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# EVALUATION AND SELECTION OF STRESS-TOLERANT DURUM-BREAD WHEAT PROGENIES DERIVED THROUGH HYBRIDIZATION OF PERENNIAL AND ANNUAL WHEAT

**A. AMANOV[1], D.Y. MUSIRMANOV[2], S.M. ALIKULOV[3], F.KH. ABDULLAEV[1], M.B. RASULOV[4], and A.E. HAKIMOV[4*]**

[1]Center for Innovation and Technology Implementation LLC, Tashkent, Uzbekistan
[2]Research Institute of Plant Genetic Resources, Tashkent, Uzbekistan
[3]Scientific Research Institute of Vegetables, Melons and Potatoes, Tashkent, Uzbekistan
[4]Oilseed and Fiber Crops Research Station, Tashkent, Uzbekistan
[*]Corresponding author's email: xakimovabdumurod148@gmail.com
Email addresses of co-authors: amiramanov999@gmail.com, musirmanovdilshod@gmail.com, safaruzripi@mail.ru, marat.rasulov.24@gmail.com, f_abdullaev@yahoo.com

## SUMMARY

Climate-induced abiotic stresses, such as drought, heat, and declining soil fertility, considerably threaten wheat productivity in arid regions. Perennial wheat relatives, including the species *Thinopyrum* and *Agropyron*, possess the vigorous root system and robust abiotic-stress tolerance, proving them more valuable donors for introgression breeding. The consequent study aimed to develop and evaluate stress-tolerant durum-bread wheat progenies derived from perennial × annual crosses under arid conditions in Uzbekistan. Diverse $G_2$–$G_3$ hybrid generations underwent assessment for viable agronomic traits such as tiller number, plant height, grains per spike, 1000-grain weight, and root development. Significant phenotypic variations were evident among the hybrid combinations. Several progenies involving the species *Thinopyrum intermedium* and *Agropyron ponticum* partial amphiploids showed improved grain-number stability (48–53 grains) and a deeper root system than annual parental genotypes. Grain-weight analysis revealed the mid-range classes (38–51 g) predominated in most $G_2$ hybrids, whereas multi-parent combinations displayed wider segregation and higher variations (18%–36%). Root-length analysis disclosed robust transgressive inheritance, with perennial-derived hybrids producing roots up to 90 cm, far exceeding annual cultivars (20–21 cm), highlighting their breeding potential for stress-resilient wheat.

**Keywords:** Perennial and annual wheat, hybridization, introgression breeding, stress tolerance, $G_2$–$G_3$ hybrids, key traits, grain number, root length

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**Key findings:** Perennial wheat relatives (*Thinopyrum* and *Agropyron* spp.) transferred drought- and heat-tolerance traits to $G_2$–$G_3$ hybrids, producing superior lines with stable grain numbers and deep roots. These hybrids were identified as promising donors for breeding climate-resilient wheat adapted to water-deficit environments.

## INTRODUCTION

Wheat productivity across arid and semi-arid regions faces considerable threats from water scarcity, heat stress, soil degradation, and salinity, and these factors severely limit the performance of *Triticum aestivum* and *T. durum* genotypes. Under these climatic conditions, developing germplasm with stable performance and enhanced stress resilience has become a challenging breeding priority globally (Ergashev *et al.,* 2021; Jabborova *et al.,* 2025). Perennial wheat relatives, such as *Thinopyrum intermedium* and *Agropyron ponticum,* possess the deep and robust root systems, drought tolerance, nutrient-scavenging capacity, and perennial regrowth ability, proving them as valuable donors for wide hybridization and introgression breeding in stress-prone environments (Sharma *et al.,* 2021; Placido *et al.,* 2013).

Introgression of perennial traits into annual wheat has produced hybrid derivatives capable of stable survival under moisture-limited conditions. However, the early-generation progenies often showed extensive segregation, and their agronomic performance requires thorough evaluation through advanced generations to ensure efficient selection. Seed vigor and germination uniformity were the recognized earliest indicators of hybrids' viability. As highlighted by Bradford (2002), hydrothermal-time responses and germination kinetics provide the critical insights into physiological stability, particularly in early-generation segregating breeding material. This was consistent with reports about hybrid populations with broad phenotypic variability in Uzbekistan (Makhmudov *et al.,* 2023).

Root architecture is another decisive trait determining plants' adaptation under drought stress conditions. Deep-rooting genotypes can access moisture from deeper soil layers, contributing to improved drought stress tolerance (Lynch *et al.,* 2019). The DEEPER ROOTING 1 (*DRO1*) gene with functional characterization further demonstrated that enhanced root depth can significantly improve grain yield under water-limited conditions in rice (Uga *et al.,* 2013). Previous research enunciated that perennial × annual wheat derivatives often exhibit robust root penetration and improved drought resilience, validating their potential use as donors of stress-adaptive traits in wheat (Erjigitov *et al.,* 2025).

Uzbekistan is characteristic of arid and semi-arid climatic conditions, where limited precipitation, recurrent drought events, increasing temperatures, and soil salinity are major constraints to wheat production. These factors adversely affect plant growth, grain yield, and yield stability, thereby posing serious challenges to sustainable wheat cultivation. Consequently, the development of wheat genotypes with improved adaptation to drought- and salinity-prone environments has become a key objective of national breeding programs.

Despite several studies on perennial × annual wheat hybridization and stress tolerance, previous research has mainly focused on cytogenetic characterization, perennial trait introgression, or advanced-generation materials, while early-generation segregating populations ($G_1$–$G_3$) remain insufficiently explored. In particular, integrated assessments combining germination performance, yield-related trait segregation, and root architecture are still few. Therefore, the presented study addresses this research gap by providing a comprehensive evaluation of $G_1$–$G_3$ perennial × annual wheat progenies to identify promising genotypes with improved adaptation and yield stability under drought-prone conditions in Uzbekistan.

In addition to abiotic stress factors, wheat production faces challenges of viral diseases, such as barley yellow dwarf virus (BYDV) and cereal yellow dwarf virus (CYDV),

which further emphasize the need for robust and biotic stress-resilient cultivars in Uzbekistan (Makhmudov *et al.,* 2026). Wide hybridization has gained successful uses to combine stress tolerance and yield stability in various major crops, reinforcing its potential value in wheat improvement (Erjigitov *et al.,* 2025).

With these challenges and the need for drought-resilient cultivars in dryland ecosystems of Uzbekistan, this study focuses on evaluating $G_1$–$G_3$ progenies derived from crosses between perennial (*Thinopyrum* and *Agropyron*) and annual wheat cultivars. Specifically, the research aimed to a) assess germination and seed vigor, b) analyze grain-weight segregation and yield-related traits, and c) examine the root-length variations to identify promising hybrid combinations with enhanced stress tolerance. By integrating class-frequency distributions, variance parameters, and multivariate comparisons, the timely study seeks to define the most promising introgression lines for developing climate-resilient wheat cultivars under water-limited stress environments.

## MATERIALS AND METHODS

### Experimental site and breeding materials

The conduct of field trials during 2022–2023 occurred at the Research Institute of Plant Genetic Resources (UzRIPI), located in a dryland agro-ecological zone of Uzbekistan. The study utilized perennial wheat species (*Thinopyrum intermedium* and *Agropyron ponticum* partial amphiploid) crossed with elite annual bread wheat cultivars including Chillaki, Bunyodkor, Shams, Hisorak, Dustlik, and Yonbosh. Hybridization resulted in $G_1$–$G_3$ generation populations representing diverse genomic backgrounds.

### Traits studied

This experiment recorded data on various traits, including tiller number, plant height (cm), grain number per spike, 1000-grain weight (g), root length (cm), and root class distribution.

### Statistical analysis

Descriptive statistical parameters, including mean (X), standard error (SE), standard deviation (SD), and coefficient of variation (CV%), reached calculations for all measured traits. Germination performance among wheat cultivars and hybrid populations succeeded in its evaluation using boxplot analysis, while grain-size class distribution sustained visualization through heatmap analysis. Root class distribution employed illustrations using area and bar charts. Data processing, statistical analyses, and graphical visualizations proceeded using OriginPro 2021 software (OriginLab Corporation, Northampton, MA, USA).

## RESULTS AND DISCUSSION

The frequency distributions of three key agronomic traits in the $G_2$ generation population revealed substantial phenotypic segregation driven by genetic recombination between the genotypes with perennial and annual wheat genetic backgrounds (Figure 1). Such broad quantitative variations were mostly evident in early-generation wheat introgression lines, where allele reshuffling generates transgressive phenotypes beyond the parental genotype ranges (Würschum *et al.,* 2018; Zhao *et al.,* 2019). Each histogram reflects the extent to which specific traits have stabilized or remained under segregation pressure, found consistent with the patterns reported in other wide hybrid wheat populations (Gorafi *et al.,* 2016).

### Tiller number

The results revealed that tiller number also displayed a moderately skewed distribution, with the majority of segregating progenies falling into the 4–6 and 7–9 tiller classes (Figure 1). However, very low and very high tiller frequencies were rare, revealing partial stabilization at the $G_2$ stage. Such segregation

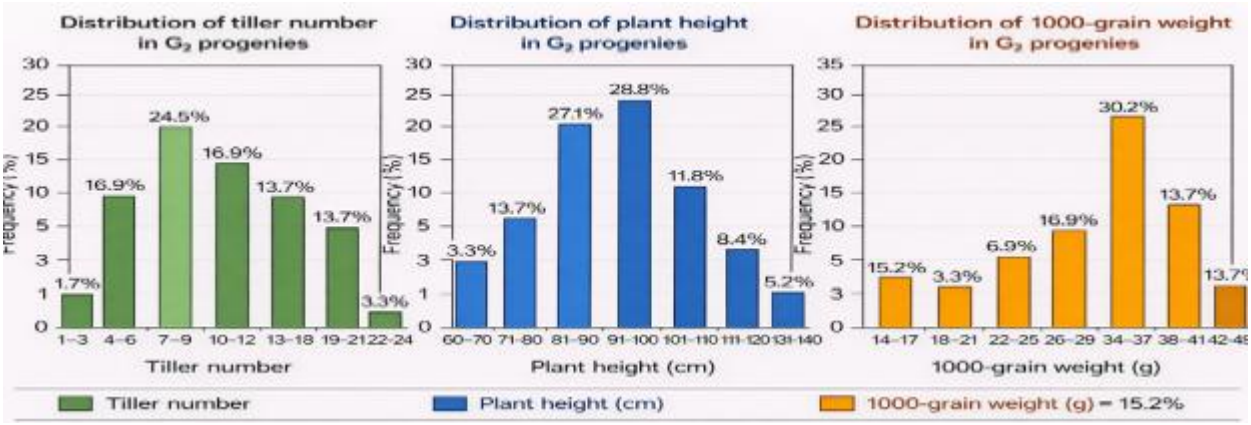


**Figure 1.** Frequency distribution of tiller number, plant height, and 1000-grain weight among the $G_2$ wheat progenies.

patterns appeared to be typical of polygenic traits, in which both additive and non-additive effects considerably influence the phenotypic expression in early hybrid generations. In previous studies, tiller number showed a moderately skewed distribution in wheat, with the most progenies concentrated in intermediate classes, reflecting that polygenic inheritance had the influence of additive and non-additive gene effects (Hao *et al.,* 2023).

Overall, the analysis of all traits (tiller number, plant height, 1000-grain weight, overall performance, germination traits, grain-weight class distribution, and root length variation) used analysis of variance (ANOVA), and differences among genotypes were statistically significant at $P < 0.05$. Trait variability across all evaluated parameters, when assessed, used standard deviation (SD), standard error (SE), and coefficient of variation (CV%), confirming the reliability of phenotypic distributions and segregation patterns in $G_1$–$G_2$ hybrid populations.

All data undergoing ANOVA gave significant differences among genotypes, determined at $P < 0.05$. Mean comparisons employed appropriate post-hoc tests, while variability of traits, expressed as standard deviation (SD), standard error (SE), and coefficient of variation (CV%), ensured statistical reliability of observed segregation patterns.

**Plant height**

Plant height exhibited a near-normal distribution, and the majority of wheat hybrid individuals were within the range of 81–100 cm (Figure 1). The symmetrical distribution and relatively narrow variance suggested the predominantly additive inheritance and revealed a tendency toward early phenotypic stabilization. Similar patterns of inheritance have been notable in durum and bread wheat recombinant inbred lines, where plant height maintained the highest heritability and stabilized earlier than other yield components (Würschum *et al.,* 2018).

**1000-grain weight**

As illustrated in Figure 1, plant height exhibited a near-normal distribution, with most hybrid progenies observed within the range of 81–100 cm. In contrast, the progenies' distribution for 1000-grain weight was more heterogeneous, showing an obvious evidence of transgressive segregation, particularly ranging from 38 to 41 g, and comprising the largest proportion of the hybrid progenies. Moreover, the occurrence of extreme classes (< 18 g and > 42 g) further reflected ongoing genetic recombination and incomplete allelic fixation at the $G_2$ stage. These results greatly aligned with previous findings, indicating that grain weight was

highly polygenic and broadly segregated in early-generation hybrid populations (Gorafi *et al.,* 2016; Zhao *et al.,* 2019).

**Overall performance**

The combined distribution patterns suggested that plant height occurred to be the most stabilized trait, tiller number showed moderate segregation, while 1000-grain weight remained highly variable, being recognized as an ideal trait for early-generation selection. These results supported the established understanding that quantitative traits segregate widely during early hybrid generations, driven by recombination and potential transgressive inheritance in wheat populations (Würschum *et al.,* 2018; Zhao *et al.,* 2019).

The boxplot revealed substantial variations in seed germination percentages among the parental wheat cultivars and $G_1$ hybrid populations derived from crosses involving *Thinopyrum* and *Agropyron* genomes (Figure 2). Parental cultivars usually exhibited a higher and more stable germination, with median values ranging between 70% and 85%, reflecting their genetic uniformity and long-term domestication history. In cultivated wheat germplasm, the similar stability pattern has had previous reports, where domestication reduced the early-generation variability and enhanced the uniformity in seed vigor (Rebetzke *et al.,* 2014).

In contrast, $G_1$ hybrid populations demonstrated broader interquartile ranges and a higher frequency of outliers, exhibiting enhanced heterogeneity and genetic segregation typical of early-generation introgression lines. However, such wide variability in germination traits following wide hybridization has also been evident in synthetic and introgressed wheat populations (Sehgal *et al.,* 2015). Hybrids containing wild relatives *Agropyron ponticum* and *Thinopyrum intermedium* showed particularly variable germination responses, suggesting that their introgression introduced both advantageous and destabilizing allelic combinations affecting early seed vigor (Placido *et al.,* 2013; Sharma *et al.,* 2021).

Nevertheless, several hybrid combinations, especially those involving wheat cultivars Bunyodkor, Yonbosh, G‘ozg’on, and Yaksart as recurrent parents, relatively maintained the highest and most consistent germination percentages (≥ 60%), enunciating improved compatibility and partial stabilization of germination-related traits (Figure 2). These results align with the findings that a recurrent-parent background can buffer instability and enhance the early vigor performance in wide crosses of bread wheat (Yagdi and Sözen, 2009).

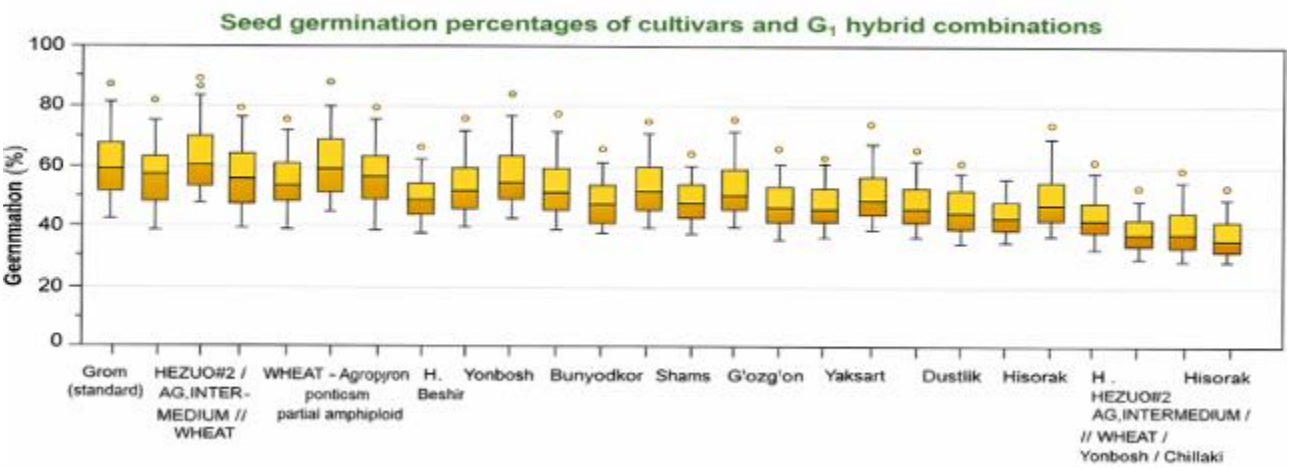


**Figure 2.** Comparative analysis of germination performance among the wheat cultivars and $G_1$ hybrid lines.

As illustrated in Figure 2, the observed distribution patterns emphasized two key findings, i.e., a) parental cultivars retain superior germination stability compared with $G_1$ hybrids, and b) genotypes characterized by narrower interquartile ranges (IQRs) and fewer outliers proved to be more suitable for advancement to $G_2$ and $G_3$ selection cycles, as these populations reflect a greater adaptation and more successful allele integration. These results highlighted the importance of evaluating seed vigor during early hybrid generations, as germination performance considerably influenced the plants' stand and subsequent yield potential under stress-prone environments—an insight widely supported by studies on early vigor genetics in wheat populations (Rebetzke *et al.,* 2014; Sharma *et al.,* 2021).

The heatmap provided a clear visualization on how grain-size classes attained distribution across the 18 $G_2$ hybrid populations. This representation both revealed the degree of phenotypic segregation and emphasized the varying influence of parental genotypes on the inheritance of grain weight. Such insights proved crucial for understanding genetic variability and guiding future breeding strategies aimed at optimizing grain yield and its quality parameters (Future 3). Similar grain-weight variation has reached documentation in wheat early-generation introgression material, where wide genomic reshuffling leads to class-wise separation of grain traits (Huang *et al.,* 2020).

Most hybrid progenies exhibited robust clustering within the mid-range grain-weight classes (31–37, 38–44, and 45–51 g), detailing that these intervals represented the central phenotypic tendency of the evaluated hybrid progenies. Several combinations, such as H4, H5, H7, H8, H10, and H17, showed the highest frequencies within these classes, suggesting relatively stable inheritance and reduced variability in grain weight (Figure 3). These inheritance patterns appeared consistent with past findings that grain weight often displayed moderate additive control, contributing to more uniform expression in stabilized backgrounds in wheat (Ayalew *et al.,* 2018).

In contrast, hybrid populations derived from more complex and multi-parent crosses (notably H11, H12, H13, H14, and H16) revealed broad segregation across the six-to-eight grain-weight categories. Such wide distribution patterns were considerably the characteristics of early-generation introgression lines undergoing active genetic recombination, suggesting that multiple allelic interactions influenced the grain weight in these populations. This trend was in high agreement with observations from multi-parent wheat populations, where recombination intensity generates the extensive phenotypic diversity in wheat lines (Iqbal *et al.,* 2021). These hybrid progenies also correspond with elevated coefficients of variation (V% = 18%–36%), supporting the interpretation that grain weight tended to be genetically unstable and subject to further segregation in subsequent generations.

Hybrid populations with narrower distributions, such as H3, H4, H5, H6, H8, and the standard cultivar (H18), expressed more concentrated grain-size frequencies. Their moderate-to-low variability (V% = 10%–12%) disclosed robust additive inheritance and suggested that these cross combinations have reached the partial phenotypic stabilization in the $G_2$ generation. Such types of genotypes were remarkably promising candidates for early selection, particularly for improving grain uniformity and yield consistency under stress-prone environments (Figure 3). Overall, the heatmap revealed three key trends, i.e., a) most $G_2$ hybrid populations exhibited dominant expression of mid-weight grain classes; b) wide segregation in multi-parent hybrids reflects the active recombination and potential for selecting transgressive phenotypes; and c) low-variability hybrids expressed phenotypic stability suitable for advancement in $G_3$ and later selection cycles.

The grain-weight class distribution of the 18 $G_2$ hybrid combinations revealed substantial diversity in phenotypic expression, reflecting the degree of segregation following introgression from perennial (*Thinopyrum intermedium* and *Agropyron ponticum*) and annual wheat backgrounds. These included

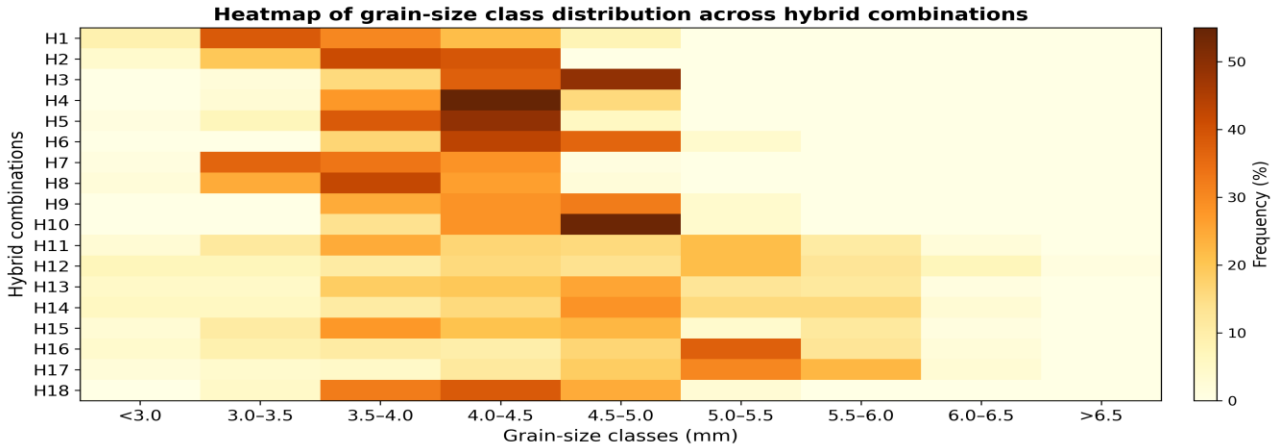


**Figure 3.** Heatmap illustrating the distribution of grain-weight classes among the 18 hybrid combinations (H1–H18) in the $G_2$ generation. Columns represent grain-weight classes, while rows correspond to individual hybrid combinations. The color gradient indicates the frequency of progenies within each grain-weight class, with darker colors representing higher frequencies and lighter colors indicating lower frequencies.

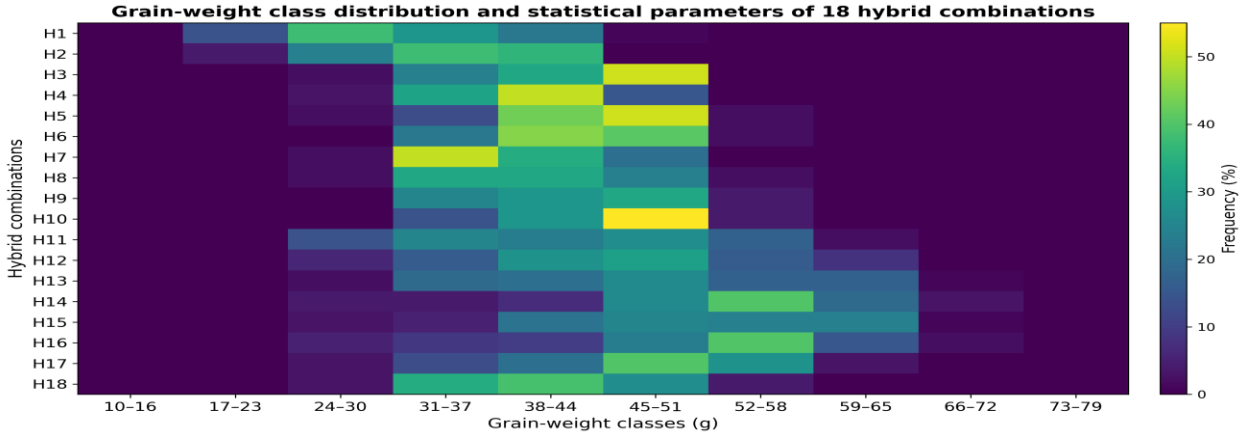


**Figure 4.** Grain-weight class distribution and statistical parameters of the 18 hybrid combinations ($G_2$ generation).

Chillaki, Bunyodkor, Shams, Hisorak, Dustlik, and Yonbosh. In early-generation introgression lines, such wide segregation was consistent with observations in wheat genetic studies, where wild-relative alleles considerably interact during recombination (Grewal *et al.,* 2018).

The majority of hybrid populations accumulated within the central grain-weight categories—particularly the 31–37, 38–44, and 45–51 g classes—indicated that these ranges represent the predominant expression of grain weight in the studied material. Hybrids, such as Yonbosh (H3), Bunyodkor (H5), Shams (H6), G‘ozg’on (H7), Yaksart (H8), and Hisorak (H10), demonstrated narrow class distributions, aligning with their low coefficients of variation (CV = 10%–13%). This inheritance pattern suggested that grain weight was approaching phenotypic stabilization in these cross combinations and possessed the improved potential for selection in early breeding stages. The same trend was also in a report stating stabilized recombinant inbred wheat populations in past studies (Golan *et al.,* 2019).

As illustrated in Figure 4, in contrast, several complex multi-parent hybrids, including H11, H12, H13, H14, H15, and H16, revealed

broader segregation across six-to-eight grain-weight classes. Their high CV values (17%–22%) further highlighted considerable genetic recombination and allelic reshuffling. Similar clustering and wide variability patterns have successful documentation in multi-parent wheat lines, where recombination intensity generates the highly diverse grain-weight outcomes (Scott *et al.,* 2021). Such combinations, although phenotypically heterogeneous, represent valuable breeding material for selection of transgressive genotypes with superior grain-size traits. In these hybrid populations, the wider variation enunciated that grain weight remains genetically unstable at the $G_2$ stage, requiring additional selection cycles for stabilization.

Hybrid populations with the highest mean grain weights, such as H17 (53.0 g), H12 (51.0 g), H14 (50.9 g), and H10 (50.0 g), disclosed both elevated grain weight and moderate phenotypic variability, proving their potential as promising donor lines for improving grain size under stress-prone environments. Conversely, the cross combinations (H1 and H2) with low average grain weight exhibited wider segregation and higher variability, suggesting weaker stabilization and incomplete integration of the donor alleles (Figure 4). These results align with the grain-weight inheritance studies, revealing that large-grain phenotypes often require several recombination cycles before achieving their consistent expression (Grewal *et al.,* 2018; Golan *et al.,* 2019).

Overall, the grain-weight distribution patterns evidently differentiated the hybrids with stable inheritance from those undergoing active genetic segregations. This combined evaluation of class frequency, average grain weight, standard deviation, and coefficient of variation (CV%) provides a robust framework for selecting elite genotypes. It also guides further advancement of perennial-annual wheat introgression lines, in accordance with recommendations from multi-parent wheat breeding research (Scott *et al.*, 2021).

The analysis of root-length distribution across the cultivars and perennial-annual wheat hybrid populations revealed considerable differentiation in root system architecture (Figures 5A–B). As expected, the wild wheat relative, *Thinopyrum intermedium,* exhibited the deepest rooting profile, reaching a mean of 0.90 m, clearly separating from all annual wheat cultivars. Such extreme rooting depth proved consistent with past reports describing perennial grasses as possessing highly developed axial roots capable of penetrating deep soil layers under moisture-deficit conditions (Kell, 2011). In contrast, the standard bread-wheat cultivars, such as Dustlik and Yonbosh, displayed substantially shorter roots (0.20–0.21 m), confirming their limited adaptation to deep-soil moisture extraction and drought resilience.

Perennial-by-annual hybrid combinations demonstrated intermediate yet significantly enhanced rooting capacities relative to annual parents. In these hybrid populations, the average root length ranged between 0.35 and 0.47 m, suggesting successful introgression of perennial root-system traits into annual backgrounds. Notably, the hybrids *A. ponticum* × Hisorak, *A. ponticum* × Elomon, and *A. ponticum* × G‘ozg’on produced the longest roots (0.40–0.47 m) among all the hybrids, highlighting these lines as promising donors for improving root penetration and subsoil water acquisition. The observed enhancement aligns with studies showing that introgression from wild wheat relatives increases root depth, angle plasticity, and drought-adaptive behavior (Wasson *et al.,* 2012; Golan *et al.,* 2018).

The root-class area chart (Figure 5) classified the wheat cultivars and hybrid progenies as a) annual cultivars remained confined to shallow-root classes (0–30 cm); b) most perennial-derived hybrids dominated the 41–50 and 51–60 cm classes; and c) only *Thinopyrum intermedium* extended into the 61–160 cm class, confirming its exceptional root-depth potential. This clear stratification of root classes across the hybrid groups validated successful transmission of deep-rooting alleles from perennial wheat relatives (Figure 5). Root-system introgression proved crucial for improving water-use efficiency, hydraulic lift, and drought survival strategies in wheat breeding programs. These results appeared greatly analogous to the parallel global findings

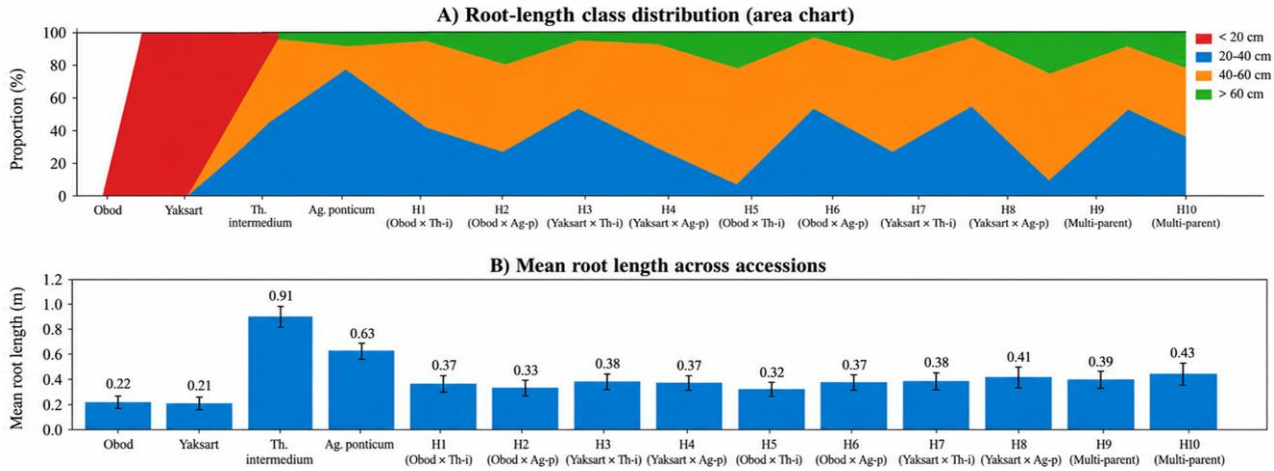


**Figure 5.** Root system variation across the cultivars and hybrid combinations ($G_2$ generation).

that deep-rooted wheat genotypes significantly enhanced yield stability under water-limited environments (Wasson *et al.,* 2012; Lynch *et al.,* 2019).

## CONCLUSIONS

Perennial wheat donors, including the species *Thinopyrum intermedium* and *Agropyron ponticum*, effectively transmitted drought-tolerant traits to their progeny. Several $G_2$–$G_3$ hybrid lines exhibited stable grain numbers (48–53 grains per spike), coupled with robust root systems. Notably, the HEZUO#2- and *Agropyron*-derived cross combinations demonstrated superior performance, highlighting their potential as valuable breeding materials. These lines offer a promising resource for developing climate-resilient wheat cultivars adapted to dryland environments.

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