sensitivity signatures.

Linear discriminant modeling revealed a clear dose hierarchy for both mutagens. For EMS, the mid and upper concentrations (0.05% and 0.1%) yielded comparable rates of favorable variants and consistently strong reactions across cultivars, whereas 0.025% EMS produced markedly fewer changes and a weaker mutagenic imprint.

For SA (Fig. 2), concentrations included three levels: the lowest level was underpowered; the intermediate pair (0.025% and 0.05%) showed similar effects and most productive genetic activity; and the highest dose, while highly active, translated into fewer practically useful outcomes, suggesting diminished efficiency at high concentrations.

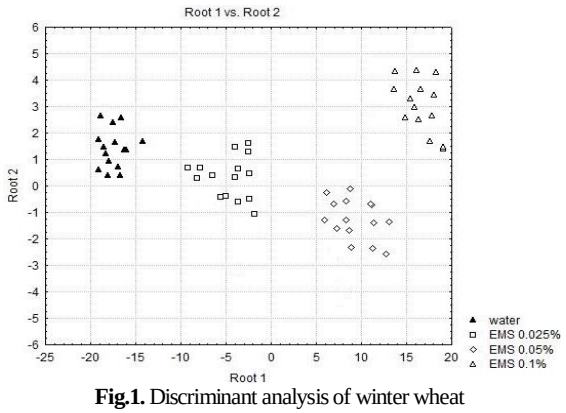

Fig.1. Discriminant analysis of winter wheat by EMS concentration, using the rate of positive changes

Using the same discriminant framework, traits were prioritized by their ease of induction after accounting for both mutagen identity and concentration. Two domains proved most tractable: developmental timing (earliness) and grain quality, which repeatedly showed strong, positive changes. A second group, including disease tolerance, semi-dwarf stature, and elongated spike architecture, displayed moderate but practically important. Unresponsive traits were uncommon. However, the analysis emphasized pronounced genotype × mutagen interactions. Consequently, the most effective breeding strategy is to pair responsive genotypes with SA 0.025–0.05% or EMS 0.05–0.10%. Higher SA doses must be used with caution, given that they reduced conversion of raw activity into desirable, selectable changes.

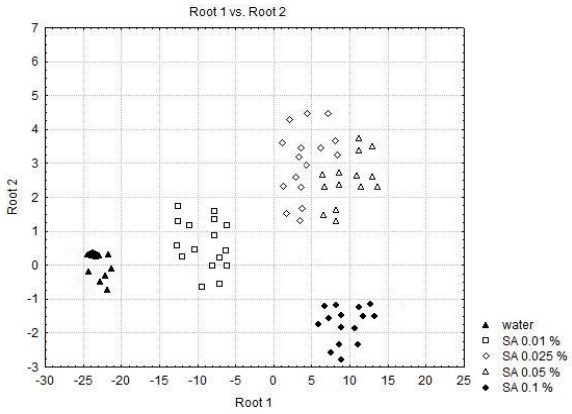

Fig.2. Discriminant analysis of winter wheat by sodium azide (SA) dose, using the rate of positive changes

The complementary classification (Table 3) attributed trait classes to the most responsive genotype–dose combinations. In general, Ihrysta was the more reliable source of end-use quality improvements, lines with enhanced gluten architecture (better HMW/LMW balance), and elevated protein. Ihrysta also responded well in terms of reduced stature, delivering semi-dwarf phenotypes at useful frequencies. By contrast, Vezha, excelled where phenology and adaptation were the focus, earlier heading/maturity appeared repeatedly at effective doses. Furthermore, this variety also exhibited disease-tolerance gains and spike-type remodeling (longer or larger ears). Traits linked to epicuticular wax proved comparatively easy to induce in both genotypes, indicating that cuticular modification is an attainable target across these backgrounds.

Increasing EMS to 0.1% consistently broadened the observable spectrum, both morphoarchitectural and biochemical, compared with 0.025–0.05% concentrations, while still allowing a sufficint proportion of recoverable, agronomically viable lines. For sodium azide, a clear performance plateau was observed at 0.025–0.05%: Within this interval, the share of agronomically valuable variants increased sharply without the efficiency losses seen at the top dose. Although 0.10% SA was highly mutagenic, the resulting conversion rate to advanceable selections was poorer, making it a less attractive option for breeding programs that prioritize consistent improvement.

Translating these patterns into practice suggests a targeted deployment strategy. If the breeding goals are earlier maturity, longer spikes, or enhanced disease tolerance, Vezha under SA 0.025–0.05% is a good option: This pairing repeatedly generated selectable material in those domains. If the program emphasizes flour/bread quality, protein level, and glutenin profile, Ihrysta and SA 0.025–0.05% could be used: those combinations delivered highly favorable biochemical changes. Ihrysta combined with EMS 0.10% produced semi-dwarf ideotypes, balancing mutation breadth with recoverability. To increase epicuticular wax (with potential drought and heat benefits), both genotypes are usable under EMS 0.05–0.10%, which consistently produced wax-intense variants.

Across targets, the results underscore a strong genotype × concentration relationship. The same chemical level can be productive in one background and inefficient in another. As a result, selecting the mutagen and concentration and the variety should be carried out considering the baseline genetics and the desired traits.

We screened mutagen-derived candidates for yield and bread-making quality (Tables 3–4) and found at least one standout from each source variety. From Vezha, three lines were advanced to intensive testing (from variants with EMS 0.1%, SA 0.025%, SA 0.05%). From Ihrysta, four lines progressed, one from EMS 0.1%, two from SA 0.025%, and one from SA 0.05%. Across three seasons, every selected line outperformed the standard for grain yield, although the magnitude of gain varied among genotypes.

Table 3
Modeling for changed traits in factors space

Trait at model	Wilks Lambda λ	Concentration at model	Genotype at model	$F_{0.05}$	P-level
Thick stem	0.513	Non	non	0.99	0.166
Short-stem	0.211	EMS 0.1%	Vezha	5.15	0.042
Semi-dwarf	0.170	EMS 0.1%	Ihrysta	7.11	0.035
Dwarf	0.374	Non	non	2.43	0.085
Intense epicuticular wax accumulation	0.219	EMS 0.05–0.1%	non	5.00	0.045
Large-size grain	0.443	Non	non	1.34	0.142
Long spike	0.170	SA 0.025–0.05%	Vezha	7.09	0.036
Large-size spike	0.416	Non	non	1.40	0.139
Early ripeness	0.120	SA 0.025–0.05%	Vezha	12.45	0.004
Tolerance for diseases	0.149	SA 0.025–0.05%	Vezha	7.55	0.028
Productivity	0.467	Non	non	1.20	0.153
Tillering capacity	0.411	Non	non	1.39	0.147
Higher protein content	0.120	SA 0.025–0.05%	Ihrysta	12.11	0.005
Positive changes in protein components	0.120	SA 0.025–0.05%	Ihrysta	12.14	0.005
Positive changes in microelement content	0.101	SA 0.025–0.05%	Ihrysta	14.99	0.001

Year-by-year grouping against the standard revealed consistent top performers. In 2024, lines 41 and 44 constituted the top productivity class. Line 32 formed its own intermediate tier, while the remaining selections occupied a second intermediate tier; the reference cultivar Podolianka ranked lowest. The pattern intensified in 2025: The differences increased, the elite group again separated clearly, and lines 41 and 44 remained at the forefront. Under that season's semi-intensive conditions, lines 35 and 55 also joined the leaders. The rest grouped into a distinct second echelon, clearly below the top performers, but above the control.

Synthesys of the multi-year evidence revealed that mutagen selections reliably exceeded the control and maintained their advantage under moderate shifts in seasonal intensity. Vezha's best outcomes aligned with the low–mid dose window (SA 0.025% and EMS 0.1%). Several strong performers of Ihrysta were yielded using SA 0.025–0.05% or EMS 0.1%. The lines 41 and 44 point continuously stood out, indicating an actual genetic improvement rather than transient seasonal effects. Lines 35 and 55, while not consistently elite, occupied a stable second tier and are promising as parents for recombination or as targeted candidates for environments favoring semi-intensive ideotypes.

Across the three seasons, the candidates grouped into three distinct yield strata. Lines 41 and 44 formed the elite, high-stability tier ($F = 12.43$; $F_{0.05} = 4.01$; $P = 0.002$). A second, mid-performing tier comprised lines 35 and 55 ($F = 5.91$; $F_{0.05} = 4.01$; $P = 0.03$). Lines 11, 31, and 32 consistently surpassed the standard ($F = 8.41$; $F_{0.05} = 4.01$; $P = 0.009$), but remained significantly below the top pair when contrasted directly ($F = 7.11$; $F_{0.05} = 4.01$; $P = 0.01$). Notably, lines 41 and 44 expressed yields with minimal year-to-year drift, while the remaining genotypes were more season-sensitive.

Table 4
Results from field tests for grain yield of winter wheat mutants (DSAEU, 2024–2025, x ± SD, n = 3, t/ha)

Variant	Origin	2024	2025
1	Podolianka, standard	6.10 ± 0.12^{a}	5.53 ± 0.11^{a}
11	Vezha, EMS 0.1%	7.05 ± 0.13^{b}	6.06 ± 0.13^{b}
21	Vezha, SA 0.025%	6.85 ± 0.12^{b}	6.06 ± 0.12^{b}
32	Vezha, SA 0.05%	6.60 ± 0.12^{c}	6.06 ± 0.12^{b}
35	Ihrysta, EMS 0.1%	6.95 ± 0.11^{b}	6.45 ± 0.12^{c}
41	Ihrysta, SA 0.025%	7.55 ± 0.16^{d}	7.11 ± 0.15^{d}
44	Ihrysta, SA 0.025%	7.48 ± 0.16^{d}	7.10 ± 0.15^{d}
55	Ihrysta, SA 0.05%	6.90 ± 0.11^{b}	6.46 ± 0.11^{c}

Note: see table 1.

Quality evaluations confirmed these distinctions. Lines 32, 35, 41, and 44 ranked highest for both grain protein and gluten, reflecting a close relationship between these parameters. All lines met bread-making suitability, yet lines 11 and 21, despite solid yields, had comparatively weaker technological quality. Line 41 stood out according to all the quality metrics as a strong donor for improving bread-making performance.

The quality advantage was mechanistically associated with higher high-molecular-weight (HMW) glutenin content, reduced low-molecular-weight (LMW) glutenins, and only moderate shifts in gliadins. Lines 11, 32, 41 and 44 were superior according to HMW glutenins; and lines 32, 35, 41, and 44 also exhibited reduced LMW fractions. Line 21 underperformed according to quality due to an elevated LMW component. Gliadins were comparatively stable overall, though line 41 trended slightly higher without compromising baking suitability.

Table 5
Technological grain quality of winter wheat mutants (results from field tests,DSAEU, 2025, x ± SD, n = 5)

Variety/line	Protein, %	Gluten, %	Glutenins		Gliadins
			HMW	LMW	
Podolianka	13.76 ± 0.11^{a}	24.70 ± 0.34^{a}	0.15860 ± 0.00270^{a}	0.45442 ± 0.00818^{a}	0.45600 ± 0.00821^{a}
1	13.80 ± 0.09^{a}	24.86 ± 0.51^{a}	0.15555 ± 0.00327^{a}	0.45146 ± 0.00948^{a}	0.44980 ± 0.00495^{a}
11	13.98 ± 0.10^{a}	24.75 ± 0.30^{a}	0.15234 ± 0.00320^{a}	0.46100 ± 0.00968^{a}	0.45110 ± 0.00496^{a}
21	13.94 ± 0.17^{a}	24.44 ± 0.41^{a}	0.20011 ± 0.00440^{b}	0.49499 ± 0.01089^{b}	0.45890 ± 0.00551^{a}
32	14.31 ± 0.14^{b}	26.14 ± 0.48^{b}	0.21123 ± 0.00485^{b}	0.40001 ± 0.00920^{c}	0.45140 ± 0.00587^{a}
35	14.32 ± 0.10^{b}	26.01 ± 0.32^{b}	0.16131 ± 0.00338^{a}	0.40954 ± 0.00860^{c}	0.45460 ± 0.00500^{a}
41	15.09 ± 0.17^{c}	27.99 ± 0.27^{c}	0.20432 ± 0.00225^{b}	0.41101 ± 0.00617^{c}	0.49143 ± 0.00737^{b}
44	14.23 ± 0.18^{ab}	25.98 ± 0.30^{b}	0.21100 ± 0.00422^{b}	0.40861 ± 0.00817^{c}	0.45100 ± 0.00451^{a}

Note: see Table 1; HMW – high molecular weight glutenins, LMW – low molecular weight glutenins.

For breeding deployment, line 41 concentrates multiple quality advantages but achieves only mid-tier yield; it is therefore best positioned as a quality donor for conventional crossing to boost baking strength. Lines 32, 35, 41, and 44 pair combine superior end-use traits (elevated protein, strong gluten, high HMW with moderate LMW) with competitive productivity, making them credible advancement candidates. By contrast, line 21, although agronomically sound, exhibits suboptimal protein-gluten composition and would need targeted quality improvement prior to consideration for release.

Discussion

Long-running experience shows that advantageous mutational outcomes are not accidental; they recur in consistent patterns that advanced programs can exploit (Kantoğlu et al., 2024; Hekal et al., 2025). Under precise dosing and selection, induced variability produces genetic materials that is simpler to enhance and integrate into breeding workflows (Liang et al., 2024). For regional germplasm, mutagenesis acts as a reliable, heritable generator of novel alleles (Chetto et al., 2025) and has repeatedly yielded targeted phenotypes, from pronounced height reduction to longer, grain-rich spikes and earlier maturity, when applied to well-chosen local genotypes (Winkler et al., 2023; Mutanda et al., 2025; Naserian Khiabani et al., 2025).

Our data indicate that sodium azide (SA) and ethyl methanesulfonate (EMS) play complementary rather than redundant roles. In our experiments, SA acted as an effective mutagen across domestic and introduced lines, frequently producing stable, inheritable improvements in performance and quality with a favorable proportion of desirable to neutral out-

comes (Harb et al., 2025). EMS, by contrast, excelled as a diversity engine: It consistently expanded allelic options and delivered strong donor lines for recombination and subsequent selection, even if immediate release-ready candidates were less common (Chetto et al., 2025; Han et al., 2025). In summary, SA tended to supply near-deployment material, while EMS widened the breeding palette for strategic crosses; both substantially enriched the diversity base (Horshchar & Nazarenko, 2024; Diallo et al., 2025).

Earliness and quality-oriented indices (grain protein, gluten architecture, and micronutrient profiles) showed the most consistent responsiveness across genotypes, especially under SA 0.025–0.05%. Architecture-related traits (short-stem, semi-dwarf, dwarf, long spike) responded to both agents, with EMS tending to favor stature reduction and SA proving particularly effective for extended spike and disease-tolerance variants at mid-low concentrations. The biochemical domain was especially promising: Multiple genotypes displayed increases in HMW glutenins paired with restrained LMW fractions, a pattern associated with stronger dough properties, while micronutrients such as Zn, Fe, and Mn often rose within the same operational windows (Bayhan et al., 2024).

Crucially, responses were genotype-conditioned. Local backgrounds and western ecotypes did not behave identically. Some varieties converted positive changes into perspective lines more efficiently under SA, whereas others did so under EMS, and the most productive settings for one genotype were not necessarily optimal for another. This genotype variability is not a drawback; rather, it is the practical signature of the site-specificity that makes chemical mutagenesis attractive for directed improvement. Programs that aknowledge this reality, by screening a small grid of doses per variety and aligning targets with each genotype's tendency, will harvest more value than those seeking a universal recipe (Putra & Prasetya, 2024; Liu et al., 2025).

Finally, the climatic context makes the case urgent. Winter wheat must combine winter survival with resilience to irregular water regimes and sudden heat waves. Mutation-derived diversity expands the solution space for these interconnected challenges. By integrating induced variability, careful phenotyping, and trait-informed selection, breeding programs can assemble ideotypes that deliver both higher grain output and stronger end-use quality across a wider envelope of environments. The route is empirical rather than prescriptive: testing a calibrated set of mutagen-dose combinations per genotype; measuring responces according to traits, especially in biochemical quality and architecture; quickly introducing lines into recombination or pre-varietal testing; and engagingg in iterating cycles (Liang et al., 2024; Nilahayati et al., 2024; Stearns et al., 2025).

A central takeaway is that mutagen performance is inseparable from the genetic backdrop. Outcomes hinged on the recipient genotype, likely through sequence context, chromatin organization, and the configuration of DNA repair pathways. We repeatedly observed cultivar-specific thresholds: Some backgrounds yielded useful variants rapidly and safely, while others reached toxicity or inefficiency at the same dose. This underscores strong site-specificity and genotype × mutagen interactions, the "right" concentration for one variety can be marginal or detrimental in another. Practically, that precision is advantageous: where SA aligned with the genome, we consistently recorded gains in end-use quality, with lines showing food-relevant biochemical profiles (Prasad & Kumar, 2024).

Dose framing proved decisive. Intermediate SA levels (particularly 0.025% and 0.05%) were the most productive, unlocking clear agronomic improvements while constraining side effects (Nanggia & Manimozhi, 2025; Nazarenko & Okselenko, 2025). At these concentrations, traits often vwere iewed as unresponsive (protein functionality and mineral micronutrient enrichment) shifted steadily in the desired direction. Relative to EMS, SA in this mid-range produced a more significant responce in our material. Nonetheless, the preferable agent remained dependent on breeding targets and the host genome.

SA produced a broader range of mutations, compared with previous studies of supermutagens, indicating that, in receptive genomes, certain agents can steer (or bias) outcomes toward usable categories (Liu et al., 2025; Okselenko et al., 2025). For breeders, the process follows a two-step rule: identify responsive germplasm; and then match it to the mutagen-dose pair that best aligns with the target trait class.

Trait-wise, SA's clearest advantages were biochemical. We observed consistent improvements in baking-relevant metrics, not just total protein or bulk gluten, which can be variety-limited, but also in the internal composition of the glutenin complex. Increases in high-molecular-weight (HMW) glutenins without parallel rises in low-molecular-weight (LMW) fractions were common at productive SA doses, shifting dough strength favorably (Arumingtyas et al., 2023; Phadungsawat et al., 2025). Concurrent, moderate gains in Zn, Fe, Cu, and Mn addressed typical wheat nutritional gaps (Kantoğlu et al., 2024). Notably, these biochemical upgrades often occurred without notable architectural changes, offering an attractive path to enhance established varieties while preserving farmer-preferred phenotypes (Nanggia & Manimozhi, 2025).

Conclusion

A central practical conclusion emerging from our analyses echoes patterns seen across other crops: Mid-low dosage windows are typically optimal. For SA, the range 0.025–0.05% consistently produced the best combination of positive-change rate and conversion to perspective lines, with manageable physiological costs. For EMS 0.05% (and, for some trait classes, 0.1% under careful screening) delivered broad, agriculturally relevant spectra. Increasing SA to 0.1% did increase raw mutation count, but the share of desirable outcomes decreased and stand health indicators deteriorated – the hallmark of a toxicity threshold. In other words, more changes does not automatically translate to more useful changes. From a risk-management perspective, our findings reinforce the rule of starting in the mid-low window (SA 0.025–0.05%; EMS 0.05%). These settings maximize the probability of usable variants while minimizing viability issues. Concentration should be increased cautiously and only when the target trait proves resistant; When using higher doses (e.g., EMS 0.1%), they should be paired with stringent selection for vigor and fertility to prevent the propagation of hidden liabilities. SA 0.1% should be avoided as a routine treatment. Although it boosts the frequency of changes, the efficiency of producing perspective material declines, and negative trait combinations become more common. Mutation breeding is sometimes portrayed as a blind search. Our results and the data of the modern literature suggest a different picture: with the right agents, at calibrated doses, and with genotype-aware deployment, mutagenesis can be steered. That steering may not yet match the nucleotide precision of genome editing, but it is sufficiently directional to shift complex phenotypes, quality architecture, micronutrient balance, spike structure, within timeframes compatible with practical breeding. In summary, mutation is the original engine of plant evolution and remains a powerful, vital resource for breeders. Chemical supermutagens such as SA and EMS applied judiciously and interpreted through a genotype-sensitive lens, provide a reliable means to generate targeted, heritable change. By quantifying response rates, mapping trait spectra, and exploiting the mild site-specificity inherent to these agents, programs can shorten the path to winter wheat types that are more productive, more resilient, and superior in processing quality, an essential outcome in an era of climatic uncertainty and rising performance demands. Future studies will include drought-tolerance phenotyping (photosynthetic activity on important stages of ontogenesis, temperature dynamics and length period of photosynthetic activity), winter-tolerance identification (survival at winter period), analysis of nutrient uptake in winter wheat plants for the purposes of identification of mechanisms of microelement metabolism.

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