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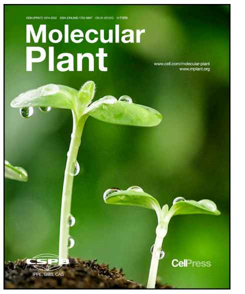

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Toward a "Green revolution" for Tartary buckwheat through ideotype breeding

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Main text

Tartary buckwheat (TB, *Fagopyrum tataricum*) is an annual crop in the genus *Fagopyrum* of the family Polygonaceae. It originated in the Himalayan mountains and subsequently spread along the Himalaya–Central Asia–Eastern Europe corridor, leading to widespread cultivation. Because of its strong tolerance to poor soils and broad environmental adaptability, it has long been used as an important crop for disaster relief and for making use of marginal land (He et al., 2024). TB grain is rich in bioactive compounds, especially flavonoids, which give it multiple medicinal and health-promoting effects (Zhang et al., 2021). The Food and Agriculture Organization of the United Nations has emphasized the importance of TB for food diversification, mountain food security, and sustainable agricultural systems (Huang et al., 2025). Despite this agronomic and nutritional potential, current TB cultivars still exhibit many primitive traits that prevent it from fully serving as a modern staple crop. To address these challenges, adopting ideotype design, exploiting crop wild relatives (CWRs), and developing easy-dehulling varieties will serve as core strategies. Meanwhile, emerging genomics and gene editing technologies offer powerful tools to expedite such breeding efforts.

Breeding progress: challenges of a semi-domesticated crop

Despite ~ 4000 years of cultivation, TB remains a "semi-domesticated" crop retaining wild traits that limit modern production (He et al., 2024). The primary issue is plant architecture: tall, slender stems with weak mechanical strength make plants prone to lodging (Figure 1A left; Shimizu et al., 2020). Additionally, strong seed shattering and indeterminate inflorescence—where flowers and seeds coexist—cause uneven ripening, hindering mechanical harvesting (Jha et al., 2024). Furthermore, removing the hard, tight hulls requires thermal processing, often damaging kernels and reducing nutritional quality (He et al., 2024).

These constraints explain why past breeding progress has been modest (Chettry and Chrungoo, 2021). Current efforts remain fragmented, targeting single traits rather than an integrated redesign of plant architecture (Shimizu et al., 2020). Transforming TB into a fully domesticated crop requires an urgent shift from empirical selection to genomics-guided design (Zhang et al., 2021). To support this, establishing a clear, widely agreed modern "ideotype" is essential for the next phase of breeding.

Future breeding strategies: ideotype design and germplasm innovation

To overcome these bottlenecks and meet future food demands, we propose three strategic pillars for TB breeding that combine field observations with genomic insights. These pillars will provide a coherent framework for transforming TB from a semi-domesticated orphan crop into a high-performing, climate-resilient smart crop.

Refining the ideotype: Dwarf, compact, and determinate

Within this framework, redesigning plant architecture is the main goal. We define the ideal TB ideotype as "Dwarf and compact, lodging-resistant, low-shattering, and determinate". Compared to current cultivars (Figure 1A left), the ideotype should have reduced plant height (optimally 50–80 cm) to lower the center of gravity and stronger, more lignified (Culm Lodging Resistant Index, CLRI $\geq$ 2.0) stems to resist lodging. The leaves should be bigger to improve light capture and photosynthetic efficiency under high planting density. At the same time, the spikes should show greatly reduced seed shattering to minimize harvest loss. Most importantly, a determinate growth habit is essential. This will synchronize flowering and seed set, promote uniform maturity and allow efficient, low-loss mechanical harvesting (Figure 1A right).

Developing perennial and high-flavonoid varieties *via* CWRs

While plant architectural optimization is foundational, enhancing perenniality and nutritional quality represents a second, complementary direction. CWRs are key genetic resources for crop improvement. The CWRs of TB, especially *F. cymosum*, carry valuable traits that were lost during domestication. *F. cymosum* has a strong rhizomatous root system and extremely high flavonoid content (He et al., 2022). A major strategy is to hybridize the TB ideotype with *F. cymosum* to introgress these traits and develop "Perennial TB." Such varieties would regrow from underground stems after a summer harvest, allowing a second harvest in autumn, and could overwinter and resume growth the following year (Figure 1B). This perennial growth habit, combined with the enhanced flavonoid profiles inherited from the wild parent, would greatly increase both the economic value and ecological sustainability of buckwheat cultivation.

Generalizing the easy-dehulling trait for high-quality groats

In parallel with improvements in plant architecture and perenniality, grain processing quality must also be upgraded to fully realize TB's nutritional advantages. To fully benefit from the nutritional value of whole-grain TB, it is essential to develop varieties that are easy to dehull. We therefore advocate the broad use of the easy-dehulling trait found in the rare landrace Rice-Tartary buckwheat. Recent genomic studies have linked this trait to structural variation in the *FtXIP* gene promoter (He et al., 2024). However, the application of *FtXIP* in breeding remains fairly limited as observations indicate that it may compromise lodging resistance. Fortunately, high-yielding ideotypes harbor multiple key genes associated with robust morphological traits, which can effectively alleviate the adverse effects of *FtXIP*. By combining the high-yielding ideotype with this easy-dehulling trait, breeders can develop varieties that produce whole, intact kernels (high-quality groats) through simple mechanical threshing (Figure 1C). This will reduce nutrient loss, lower processing costs, and maintain grain integrity for high-value food products without compromising lodging resistance.

Pathways to realization: multi-omics driven precision breeding

Achieving these goals will require a shift from traditional selection to data-driven, precision breeding, similar to progress already made in major crops like rice and maize. To operationalize this shift, several complementary approaches must be implemented in a coordinated manner.

Large-scale germplasm screening and pre-breeding

As a first step, broad exploration and pre-breeding are needed to capture existing diversity for ideotype traits. Through international collaboration within International Buckwheat Research Association (IBRA), we can carry out high-throughput phenotypic and genotypic screening of global TB germplasm. The aim is to identify rare accessions that already show parts of the target ideotype, such as natural dwarfs or determinate lines, and use them as key parents. In parallel, developing multi-parent advanced generation inter-cross populations will help combine favorable alleles for ideotype traits into single, superior backgrounds. Phenomics technologies provide powerful tools for efficient germplasm resource evaluation. Leveraging platforms such as remote sensing systems, unmanned aerial vehicles, and phenotyping robots, integrated with deep learning and artificial intelligence, enables the rapid and precise acquisition of phenotypic data, thereby enhancing the efficiency and accuracy of phenotypic characterization.

Targeted mutagenesis and genome editing

However, natural variation alone is unlikely to provide all the alleles needed for a rapid green revolution in TB. To quickly introduce traits missing from elite germplasm, chemical mutagenesis serves as a robust strategy. Based on successful work in other crops (Liu et al., 2025), saturated mutant libraries can be screened to discover new alleles controlling plant architecture. Given TB's reputation as an organic crop, the direct commercialization of gene-edited varieties currently faces significant hurdles regarding public acceptance and regulatory restrictions. Nevertheless, CRISPR/Cas9 remains an indispensable instrument for fundamental research. It enables the precise functional characterization of candidate genes—such as *FtHPCA1* (plant height), *FtAP2YT1* (grain weight) (Zhang et al., 2021), and the *FtXIP* promoter (easy-dehulling) (He et al., 2024)—thereby guiding the precise selection of desirable, non-transgenic mutants derived from radiation breeding.

Pan-genome assisted allele mining and genomic selection

Genome-wide diversity resources are essential for deploying favorable alleles. Moving beyond single reference genomes to exploit the TB pan-genome allows for the identification of rare alleles lose during domestication, particularly those retained in Himalayan wild TB (Shi et al., 2025). Integrating multi-omics data (GWAS, transcriptomics, metabolomics) helps resolve the regulatory networks for key traits like rutin biosynthesis (*FtUFGT3*) and abiotic stress tolerance (*FtPAK*) (Huang et al., 2024). Building genomic selection models on these datasets will further accelerate genetic gain for complex traits (e.g., yield stability, flavonoid content) and shorten breeding cycles, creating an "intelligent breeding" system. Furthermore, to circumvent inefficiencies arising from redundant sequencing efforts, establishing a centralized bioinformatics data-sharing database for buckwheat is equally crucial. Currently, under the leadership of the IBRA, a dedicated data-sharing platform is being developed to enable the exchange of bioinformatics datasets, thereby collectively advancing global buckwheat breeding progress.

Expedited Exploitation of CWRs

In addition to mining diversity within cultivated TB, genomic sequencing and systematic screening of CWRs are equally important. For example, the use of *F. cymosum* to improve cultivated buckwheat is currently limited by strong pre-zygotic and post-zygotic reproductive barriers. The recently proposed homoploid hybrid speciation (HHS) identification model offers a novel approach to advancing this line of research (Wang et al., 2021). We propose a new strategy: first, use whole-genome sequencing to identify specific HHS accessions within the complex *F. cymosum* population that are phylogenetically closer to cultivated TB; then use these selected accessions as "bridge parents" for crossing with the cultivated species. This approach can substantially reduce reproductive isolation and increase the success rate of obtaining superior hybrid progenies (Shi et al., 2025). Furthermore, these initial hybrids can be crossed with diverse *F. cymosum* accessions and subjected to systematic selfing or backcrossing, like the use of *Aegilops tauschii* in common wheat (Li et al., 2024). This allows for the accumulation of diverse superior genes from the wild gene pool into the hybrid background, thereby speeding up the use of beneficial alleles from CWRs.

Complementarily, *de novo* domestication of wild species represents a transformative strategy, as successfully demonstrated in wild rice and tomato (Yu et al., 2021; Zsögön et al., 2018). By directly editing genes associated with key domestication traits such as shattering habits, flowering time, and seed setting rate in the diploid wild progentior *F.*

cymosum, we can theoretically create new germplasms suitable for field production. However, it must be noted that unlike major crops, the genetic basis of these traits in buckwheat is not yet fully understood. Therefore, while promising, this approach requires extensive foundational work to identify the precise regulatory targets before it can be widely applied.

In summary, TB is uniquely positioned at the crossroads of nutrition, health, and ecological resilience. The ideotype and breeding roadmap outlined here offer a clear and practical path toward a "Green revolution" in TB.

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Author contributions

M.Z. conceived and supervised the study. W.L., H.L., L.X., and L.Y. drafted the manuscript. Y.H., Z.W., K.Z., M.Q., S.W., D.J., N.M., M.G., and I.K. contributed to discussion and critical revision of the manuscript.

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All authors declare no potential competing conflicts associated with this work.

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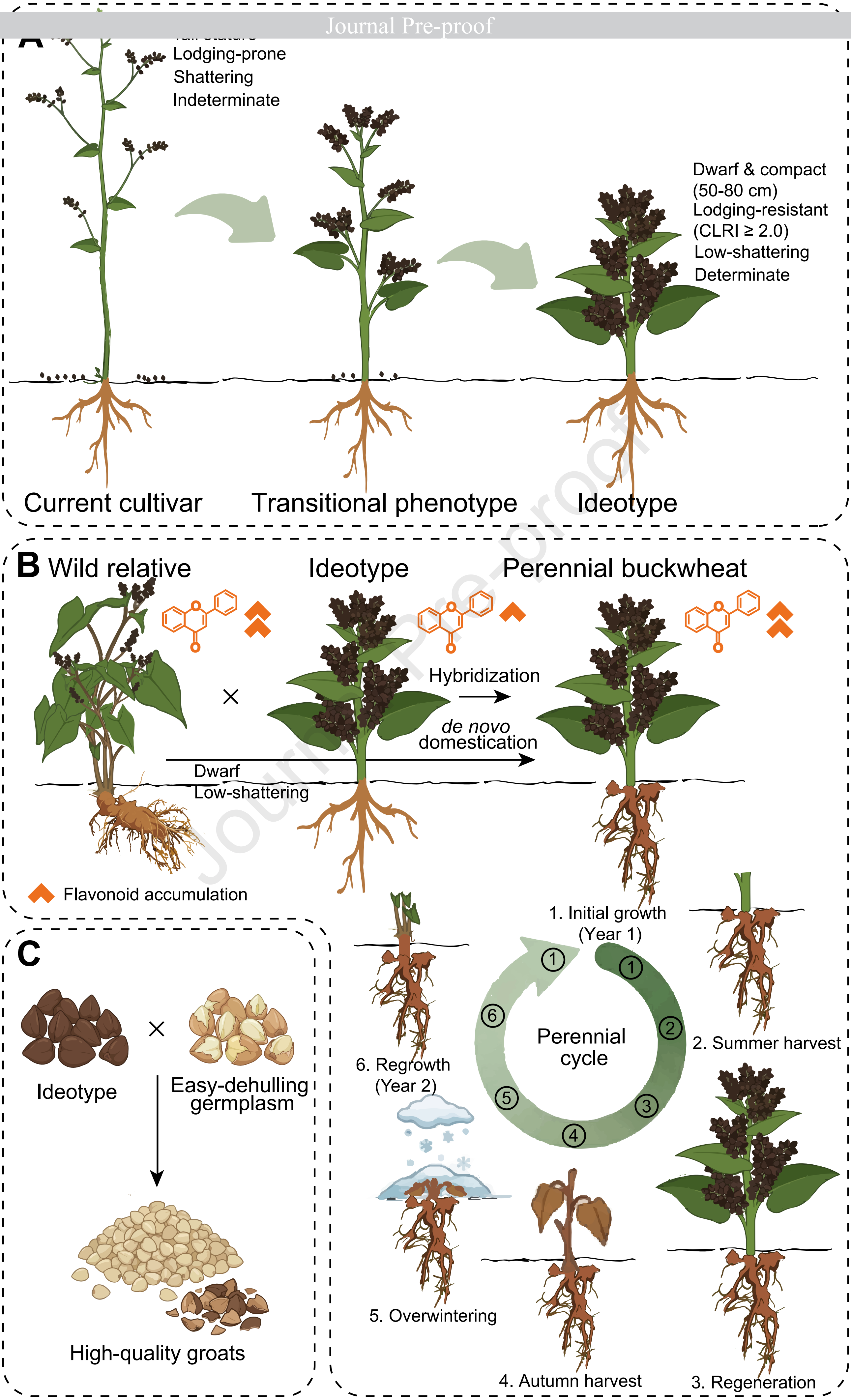
Figure legend

Figure 1. Breeding objectives and strategies for the genetic improvement of Tartary buckwheat (*Fagopyrum tataricum*).

(A) Transition from the current cultivar to an improved plant architecture (ideotype). The panel illustrates the progression from the "Current cultivar" (left) to the ideal "Ideotype" (right). The current cultivar is characterized by tall stature, lodging-prone stems, shattering and indeterminate inflorescences. In contrast, the proposed ideotype displays a dwarf and compact architecture, thicker lodging-resistant stems, low-shattering, and determinate inflorescences. The green arrows indicate the direction of genetic improvement.

(B) Breeding pathway toward perennial, high-flavonoid varieties. Two distinct strategies for utilizing crop wild relatives (CWRs) are depicted. The primary route involves interspecific hybridization between the ideotype and its wild relative. The wild relative contributes traits such as an enlarged rhizomatous root system and high flavonoid content (indicated by the increasing size of the orange molecule icons). Alternatively, as indicated by the labeled arrow, direct *de novo* domestication of CWRs offers another pathway to develop perennial buckwheat. The resulting perennial buckwheat combines a robust root system with substantially elevated flavonoid levels. The "Perennial cycle" diagram explicitly illustrates six key stages: (1) Initial growth in the first spring (Year 1); (2) Summer harvest; (3) Regeneration of new shoots (Ratooning); (4) Autumn harvest; (5) Overwintering of underground rhizomes; and (6) Regrowth in the subsequent spring (Year 2).

(C) Breeding pathway for easy-dehulling varieties. Hybridization between the ideotype and easy-dehulling germplasm enables the development of new varieties that combine high yield with improved processing quality. This pathway aims to produce high-quality groats (dehulled kernels) that are large and readily separated from the hull.


A
Lodging-prone
Shattering
Indeterminate
Dwarf & compact
(50-80 cm)
Lodging-resistant
(CLRI ≥ 2.0)
Low-shattering
Determinate
Current cultivar
Transitional phenotype
Ideotype
B Wild relative
Ideotype
Perennial buckwheat
×
Hybridization
de novo
domestication
Dwarf
Low-shattering
Flavonoid accumulation
C
Ideotype
×
Easy-dehulling
germplasm
High-quality groats
1. Initial growth
(Year 1)
2. Summer harvest
3. Regeneration
4. Autumn harvest
5. Overwintering
6. Regrowth
(Year 2)
Perennial
cycle
1
1
2
3
4
5
6