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ORIGINAL ARTICLE

Phenotyping and identification of target traits for de novo domestication of wheat wild relatives

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Abstract

De novo domestication—the modification of domestication genes in crop wild relatives via genome editing—is an approach for harnessing the beneficial genetic diversity of crop wild relatives. A prerequisite for de novo domestication is phenotyping to identify genetic materials suitable for cultivation in the respective environment. Taxa from the wheat genepool (*Triticum aestivum*, *Triticum durum*, *Triticum monococcum*) are a staple food; these taxa comprise wild relatives of different ploidy levels. The diploid *Triticum boeoticum* and *Triticum urartu* and the tetraploid *Triticum dicoccoides* and *Triticum araraticum* harbor desirable traits such as high grain quality and abiotic and biotic stress tolerance. Hence, they are candidates for de novo domestication. Here, we grew 111 wild wheats and 38 landraces originating predominantly from the Fertile Crescent and six modern wheat cultivars in a field in Giessen, Germany, to evaluate their environmental adaptability to the central European climate and to identify potential candidates and target traits for de novo domestication. We demonstrate that several wild taxa are suitable for cultivation in the central European environment and that they have distinct characteristics that need to be modified during de novo domestication. The normalized difference vegetation index and the thermal time to heading and flowering indicated excellent adaptability of some wheat wild relatives to central European conditions. The values of yield parameters such as grain weight per plant, number of tillers, and thousand kernel weight were lower in the wild wheats than in the landraces. Therefore, these traits should be targeted for improvement during the de novo domestication of wild wheats.

KEYWORDS
de novo domestication, domestication genes, landraces, phenotyping, wheat wild relative

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1 | INTRODUCTION

Crop diversification is an essential strategy for agricultural production and food systems to ensure food security and nutritious food for a growing population under climate change. Currently, maize, wheat, and rice are the major staples to feed the world, and food systems' homogeneity has increased over the last 50 years (Khoury et al., 2014). Because the global diet relies on a minority of crops compared with the vast array of plant species (Milla & Osborne, 2021; Østerberg et al., 2017), options to re-introduce and increase diversity should be pursued. A common approach for broadening the diversity of modern crops is using crop wild relatives (CWRs) in breeding programs (Dempewolf et al., 2017; Kilian et al., 2021). CWRs harbor vast genetic diversity in terms of biotic and abiotic stress tolerance and resistance and nutritional composition. Usually, the introgression of favorable traits from CWRs is time-consuming, and linkage drag involving undesirable wild genes impairs the performance of the modern crop variety (Bohra et al., 2022; Chen et al., 2019; Dempewolf et al., 2017).

Genome editing of plants enables the more rapid use of CWRs as novel crops, in a process called de novo domestication. It is defined as the introduction of domestication alleles into non-domesticated plants (Fernie & Yan, 2019). De novo domestication using genome editing was successfully applied by Li et al. (2018) and Zsögön et al. (2018), who altered domestication genes affecting fruit size and synchronous flowering in wild tomato (*Solanum pimpinellifolium* L.). Lemmon et al. (2018) edited similar domestication genes in *Physalis pruinosa* L.; thus, de novo domestication via genome editing is feasible. However, there are several obstacles to de novo domestication. Scientific prerequisites for de novo domestication include transformation protocols (Østerberg et al., 2017; van Tassel et al., 2020), annotated reference genome sequences, and identification of suitable orthologs of domestication genes in wild plants (Fernie & Yan, 2019; Østerberg et al., 2017). Agronomic, cultural, social, and legal aspects should also be considered (Østerberg et al., 2017; van Tassel et al., 2020). This implies that genome-edited crops need to be accepted by consumers and comply with relevant laws.

Furthermore, newly domesticated crops need to compete with long-adapted high-yielding crops in terms of land-use and economic value (Luo et al., 2022; Østerberg et al., 2017). The process of obtaining a de novo domesticated crop can be distinguished into several phases, including the editing of (monogenetic) key domestication genes such as loss of shattering (Østerberg et al., 2017), followed by a subsequent breeding program to increase the performance of the novel crop (van Tassel et al., 2020). However, before these steps, the essential prerequisite is phenotyping to determine the new crop's ability to grow in the region(s) of interest, its abiotic and biotic stress resistance or tolerance, its advanced nutritional profile, and its non-toxicity to humans (Østerberg et al., 2017; van Tassel et al., 2020).

Wheat (*Triticum aestivum* L., 2n = 6x = 42, BBAADD) is one of the major staples (Langridge et al., 2022). The *Triticum* genepool consists of di-, tetra-, and hexaploid taxa. Two wild diploid and two wild tetraploid *Triticum* taxa have been found in nature: *Triticum urartu* Thumanjan ex Gandilyan (2n = 2x = 14, A^uA^u) and *Triticum boeoticum* Boiss. (2n = 2x = 14, AA, wild einkorn wheat), *Triticum dicoccoides* (Korn. ex. Aschers. & Graebner) Schweinf. (2n = 4x = 28, BBA^uA^u, wild emmer wheat), and *Triticum araraticum* Jakubz. (2n = 4x = 28, GGA^uA^u). Because no wild hexaploid *Triticum* taxa have been found so far, the role of the four wild *Triticum* taxa is of great importance (Zeibig et al., 2021). These taxa have been used as a source of genetic material for introducing biotic and abiotic stress resistance and tolerance into modern bread wheat and are a rich resource of genetic diversity (Dempewolf et al., 2017; Kilian et al., 2011). However, as explained above, introgressing selected traits from wild wheats into modern cultivars can hamper the latter's performance. Because of their strong ability to adapt to marginal environments, their superior grain quality, and their tolerance to pests and diseases, wild wheats could be good candidates for de novo domestication (Yaqoob et al., 2023). They represent important alternatives to modern wheat cultivars from the perspectives of increasing agrobiodiversity, cultivation in marginal locations that are unsuitable for bread and pasta wheat, and supplying nutrients, especially micronutrients.

Before performing de novo domestication, the suitability of wild wheats for cultivation in the respective environment and agricultural system must be evaluated. In terms of their survival, growth, phenology, and productivity, little is known about their adaptability to temperate central European regions. To fill this knowledge gap, we grew a diverse collection of wild diploid and tetraploid wheats, landraces, and modern wheat varieties in a field trial in Giessen, Germany. Our study aimed to identify candidate wild taxa for de novo domestication. For this purpose, we tested the following hypotheses: (i) the temperate central European climate is a suitable environment for wild wheats; and (ii) the phenotypic traits of wild wheats differ from those of modern cultivars and some of these traits should be priority targets for de novo domestication.

2 | METHODS

2.1 | Plant materials

The wild and landrace *Triticum* panel comprised 149 samples (Table 1, Table S1). The wheats were classified

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TABLE 1 Taxa, number of accessions sown in the field, classification of biological status and ploidy level of materials used in this study.

Taxon	Number of accessions	Biological status	Ploidy
Triticum boeoticum	7	Wild	2n
Triticum urartu	6	Wild	2n
Triticum dicoccoides	9	Wild	4n
Triticum araraticum	89	Wild	4n
Triticum monococcum	7	Landrace	2n
Triticum dicoccon	14	Landrace	4n
Triticum timopheevii	6	Landrace	4n
Triticum durum	4	Landrace	4n
Triticum aestivum	5	Landrace	6n
Triticum zhukovskyi	2	Landrace	6n
Triticum durum cv.	2	Modern cultivar	4n
Triticum aestivum cv.	4	Modern cultivar	6n

according to Dorofeev et al. (1979) (Kilian et al., 2010). The panel covered four wild taxa and six landrace taxa (Figure 1). The biological status group landrace comprise taxa thar are domesticated descendants of the wild taxa. For comparison, we also grew four modern winter wheat cultivars: cv. Apostel (I.G. Pflanzenzucht), cv. Julius (KWS SAAT SE & Co.), cv. Nordkap (SAATEN UNION), and cv. RGT Reform (RAGT Saaten), and two modern *T. durum* cultivars: cv. Sambadur (Hauptsaaten) and cv. Wintergold (SAATEN UNION).

2.2 | Experimental site

The field (7 m × 36 m) was located at the research station Weilburger Grenze (50°36′ N, 8°39′ E) in Giessen, Germany. The soil was a Fluvic Gleyic Cambisol with 40 kg Nmin/ha. The long-term average annual precipitation was 700 mm/a, and the annual air temperature was 9.7°C, measured from 1981 to 2010. During the experiment, the precipitation was 613.7 mm from planting in November 2020 until harvest in August 2021, and the mean temperature was 9.4°C. The coolest month was February 2021, with a mean monthly temperature of 1.3°C, and the hottest month was June, with a mean monthly temperature of 20.4°C (Figure S1). Climatic data were recorded daily with a weather station at the field station.

2.3 | Plant cultivation

In October 2020, four single seeds per genotype were pre-cultivated in a greenhouse. Seed trays were placed in a vernalization chamber (Weiss Umwelttechnik GmbH, Reiskirchen-Lindenstruth) for stratification for 48 h under an 8-h light/16-h dark photoperiod at 5°C and 60%–70% relative humidity. Afterward, they were transferred to a greenhouse and kept under a 10-h light/14-h dark photoperiod with day/night temperatures of 15°C/10°C. After 1 week, the temperature was decreased to 10°C during the daytime and 5°C during the nighttime, with a 16-h light/8-h dark photoperiod. Within the 2 weeks in the greenhouse, plants reached the two- or three-leaf stage and were then moved outside to acclimatize for 2 days before transplanting into the field in November. The field was arranged in a randomized block design, comprising two blocks with two sub-replicates for each accession in each block.

If only three seedlings emerged, they were separated into two groups (2 + 1), and in case of two seedlings, one was placed in each of the two blocks. The distance between seedlings of the same genotype was 25 cm and that between different genotypes was 50 cm. At the beginning of June, *Drechslera tritici-repentis* was detected, and lice were a major problem at the end of June. Therefore, the plants were sprayed with half-strength solutions of GIGANT® (ADAMA Deutschland GmbH) to treat *D. tritici-repentis* and PIRIMOR® G (ADAMA Deutschland GmbH) to control lice.

2.4 | Phenotyping and physiological measurements

For phenotyping the development of the different taxa, the Zadoks growth scale was used (Zadoks et al., 1974). The heading date was recorded as soon as Zadoks stage 50 (Z50) was reached. The Normalized Difference Vegetation Index (NDVI) was measured for each plant at the heading date at the flag leaf. Duplicate measurements were taken with a Polypen RP140 UVIS Spectroradiometer (PSI

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FIGURE 1 Spikelets of wild taxa and spikes of landrace taxa.

Instruments, Drasov, Czech Republic). After that, each plant was covered with a large Crispac microperforated plastic bag (Baumann Saatzuchtbedarf) to avoid cross-fertilization and to ensure that shattered ears and spikelets were retained and could be assigned to a single plant. The majority of the above-ground parts of the plant was covered by a single large micropore bag. Later-emerging side tillers were covered later with smaller bags. The anthesis was recorded as soon as flowering (Z60) was observed. The thermal time (°Cd) needed for heading and anthesis was calculated by adding the daily mean temperature. The base temperature was set to 0°C. Plant height was measured in June after all plants had flowered. Because of the wild relatives' brittle rachis, the height of the stem, from the bottom to the start of the spike, could be measured. The rachis phenotype was recorded at harvest as brittle when all spikelets had disarticulated from the spike at maturity.

2.5 | Analysis of harvest fractions

After harvest, the plants were dried to constant weight at 30°C. The number of tillers was counted, and the spikelets, spikes, and straw of each individual plant were weighed. The spikelets of the landrace and modern wheats are attached to the spike (Figure 1), so the whole spike was weighed. The weights of the wild wheats' spikelets and of the landrace and modern wheats' spikes were recorded as hulled grain weight.

For further analysis, only genotypes with at least three surviving plants were selected, and one sub-replicate in each block was chosen. The spikelets and spikes were threshed using an electric coffee mill. Only the seeds retained in the large microperforated bag, which were most of the seeds produced by the plant, were threshed. The hulless grain weight from the threshed sample was weighed for each plant. To calculate the share of the hulless grain weight to the hulled grain weight, we divided the hulles grain weight by the hulled grain weight. To estimate the total hulless grain weight, the hulled grain weight from the unthreshed samples of the side tillers was multiplied by the share of the hulless grain weight. The thousand kernel weight (TKW) was analyzed by counting three replicates of 50 seeds for each plant. The harvest index (HI) for each plant was calculated as follows: HI = total hulless grain weight ÷ total above-ground biomass (weight of grain, straw, and husks).

We calculated the survival rate of plants to determine how suitable the growing environment was for the different taxa. The survival rate was calculated by dividing the number of plants of each taxon that reached heading and flowering by the number of plants transplanted into the field in November.

2.6 | Statistical analyses

For statistical analysis of the heading and flowering date, stem height, and the number of tillers, one plant in each

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block had to survive per genotype. Others were excluded from the analysis. If both replicates survived in one block, their mean was calculated for further analysis. For statistical analysis, ANOVA was used to integrate the taxa or biological status as fixed effects and the block as a random effect. Principal component analysis (PCA) was computed. Statistics were performed in R Studio with R version 4.2.0 (www.r-project.org). The packages emmeans, multcomp, and nlme were used for ANOVA, and the packages FactoMineR, factoextra, and corrplot were used for PCA. Figures were generated with ggplot2 and Microsoft Excel.

3 | RESULTS

3.1 | Morphological observations

Different wheat relatives exhibited characteristic panicle stand and spike shapes (Figure S2). During maturity and ripening, spikelet shattering occurred in the wild wheats, and the shattered spikelets and seeds were retained in the microperforated bags. The seeds of the landraces and modern cultivars did not disarticulate from the spike (Figure 1).

3.2 | Survival rate

The wild wheats showed a survival rate (to the heading date) of 98.4%, compared with only 94.3% for the landraces. Among the wild taxa, the diploid *T. boeoticum* and *T. urartu* showed higher survival rates than the tetraploid wild taxa. Among the landraces, *T. monococcum*, *T. timopheevii*, and *T. zhukovskyi* showed a 100% survival rate, whereas *T. durum* (92.3%), *T. aestivum* (88.2%) and *T. dicoccon* (85.2%) lost some plants during the cold period.

3.3 | NDVI

The NDVI differed significantly between the wild taxa and the landraces, but not between the wild taxa and the modern cultivars. Among the wild taxa, the diploid *T. boeoticum* and *T. urartu* performed slightly better than the tetraploid *T. dicoccoides* and *T. araraticum*. Among all the taxa, domesticated einkorn showed the highest NDVI, followed by *T. timopheevii* (Figure S3, Table S3).

3.4 | Heading and anthesis date

All of the samples that survived the winter reached the heading stage (> Z50) and completed anthesis (Z60 and higher). The wild taxa group was the first group to reach the heading stage (Z50) at the beginning of June (mean, 1363 °Cd), followed by the modern cultivars (mean, 1414 °Cd). The landrace group was the latest group to head (mean, 1462 °Cd). The same pattern was found for the thermal time to flowering (Z60). The wild taxa reached anthesis after 1498 °Cd (mean), followed by the modern cultivars (mean, 1556 °Cd) and then the landraces (mean, 1583 °Cd). Compared with the wild and landrace taxa, the modern cultivars showed a more even distribution for both phenological dates. The thermal time to heading (Z50) and flowering (Z60) differed significantly only between the landraces and wild wheat group.

Focusing on the individual taxa in our panel, the wild *T. dicoccoides*, *T. urartu*, and *T. araraticum* were the first to reach the heading stage, whereas *T. monococcum*, *T. timopheevii*, and *T. zhukovskyi* were the last (Figure 2, Table S3). There was no significant difference in the thermal time to heading or to flowering among the taxa in the wild group. The thermal time to flowering in *T. zhukovskyi*

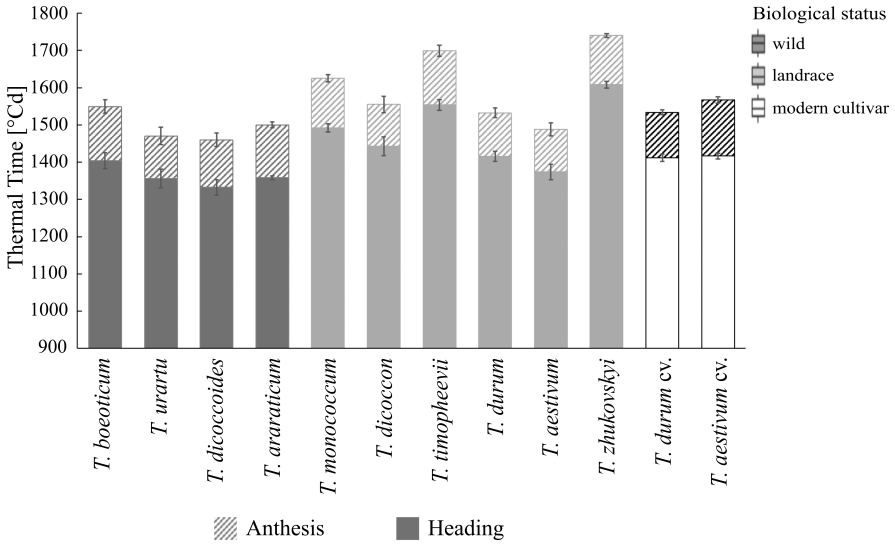

FIGURE 2 Thermal Time [°Cd] required for heading (Z50) and anthesis (Z60) for wild taxa, landraces, and modern cultivars. Bars indicate standard error for each parameter.

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and *T. timopheevii* differed significantly from those in all wild and landraces except for *T. monococcum*.

3.5 | Stem height

Plant height is important since it determines the plant's susceptibility to lodging. Modern cultivars showed the lowest average height (63.8 cm), followed by the wild taxa (93.8 cm), and the landraces showed the highest average stem height (104.4 cm). These values differed significantly among the three groups.

Modern bread wheat cultivars were the shortest (61.3 cm) and were significantly shorter than all other taxa except modern durum wheat cultivars. *T. araraticum* was the shortest wild taxon with an average height of 91.5 cm, whereas its domesticate *T. timopheevii s. str.* was the tallest, with an average height of 121.9 cm (Figure 3, Table S2). This follows the pattern that occurred in the groups based on biological status and highlights that the wild taxa are shorter than their domesticated descendants. This was also true for *T. dicoccoides* (93.0 cm) and *T. dicoccon* (106.2 cm) (Figure 3). However, this difference was only significant for *T. araraticum* and *T. timopheevii*. *T. araraticum* was also significantly shorter than the two diploid wild taxa, *T. boeoticum* and *T. urartu*.

3.6 | Number of tillers per plant

Tillers are an important yield component. The median number of tillers per plant was 33 in the wild taxa and 39 in the landraces. The modern cultivars had fewer tillers per plant, with a median of 24. The number of tillers per plant in the landraces differed significantly from those in the wild taxa and modern cultivars. The wild and landrace group showed large variations in the number of tillers. The highest number of tillers was found in *T. monococcum* (58 tillers per plant), followed by its wild ancestor, *T. boeoticum* (45 tillers per plant) (Figure S4, Tables S2 and S3). The number of tillers per plant was significantly different between *T. monococcum* and all other taxa except *T. boeoticum*. This high number was also accompanied by a large variation. This trait generally showed a broad distribution.

3.7 | Hulled and hulless grain weight per plant

Grains of wild and some domesticated taxa are covered by glumes. The hulled grain weight and the hulless grain weight increased from wild to landrace to modern cultivars. The proportion of hulless grain weight out of hulled grain weight increased from 51% in the wild taxa to 74% in the landraces to 87% in the modern cultivars (Figure 3, Table S3). The hulless grain weight, but not the hulled grain weight, differed significantly between the landraces and modern cultivars. However, both of the grain weight traits of the wild taxa differed significantly from those of the landraces and modern cultivars.

T. durum and the modern cultivars of *T. aestivum* cv. had similar hulless grain weights of 55.1 g and 54.5 g per plant, respectively (Figure 4, Table S2). *T. zhukovskyi* had the lowest grain weight per plant with only 7.5 g (Figure 4,

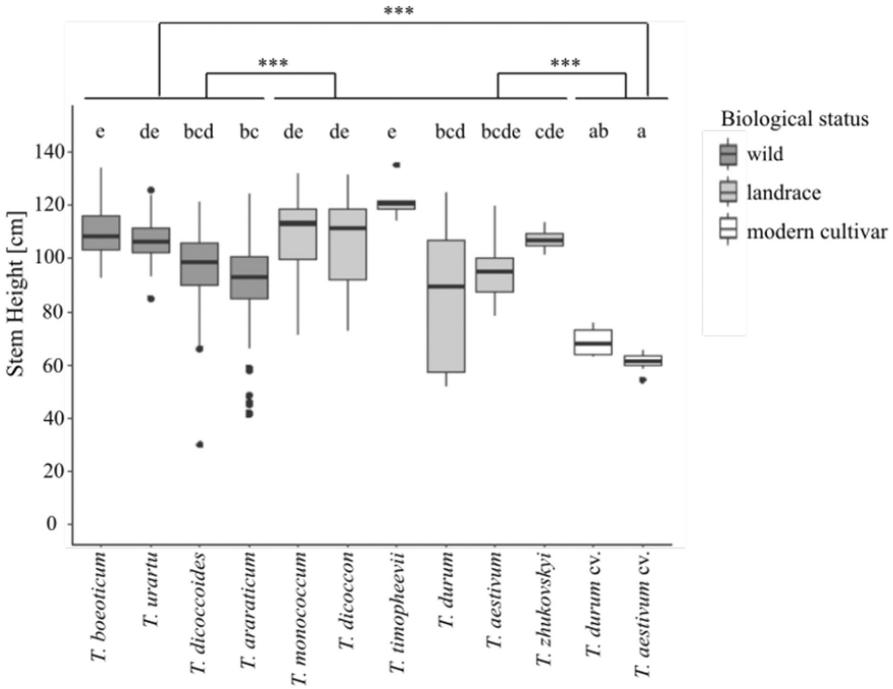

FIGURE 3 Stem height of wild taxa, landraces, and modern cultivars. Shading indicates biological status groups. Asterisks indicate significant differences between biological status groups (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$), ns. indicates no significant difference, and different letters indicate significant differences among taxa ($p < 0.05$).

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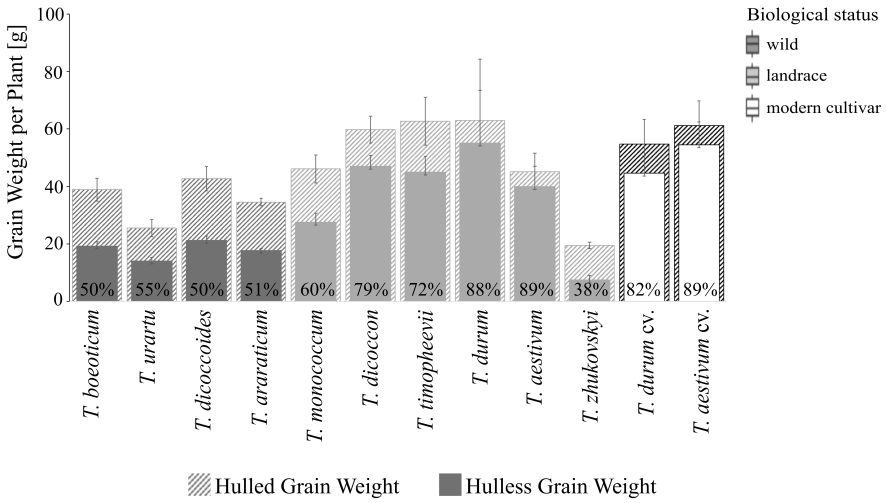

FIGURE 4 Hulled grain weight and hulless grain weight per plant for wild taxa, landraces, and modern cultivars. Percentage shows the proportion of hulless grain weight out of hulled grain weight. Bars indicate standard error for each parameter.

Table S2). The hulless grain weights of the wild taxa were in the lower range from 13.9 to 21.2 g and did not differ significantly from each other, but were significantly lower than those of all the modern cultivars and landraces except *T. monococcum* and *T. zhukovskyi*.

3.8 | Thousand kernel weight

The TKW was significantly lower with 24.8 g in the wild taxa compared to 34.3 g in the landraces and 38 g in the modern cultivars. Notably, the TKW did not differ significantly between the landraces and modern cultivars. Focusing on the taxa within the biological status groups, there was a significant difference in TKW between the diploid and tetraploid wild taxa. The TKWs for *T. boeoticum* and *T. urartu* were 13.7 g and 11.6 g, respectively, much lower than those in *T. dicoccoides* in *T. araraticum* (28.4 g and 26.3 g, respectively) (Figure 5, Tables S2 and S3). Among the landraces, the diploid *T. monococcum* had a TKW of 20.3 g, which was significantly lower than those of the tetra- and hexaploid landraces and cultivars (33.7 g). The TKW of tetraploid landraces differed significantly from those of all wild taxa, but not from those of the modern cultivars.

3.9 | Harvest index

The HI is an important characteristic for resource allocation to grain yield and its share of the above-ground biomass. The HI of the wild taxa was 0.26, but higher in the landraces (0.34) and modern cultivars (0.44). The HI differed significantly among the three groups. On the basis of hulless grain weight, *T. zhukovskyi* showed the lowest HI (0.11), which was significantly lower than those of all the other taxa. The HI of the wild taxa and *T. monococcum* ranged from 0.24 to 0.29. The HI of *T. aestivum* landraces (0.41) was similar to that of *T. aestivum* cultivars (0.45) (Figure S5, Tables S2 and S3). Again, the HI of modern cultivars was significantly higher than those of the wild taxa and *T. monococcum*.

3.10 | Connections between phenological, phenotypic, and yield parameters and different taxa

A PCA was performed to see how the taxa clustered on the basis of the variables measured in this study (Figure 6). The majority (89.4%) of the variation in the data set was explained by three principal components (PCs). The first PC (PC1) described 43.5% of the variation in the dataset and was dominated by phenotypic traits such as hulled and hulless grain weight as well as HI, plant height, and tiller number. The second PC accounted for 25.7% of the variation and was described by the thermal times to heading and flowering, that is, by phenological data. The NDVI and number of tillers per plant were the main contributors to the third PC, which explained 20.2% of the variation in the data set. The NDVI had the lowest contribution in the biplot, followed by the number of tillers (Figure 6). The number of tillers clustered on the opposite side of the yield-related traits of hulled grain weight, hulless grain weight, and proportion of hulless grain weight out of hulled grain weight. The HI and the stem height showed an opposing trend.

The wild taxa clustered together, the diploid *T. boeoticum* and *T. urartu* clustered outside the ellipse, and the wild tetraploid *T. araraticum* and *T. dicoccoides* grouped within the ellipse. The landraces were more scattered than the other taxa. *T. dicoccon* and *T. durum* clustered close to *T. aestivum* and the modern cultivars. Notably,

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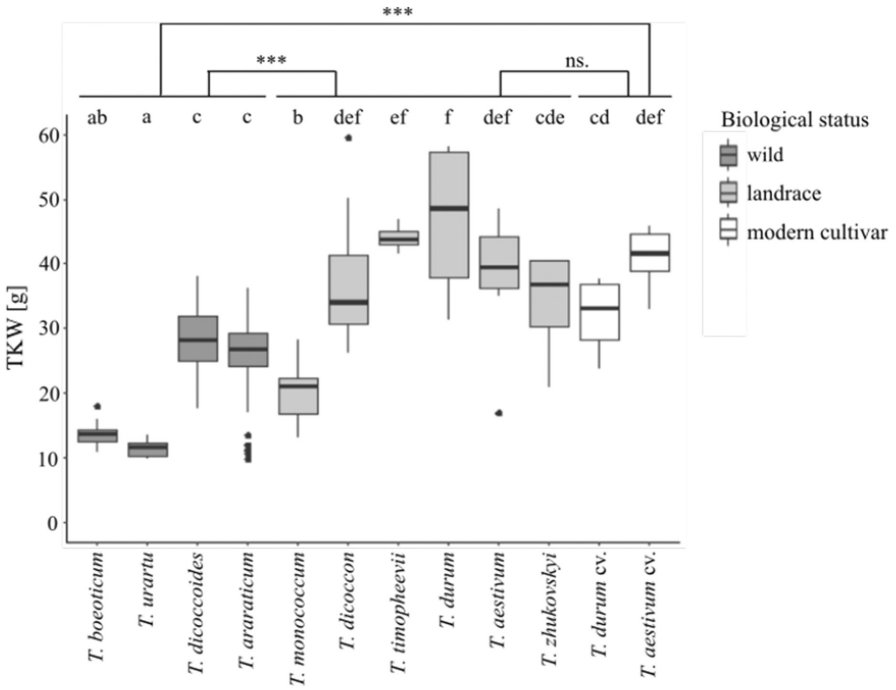

FIGURE 5 Thousand kernel weight (TKW) for wild taxa, landraces, and modern cultivars. Shading indicates biological status groups. Asterisks indicate significant differences between biological status groups (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$), ns. indicates no significant difference, and different letters indicate significant difference among taxa ($p < 0.05$).

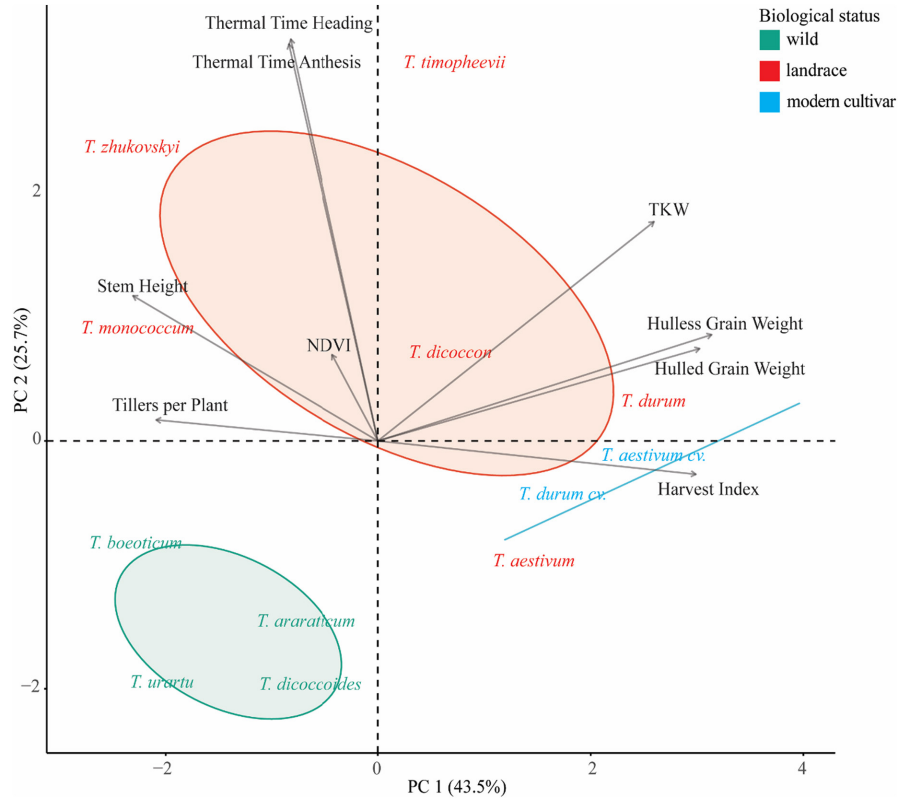

FIGURE 6 Principal component analysis of taxa and phenological, phenotypic, and yield parameters. Taxa are colored according to their biological status. Confidence ellipses are displayed for the biological status.

the modern cultivars of *T. durum* and *T. aestivum* were located near their landraces. This group was found in the proximity of yield-describing traits. The G genome-containing *T. timopheevii* and *T. zhukovskyi* were located distantly from each other (unlike *T. dicoccon* and *T. aestivum*). Still, both were aligned more with the phenological traits of PC2 than with the yield-determining traits of PC1.

4 | DISCUSSION

4.1 | The central European climate is a suitable environment for wild wheats

The survival rate is an important indicator of the adaptability of exotic germplasm to a new environment and the suitability of that environment for their cultivation (van

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Tassel et al., 2020). The wheat wild relatives in our study showed high survival rates at the field site, indicating good adaptability. Their adaptation potential is surprising when comparing the climate of their origin to that at the field station. The Fertile Crescent is primarily characterized by a semi-arid to arid climate with winter rains and a hot, dry summer (Jaradat, 2017; Kelley et al., 2015). During the cultivation period in Giessen (Nov 2020–August 2021), May and July had the highest precipitation (Figure S1), but this did not affect the wild wheats too severely. The accessions in our panel had diverse sites of origin. The *T. araraticum* accessions were mainly from Turkey and Iraq, whereas the *T. dicoccoides* accessions were collected from Israel, Turkey, Iran, and Iraq. Consequently, our panel (SI) covered geographic diversity well. Therefore, their good adaptability can also be explained by the diverse environments in their regions of origin, which are shaped by high mountains to drier deserts (Jaradat, 2017). Furthermore, wild wheats are adapted to highly variable yearly precipitation, which ranges from 150 mm to more than 600 mm in their various sites of origin (Willcox, 2005). Considering this, they will likely be suitable for cultivation in other environments in central Europe, although this needs to be tested in field experiments. Another question to be addressed in the future is whether any maternal effect caused differences between wild wheats, which means that the propagation of plants outside their natural habitat would affect seed quality and thus the performance of subsequent generations.

The NDVI is an indicator of chlorophyll content and is related to crop productivity (Thapa et al., 2019) and plant fitness. Typically the NDVI increases until anthesis and peaks at the booting and flowering stages (Hazratkulova et al., 2012; Samborski et al., 2015), consistent with our measurements (Figure S3). The NDVI did not differ significantly between the wild wheat taxa and the modern cultivars, which indicates similar fitness and productivity potential. The chlorophyll content contributes to the yield potential of wheat (Zhang et al., 2009). In this regard, it seems that the wild diploid *T. urartu* and *T. boeoticum* meet the prerequisites for high yield (Figure S3). However, other factors that contribute to yield and productivity, such as grain weight (Figure 4) had lower values in wild wheats than in the modern wheat cultivars in this study. This was expected, because the wild wheats have not been bred for these traits. Due to the similar NDVIs, it can be concluded that the wild taxa are as suitable as the modern wheat cultivars in this environment.

The thermal time can be used to assess the development of plants in response to different environmental factors and genotypic constitutions. Compared with the modern cultivars, the wild taxa tended toward slightly earlier heading (Z50) and flowering (Z60). Still, overall, the developmental stages were reached after a similar amount of degree days (Figure 2). Compared with thermal times reported in other studies, those detected for the wheat panel in this study were highly variable. A short number of degree days was reported for *T. monococcum* and *T. dicoccoides* grown in the USA (Jaradat, 2019). In contrast, modern wheat cultivars grown in Germany took a long time to reach the heading stage (Mahrookashani et al., 2017). Such variation can be attributed to the contributions of vernalization and photoperiod, which strongly influence plant development, but have not been included in the calculations in our study or other studies (McMaster et al., 2008).

Furthermore, in the study of Jaradat (2019), the domesticates were grown as summer crops, thus excluding a vernalization period. However, prolonged times to heading and flowering were found for *T. timopheevii* and *T. zhukovskyi* in the present study (Figure 2). This finding can be attributed to their origin, because they are from a specific part of Georgia (Badaeva et al., 2021). Thus, they might be suitable candidates for stay-green phenotypes and enhanced assimilation. In general, all wild wheats were able to complete their generative development in the central European climate, indicating that they are suitable for cultivation in this area.

4.2 | Wild wheats exhibit phenotypic traits that need to be targeted and modified in de novo domestication

De novo domestication via genome editing offers the opportunity to broaden the diversity of plants for cultivation and accelerate the domestication of wild plants. However, two points must be considered. First, the newly domesticated plant must be accepted by consumers and farmers. For the former, information about genome editing, including its potential and risks, needs to be delivered to, and discussed with, the public, and regulatory policies and frameworks have to be declared. For acceptance by farmers, the crop should be manageable with existing agricultural machinery, such as combine harvesters, to minimize the expense of adaption (van Tassel et al., 2020). Additionally, the de novo domesticated crops must benefit the public and farmers. Secondly, genes underlying unfavorable traits for modern cultivation need to be identified and edited (Fernie et al., 2021; Fernie & Yan, 2019). Most of these genes will comprise domestication-related loci that enable cultivation under the conditions of modern agriculture.

The loss of seed shattering is a major indicator of domestication. Accordingly, we observed the disarticulation of the spikelets of the wild taxa from the spike during

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ripening. This trait is mainly influenced by the *Brittle rachis 1* and *Brittle rachis 2* (*Btr*) genes on chromosome 3. Their loss of function enables the non-shattering phenotype (Pourkheirandish & Komatsuda, 2022). Thus, those genes should be the first target for de novo domestication of wild wheats.

Hulled grains occur in wheat wild relatives and landraces. This trait hampers threshing and has been selected against during the breeding of bread wheat and durum wheat. In our study, at least 50% of the spikelets consisted of glumes and awns in the wild wheats (Figure 4), resulting in increased biomass, decreased HI, and difficult threshing. The combination of these factors makes this a key target trait because, without straightforward harvesting, de novo domesticated wild wheats will have greater difficulty being accepted by farmers (van Tassel et al., 2020). Traits associated with ease of harvesting have been targeted during domestication, as indicated by an increasing proportion of the hulless grain weight out of hulled grain weight with the advancement in domestication status (Figure 4). Different genes influence the free-threshing character, namely *Q*, *Tg*, and *sog*. The dominant *Q* locus is a major domestication gene in wheat and is located on chromosome 5 (Simons et al., 2006). Threshability is further determined by the *Tenacious glume* (*Tg*) gene on chromosome 2 (Kilian et al., 2009; Sharma et al., 2019; Sood et al., 2009) and *soft glume* (*sog*) (Sood et al., 2009). For the complete free-threshing character, *tg* and *Q* need to be present because they have an additive effect (Sharma et al., 2019). Hulled grains is a major trait that should be targeted in de novo domestication.

Yield parameters distinguished the wild taxa from the landraces and modern cultivars (Figure 6). For successful establishment of de novo domesticated crops derived from CWRs, yield-determining and yield-influencing traits need to be identified and improved. Yield is a complex trait made up of different components (spikes per area, grain weight and size, spike architecture) (Luo et al., 2022; Voss-Fels et al., 2019). In our study, the grain weight parameters (hulled and hulless grain weight) were negatively associated with the number of tillers (Figure 6). Many of the wild samples produced a large number of tillers (Figure S4) but the hulless grain weight was low (Figure 3). This implies that the tillers do not carry a high number of grains per spike or that the TKW was low. Still, those are important traits for productivity in wheat. The number of grains per spike comprises two components; that is, the number of grains per spikelet and the number of spikelets per spike (Kuzay et al., 2019). Different genes have been identified to be responsible for these traits in wheat. The gene *WAPO-A1* on chromosome 7AL positively influences the number of spikelets per spike (Kuzay et al., 2019, 2022).

Similarly, *FT-A2* on chromosome arm 3AS further increases grain number per spike and spike yield (Glenn et al., 2022). A reduced function of *GNI1* (grain number increase) was shown to increase the number of fertile florets per spikelet and thus, the grain number (Sakuma et al., 2019). However, the alleles differ between the wild and domesticated taxa (Glenn et al., 2022; Kuzay et al., 2019, 2022). For de novo domestication, these genes and the corresponding favorable allele(s) should be targeted to increase yield.

The TKW is a highly heritable trait that is an important contributor to grain weight and flour yield (Dziki & Laskowski, 2005). Among the wild samples, the tetraploid taxa showed significantly higher TKW than did the diploid taxa. The TKW of *T. monococcum* was considerably lower than those of the tetraploid landraces and tetraploid wild taxa (Figure 5). This pattern is further supported by other studies that reported TKWs between 20 g and 30 g for *T. monococcum* (Brandolini et al., 2011; Hidalgo & Brandolini, 2017; Kulathunga et al., 2021) and between 33 g and 40 g for *T. dicoccon* (Kulathunga et al., 2021; Marino et al., 2009). Those values are consistent with our observations. Therefore, choosing tetraploid wild taxa for de novo domestication promises a higher yield potential.

The HI represents the partitioning of the grain yield relative to the above-ground biomass and has constantly been improved by breeding to increase grain yield and reduce plant height (Voss-Fels et al., 2019). In our study, the HI was negatively associated with the number of tillers and stem height (Figure 6), which are indicators of large biomass. A tall stem height is a distinctive feature of the wild taxa and landraces (Figure 3). Comparison of stem height data from our study with data reported from different environments revealed some differences. For example, *T. boeoticum* in our study was taller than *T. boeoticum* grown in Iran (Pour-Aboughadareh et al., 2017), whereas *T. urartu* in our study was slightly shorter than *T. urartu* grown in Italy (Talini et al., 2020). This could be attributed to the different environmental conditions (Royo et al., 2014), or to genotypic differences. When performing de novo domestication of wild wheat, reducing plant height is an important target to prevent plants from lodging and increase HI. Genes from the *Rht* dwarfing family would be suitable targets for reducing plant height (Hedden, 2003; Würschum et al., 2017).

The loci proposed here are a first selection of putative target genes for de novo domestication of wild wheats. However, identifying the right orthologs in the wild taxa remains a challenge (Fernie & Yan, 2019; Østerberg et al., 2017). De novo domestication is a chance to repeat the domestication process with the benefits of current knowledge. That implies that we should not abandon diversity at the expense of yield traits. Favorable traits have

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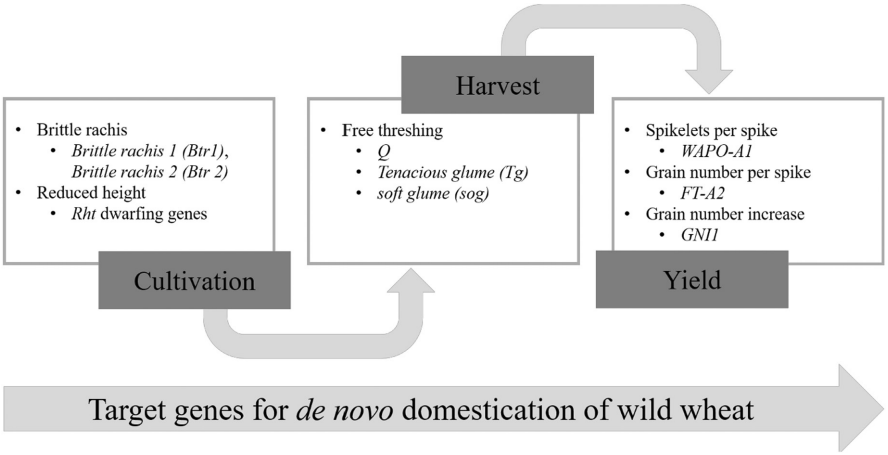

FIGURE 7 Prioritization of genes for a *de novo* domestication of wild wheat. *FT-A2, FLOWERING LOCUS T2; GNI1, GRAIN NUMBER INCREASE 1; Rht, Reduced height; WAPO-A1, WHEAT ORTHOLOG OF APO1.*

been lost unintentionally during domestication history and breeding (Fernie & Yan, 2019; van Tassel et al., 2020). Modifying and selecting target traits via genome editing can help to prevent such losses. However, each modification suggested here will interfere with the plant's physiology; therefore, trade-off effects should be screened by phenotyping afterwards. This needs to be emphasized because the domestication loci, such as the *Q* gene, have pleiotropic or additive effects, thus influencing not only the target trait, but also many other traits (Figure 7).

5 | CONCLUSION

The diversity of CWRs provides a resource for ensuring food security under climate change, which can be harnessed by de novo domestication. However, to perform de novo domestication, phenotyping to confirm environmental suitability and the identification of target genes or traits are prerequisites. As a staple food with a diverse genepool, wheat is a good crop for this approach. The wild wheats showed good adaptability to the Central European climate at the field station in Germany with high survival rates and completion of their generative development. The brittle rachis trait in wild wheats should be prioritized and edited first during de novo domestication because it will facilitate cultivation. Genes involved in yield-related traits are also important targets for de novo domestication of wild wheats. Within the wheat taxa, the tetraploid wild wheats showed a higher TKW than did the diploid taxa. Thus, they should be prioritized in future research. These wheats should be grown in different regions to further determine how they are affected by environmental factors. In addition, potential wild wheat candidates should be assessed for novel traits such as tolerance to abiotic stresses and grain quality to choose favorable genotypes for de novo domestication that will increase diversity in the wheat cropping system.

AUTHOR CONTRIBUTIONS

FZ planned the field experiment, took measurements, collected, and analyzed data, created the figures and tables, and structured and wrote the manuscript. BK consulted FZ during the field experiment and contributed to and edited the manuscript. HÖ provided the plant material, and contributed to and edited the manuscript. SP supported FZ in the yield parameter measurements and edited the manuscript. MF conceived the project, contributed to and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data relevant to this article can be found in the article and the supplementary information.

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ETHICS STATEMENT

The authors declare that the experiments comply with the current laws of Germany.

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SUPPORTING INFORMATION

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