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RESEARCH ARTICLE

An ancient super allele of the *Vrs1* gene driving the recent success in modern barley improvement through optimising spike architecture

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Highlights

- A *deficiens* morphology-associated allele, *Vrs1.t1*, was identified with two F_2 populations.
- *Vrs1.t1* in two-rowed *deficiens* barley exhibited increased spikelet length, grain number and grain size.
- The *Vrs1.t1* originated in the Fertile Crescent and dispersed with the Neolithic migrations.

Abstract

Improved yield potential is the goal of barley domestication and cultivation. During this process, two- and six-rowed barley types emerged and have been utilised in breeding and production. The six-rowed type could produce three times as many grains as its ancestral two-rowed forms, thus dominating barley cultivation for thousands of years. The *deficiens* form of the two-rowed type, characterised by extremely suppressed lateral spikelets, has gained dominance over the past few decades in barley-growing regions worldwide. We hypothesised that the absence of lateral spikelets in *deficiens* barley affects spike architecture and spike-related traits, contributing to its superior yield potential of *deficiens* barley cultivation. Currently, a *deficiens* barley variety, RGT Planet, is the most popular barley variety in the world. In this study, we used two F_2 populations derived from crossing RGT Planet with two canonical two-rowed barley and identified the functional allele *Vrs1.t1* associated with *deficiens* morphology. We observed that the *Vrs1.t1* allele may contribute to high yield potential by optimising spike architecture through increased spikelet length, grain number, and grain size. Phylogenetic analysis suggests that the *deficiens* mutation was likely present from the early stages of barley cultivation in the Fertile Crescent and spread to Ethiopia and beyond with agricultural expansion. We conclude that the ancient *deficiens* allele *Vrs1.t1* has been a critical driver for the recent success of modern barley improvement by optimising spike architecture.

Keywords: *deficiens* barley, fine mapping, *Vrs1* gene, row types, spike architecture, yield potential

1. Introduction

Barley is the fourth-largest edible grain crop in the world, following wheat, rice, and maize. It is extensively used as human food, in beer production, and as animal feed (Geng *et al.* 2022). Barley is a staple food in highland regions, such as Ethiopia and the Tibetan Plateau, China (Langridge 2018; Lyu *et al.* 2022). Over the last few decades, barley has served as a model organism for crop development due to its simple diploid genome and the availability of many different morphological mutants (Druka *et al.* 2011). The spike (inflorescence) in cultivated barley consists of three spikelets at each rachis node. In the six-rowed form, all three spikelets are fertile and produce grains, while only the central spikelets are fertile in the two-rowed form (Sakuma *et al.* 2017). *Deficiens* barley has a two-rowed spike with extremely rudimentary lateral spikelets compared to the canonical two-rowed form (Sakuma *et al.* 2017). Archaeological evidence indicates that the earliest domesticated barley (*Hordeum*

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vulgare) with two-rowed spikes dates back approximately 10,000 years (Clark 1967). Six-rowed barley diverged from its two-rowed parent shortly after cultivation began, as the six-rowed form could produce three times as many grains as the ancestral two-rowed forms (Willcox 1998). Increased seed number per spike and grain size contribute to the high yield (Guo *et al.* 2024). Consequently, six-rowed barleys have dominated many barley-growing regions for thousands of years (Clark 1967). Contrary to the historical trend, the *deficiens* form has become increasingly dominant in production across the world's barley cultivation regions, including the UK, Europe, North America, and Australia, over the last few decades (Sakuma and Schnurbusch 2020). This shift is believed to be due to the increased size of grains in the central spikelets of the *deficiens* form (Sakuma *et al.* 2017). A *deficiens* barley, RGT Planet, is the most successful barley variety grown in over forty countries.

Genes that may enhance crop traits can be found in a species "accessory" genome (Jayakodi *et al.* 2020). The genomic era is rapidly shifting from reference genomes to pan-genome analyses. Pan-genomes in various crops enable the tracking of the inheritance of ancestral alleles in wild relatives or distant ancestors to cultivars (Naithani *et al.* 2023). The construction and use of the barley pan-genome can provide new insights into the analysis of domesticated genes, such as *Vrs1*, regarding their evolution and function. Meanwhile, three key elements-grain number, grain size, and spike length-compose the spike architecture, contributing to yield potential and stress tolerance in barley (Flavell 2022). Despite the increasing popularity of the *deficiens* type barley, the effect of the extreme inhibition of lateral spikelet development controlled by *Vrs1.t1* on other traits, such as grain number per spike and spike length, remains unclear; advancing this understanding is crucial for yield improvement.

The differences in floret fertility levels, and thus row types, in barley are controlled by at least five *Vrs* locus (six-rowed spike) loci, coded *Vrs*1-5 (Komatsuda *et al.* 2007). Mutations leading to loss of function in any of these five genes result in varying levels of fertile lateral spikelet development, with the loss of function of the *Vrs1* gene causing the growth of six-rowed spikes (with alleles *Vrs1.a*) instead of two-rowed spikes with functional alleles (*Vrs1.b)* (Komatsuda *et al.* 2007). The *deficiens* phenotype was attributed to the functional allele *Vrs1.t1* (Sakuma *et al.* 2017). Previous analyses revealed that barley carrying the *deficiens* allele (*Vrs1.t1*) was derived from two-rowed types carrying the *Vrs1.b2* alleles. It has also been reported that the six-rowed spike *vrs1.a2* allele was derived from the same *Vrs1.b2* allele through a single nucleotide mutation. *Deficiens* barley is believed to be endemic to Ethiopia (Sakuma *et al.* 2017; McKim *et al.* 2018). Some researchers speculate that the Horn of Africa may be a centre of barley diversification and a potential domestication site (Orabi *et al.* 2007), which remains controversial. Further elaboration on the origin and evolution of the allele *Vrs.t1* could strengthen our understanding of barley domestication and cultivation.

Sakuma *et al.* (2017) have speculated that the optimised morphology of the central spikelet may contribute to larger grains in the *deficiens* barley. In this study, we crossed an elite *deficiens* barley variety, RGT Planet, which possesses completely degenerated and absent lateral spikelets, with two canonical two-rowed Australian varieties, Fathom and Compass, that have normal lateral spikelets, to generate two F_2 populations. We aim to: 1) investigate the association between lateral spikelet development and spike-related traits, such as spike length and grains per spike; 2) identify the candidate gene and functional allele responsible for the degeneration of barley lateral spikelet through genetic mapping; 3) elaborate on the molecular mechanism of the *deficiens* gene and the pathway of its origin and evolution.

2. Material and methods

2.1. Plant materials

RGT Planet is a *deficiens* barley variety with a lateral spikelet degeneration phenotype. It was bred in France and developed in New Zealand. RGT Planet has become a leading variety in over forty countries worldwide due to its high yield potential and broad adaptability. Australia-bred barley varieties, Fathom and Compass, possess distinct lateral spikelets. This study generated and investigated two F_2 populations, using RGT Planet×Fathom (120 lines) and RGT Planet×Compass (270 lines) as the parental lines. Phenotypic data on lateral spikelet development were observed in both F_2 populations.

2.2. Phenotypic data collection

The two F_2 populations were planted in the greenhouse, receiving sufficient fertiliser and water throughout the growth period. The number of plants exhibiting lateral and normal spikelet degeneration was recorded at the heading stage. All phenotypic data were classified into two categories: lateral spikelet degeneration (LSD, recorded as "0") and normal lateral spikelet (normal SL, recorded as "1"). At the plant maturity stage, spike length was measured from the base of the rachis to the tip of the terminal spikelet, excluding the awns. The number of grains per spike was determined using the main spike for each plant, and the average results from the selected samples were employed in data analysis.

2.3. Genotyping and fine mapping analysis

A total of 75 InDel markers distributed across seven chromosomes were designed by the software Geneious 9.0.1 and selected to test the parental genotypes, including RGT Planet and Fathom, with 21 identified as having polymorphism (primer sequences are provided in Appendix A). The PCR reaction utilised these 21 InDel markers to detect the genotype of 120 plants from the F_2 population (RGT Planet/Fathom). For the markers with larger fragments inserted or deleted, the PCR products were separated by electrophoresis on a 2% agarose gel; otherwise, they were analysed through 6% polyacrylamide gel electrophoresis (PAGE). The results in gel photos were analysed by comparing the band positions to those of the RGT Planet marker. Bands with the same position as RGT Planet were recorded as "A", while those with different positions were labelled as "B". The closest marker related to the lateral spikelet trait was identified by calculating the correlation coefficient between 21 phenotypic markers and 120 lines from the F_2 population (RGT Planet/Fathom).

2.4. Genetic map construction

Each marker's genotype data labelled "A" and "B" was imported into JoinMap 4.0 software to analyze the linkage, recombination frequency, and genetic distance between markers. The population type was set to "F2," and the maximum likelihood mapping algorithm was applied with the base 10 logarithm of the ratio. The barley reference genome Morex version 3 sequence was used to validate the final map (Mascher *et al.* 2017).

2.5. Phylogenetic analysis

Coding sequences of the *Vrs1* gene were extracted from 76 barley accessions reported in recent research (Jayakodi *et al.* 2024). The barley accessions included wild barley, landraces, and cultivars, featuring both six- and two-rowed types, as well as *deficiens* barley such as RGT Planet. The sequences were aligned using CLC Genomics Workbench (Qiagen Pty Ltd., Denmark). The phylogenetic relationship of the *Vrs1* gene among the 76 barley accessions was constructed using a maximum likelihood approach with raxmlGUI 2.0 (Edler *et al.* 2020). The GTR substitution model was implemented for the phylogenetic reconstruction.

3. Results

3.1. Phenotypic variation of lateral spikelet in F_2 population

Each F_2 line and the two parents from two populations showed significant differences in the lateral spikelet trait. In 120 lines of the F_2 population from RGT Planet×Fathom, 89 plants exhibited degeneration of the lateral spikelet, while 31 plants had distinct lateral spikelets. In 270 lines of the F_2 population from RGT Planet×Compass, 196 plants lacked lateral spikelets, and 74 plants displayed distinct lateral spikelets. The Chi-square test revealed that the proportions of lateral spikelet types in both F_2 populations followed a 3:1 segregation ratio, suggesting that a single dominant gene governs the trait of lateral spikelet degeneration in RGT Planet.

3.2. Fine mapping of the lateral spikelet degeneration gene

A recombinant inbreeding population with 120 lines (F_2), developed by crossing Fathom with RGT Planet, was selected for fine mapping. Twenty-one of 73 pairs of primers across chromosomes 1H to 7H were designed and tested by PCR, showing polymorphism between Fathom and RGT Planet in preliminary mapping. Using the 21 polymorphic primers and eight lines with two-rowed side florets for correlation analysis, we located the *deficiens* mutation on chromosome 2H and near InDel2081 (R^2=0.82) (Fig. 1). Five more pairs of primers were then designed and tested with the entire recombinant inbreeding population, allowing us to further narrow down the *deficiens* gene to between InDel2069 (2H 565,361,874) and InDel2081(2H 590,383,499).

By using more markers and testing with the recombinant inbreeding lines population, we located the deficient gene between InDel2073 (2H 569,243,062) and InDelpr02 (2H 572,478,926) (Fig. 2-A and B). In this region, 29 candidate

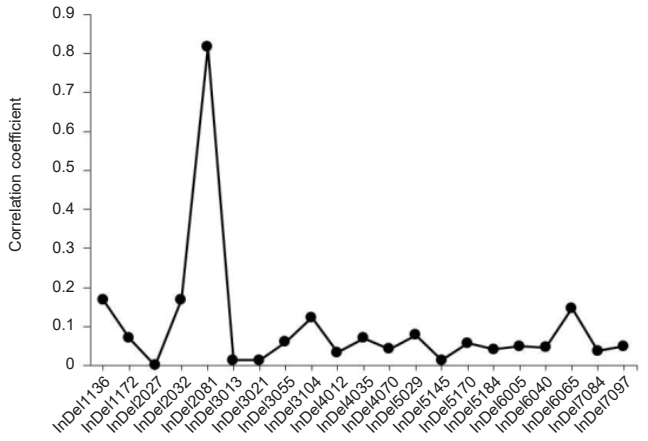


Fig. 1 Contribution of selected 21 polymorphic markers on lateral spikelet traits by correlation analysis.

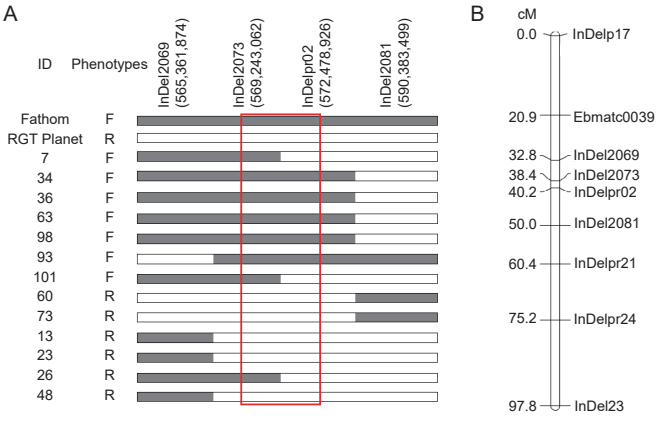


Fig. 2 Fine mapping the *deficiens* gene with recombinant inbreeding line population from crossing the canonical two-rowed Australian variety Fathom with the *deficiens* RGT Planet.

genes were identified and functionally annotated (Appendix B). One of these genes, *Vrs1*, was found to encode a protein containing a homeobox domain. The *Vrs1* gene has been reported to be associated with the development of lateral florets, determining the row type in barley. We sequenced the *Vrs1* gene in Fathom, Compass, and RGT Planet, revealing seven SNPs in this gene, with three SNPs located in the exon. At the same time, two of these SNPS were shared between RGT Planet and Compass (Fig. 3). Thus, the SNP (A/G) at 2H 570,802,479 is likely the mutation that results in rudimentary lateral spikelets in the *deficiens* barley RGT Planet. The A/G mutation is in exon 3, leading to an amino acid change from Ser (AGC) to Gly (GGC).

3.3. Effect of *Vrs1.t1* allele on yield-related traits

To examine the effects of the *Vrs1.t1* allele on yield traits, we investigated spike length and grain number per spike in both F_2 populations (Fig. 4). The spike length with lateral spikelet degeneration was 16.0% longer than that with normal lateral spikelets in the F_2 population of RGT Planet×Fathom and 11.7% longer in the F_2 population of RGT Planet×Compass. Furthermore, the number of grains

A

Genotype	570,801,107	570,801,173	570,801,191	570,801,727	570,801,906	570,802,269	570,802,479	570,802,699
Fathom	G	G	C	A	T	C	A	G
Compass	G	G	C	G	G	C	A	G
RGT Planet	C	T	T	G	G	T	G	T

B

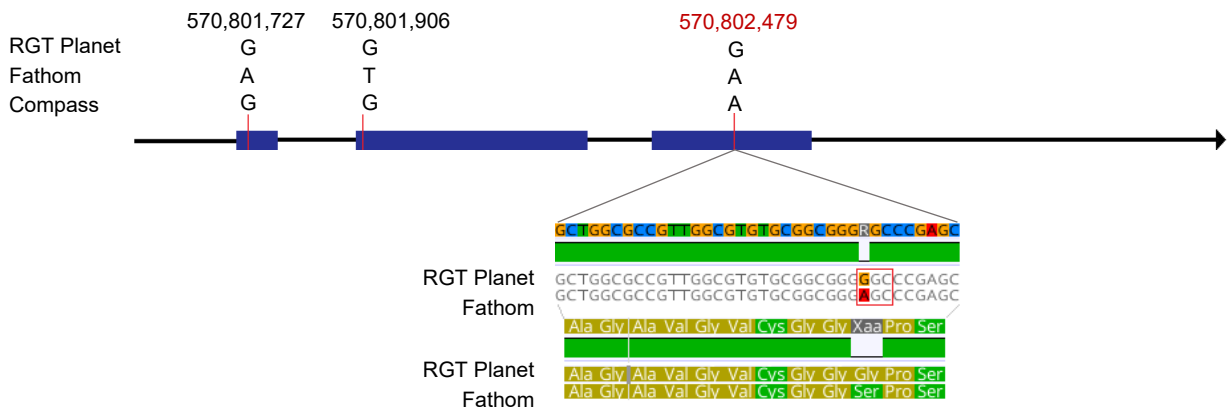


Fig. 3 The *Vrs1* gene in Fathom, RGT Planet, and Compass. A, the seven SNPs were revealed. Yellow highlights the three SNPs in the exon. B, the A/G mutation that causes an amino acid change from Ser (AGC) to Gly (GGC).

per spike with lateral spikelet degeneration was significantly higher than that with normal lateral spikelets, showing an 8.8% increase in the F_2 population of RGT Planet×Fathom and an 8.7% increase in the F_2 population of RGT Planet×Compass. These results indicate that lateral spikelet degeneration can enhance yield by contributing more assimilates to the central spikelet.

3.4. Origin of the *vrs1.t1* allele

To investigate the evolution of *Vrs1* alleles and the origin of *Vrs1.t1* between two- and six-rowed barley, we performed a phylogenetic analysis of the amino acid sequences from 76 barley accessions. Sequence alignment revealed that some *Vrs1* alleles in six-rowed barley had a single base deletion compared to two-rowed barley (Fig. 5), resulting in functionally deficient alleles (such as *Vrs1.a1-a4*). Most two- and six-rowed barley are classified into different clusters in the phylogenetic tree. However, a few six-row barley accessions, such as HOR4224, HOR495, and Aizu6, show a close genetic relationship with two-rowed barley, supporting the viewpoint that the six-rowed phenotype originated from two-rowed types multiple times in different regions and at different periods due to independent mutations in *Vrs1*. Interestingly, the single nucleotide variation (A/G) of the *Vrs1.t1* allele has been found not only in RGT Planet but also in the HOR13594 genotype from Yemen, which is also a *deficiens* type in spike morphology (Fig. 4). Moreover, the closest genetic relationship of these two *deficiens* barleys is to six-rowed barley genotypes from Middle East regions, rather than to the two-rowed type (Fig. 6), suggesting that *Vrs1.t1* may be as ancient as *Vrs1.a*. Phylogenetic analysis also indicates that there were two opposite mutation directions (from two- to six-rowed, or *vice versa*) in the *Vrs1* gene of barley in the Middle East region.

4. Discussion

4.1. *Vrs1.t1* improved yield by optimizing spike architecture

The impacts of the disappeared lateral spikelet in *deficiens* barley on the spike architecture and spike-related traits have been proposed as the driving force behind the recent surge in *deficiens* barley cultivation (Sakuma *et al.* 2017). In this study, we used two F_2 populations derived from crossing *deficiens* barley RGT Planet with two canonical two-rowed barley varieties, Fathom and Compass. We identified the functional allele *Vrs1.t1* associated with *deficiens* morphology. The *Vrs1.t1* allele has a single nucleotide mutation with an A/G substitution in exon 3 of the *Vrs 1 gene*, leading to an amino acid change (from serine to glycine) in the ser-rich motif, consistent with a previous report (Sakuma *et al.* 2017). We observed that the *Vrs1.t1* allele may contribute to high yield potential by optimising spike architecture with increased spikelet length, grain number, and grain size. Studies have reported that *deficiens* barley affects the grain size of central spikelets and may contribute to its higher yield potential of *deficiens* barley (Sakuma *et al.* 2017; Zwirek *et al.* 2019). Spike architecture directly influences grain yield (Zhang *et al.* 2022). Our results revealed that the degeneration of the lateral spikelet increases both spike length and grains per spike. Indeed, we found a 13.8% increase in spike length and an average rise of 8.7% in grains per spike in *deficiens* spikes. This could be explained by a change in the source–sink relationship or the removal of non-photosynthetic sink organs, as lateral spikelets in canonical two-rowed barley

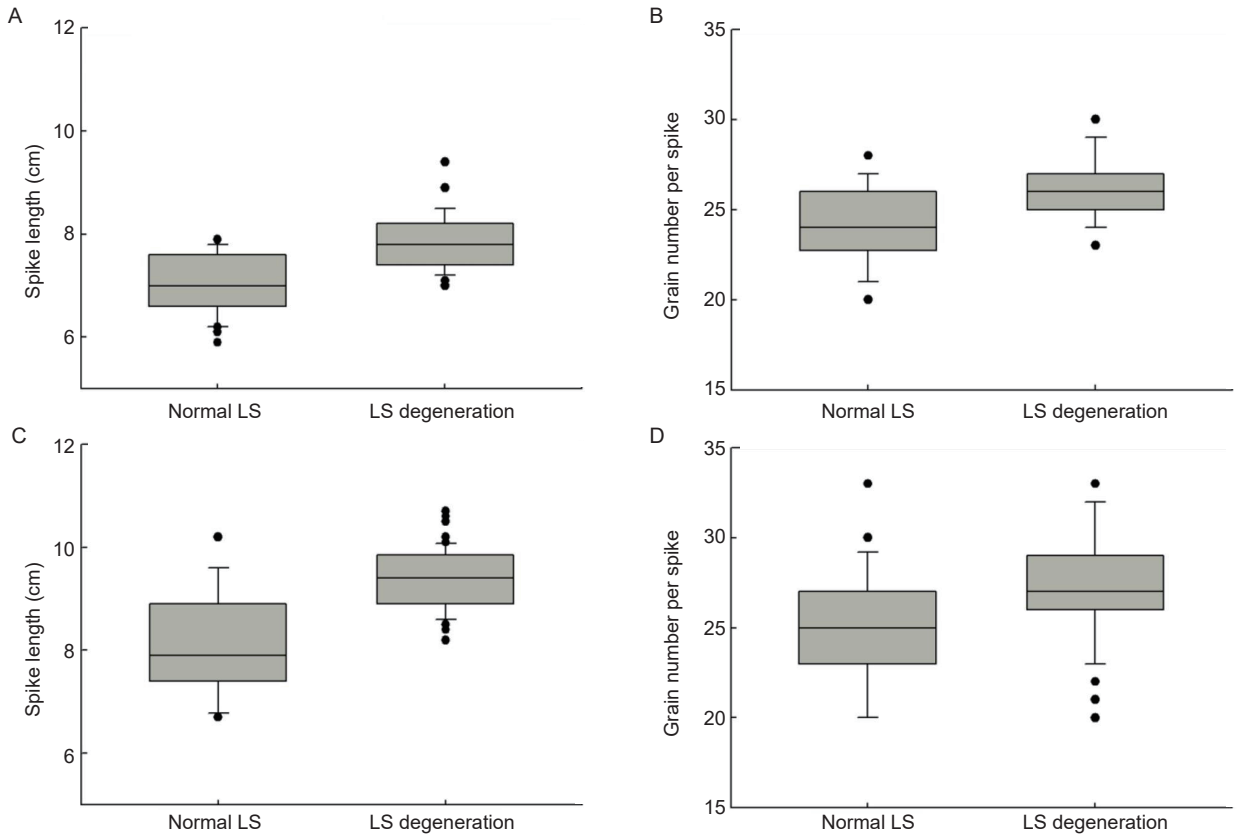


Fig. 4 Comparison of spike length and grain number per spike between barley with normal lateral spikelets (LS) and barley with lateral spikelet degeneration in the F_2 population of RGT Planet×Fathom (A and B) and RGT Planet×Compass (C and D). Boxplots represent the median (horizontal line), 25–75 quartiles (boxes), 5th and 95th percentile values (error bars) and outliers (dot).

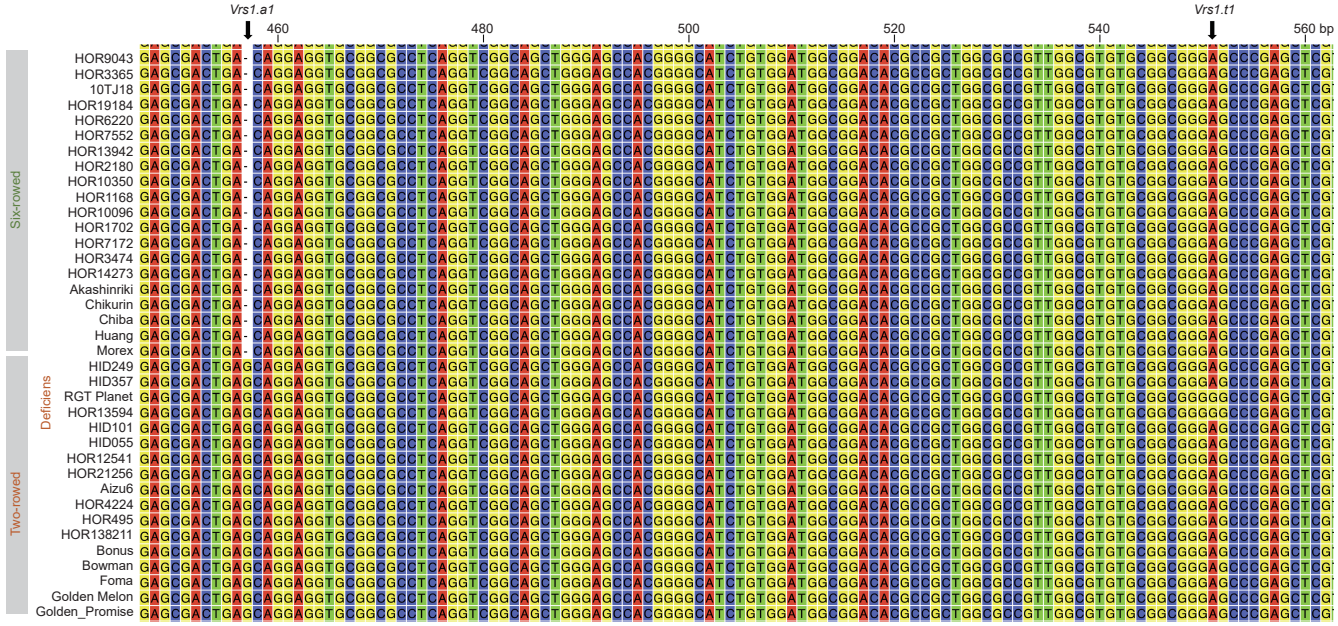


Fig. 5 Part alignment of *VRS1* gene in the pan-genome accessions showing the unique mutation (A/G) in the *deficiens* barley RGT Planet and HOR13594.

do not contribute to photosynthesis and are therefore considered assimilate consumers (Habgood and Chambi 1984). Optimised spike architecture could be achieved by suppressing the development of lateral spikelets that do not contribute to yield potential, thus enhancing yield capacity. Moreover, the grain hardness trait exhibited an opposite trend,

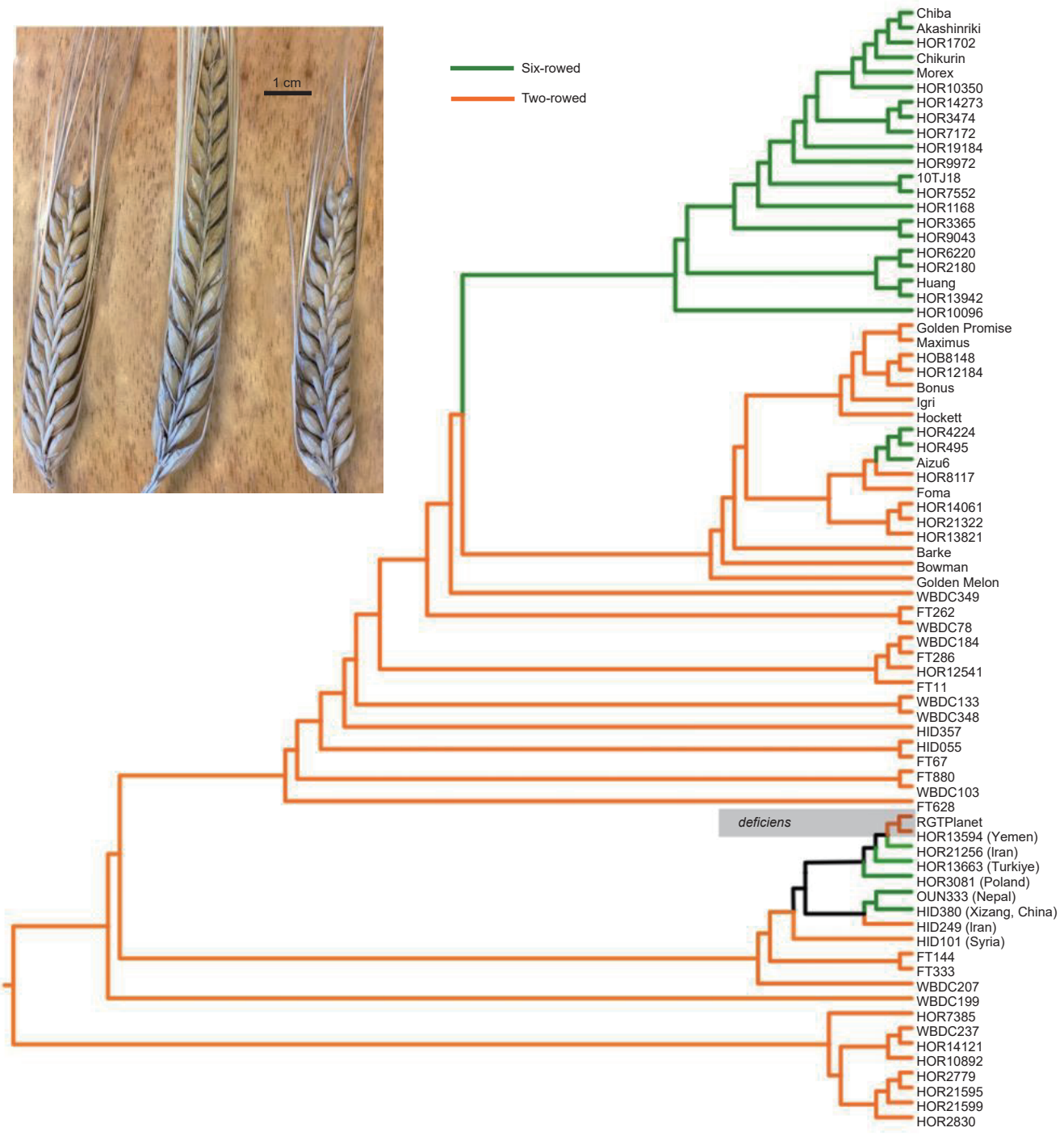


Fig. 6 Phylogenetic analysis of *Vrs1.t1* allele using 76 barley accessions.

with an 11% increase in six-rowed barley carrying the *Vrs1.1a* allele with a mutation in exon 3. This may be due to the concentration of compounds resulting from the smaller grain size. Consequently, we provide evidence suggesting that the *Vrs1* gene is closely associated with variations in grain-related traits, which could significantly impact yield potential.

4.2. *Vrs1.t1* allele analysis in translation and post-translational modification

The *Vrs1* gene encodes a transcription factor containing a homeodomain and a closely associated leucine zipper motif. *Vrs1* is a member of the homeodomain-leucine zipper (HD-Zip) family, which plays an essential role in plant development and morphogenesis. The HD-Zip family has been divided into four subfamilies (I–IV) based on DNA binding specificity and physiological functions (Sharif *et al.* 2020). HD-Zip III and IV are involved in the differentiation of epidermal cells, the development of shoot apical meristems, and the regulation of plant stems and leaves (Lin *et al.* 2024). HD-Zip I and II are considered to regulate plant development and resistance to environmental stress. *VRS1* in barley encodes a protein

belonging to HD-Zip I. Genes of HD-Zip I in *Arabidopsis* (Valdés *et al.* 2012) and rice (Zhang *et al.* 2012) are involved in phytohormone signaling to regulate biotic and abiotic stress tolerance or through gibberellin and auxin modulation to control plant height (Zhou *et al.* 2014; Liu *et al.* 2023). Hence, *Vrs1* in barley may potentially influence plant height, spike length, and stress tolerance by regulating plant hormones. Notably, the mutation site in the *Vrs1.t1* allele occurs in the carboxy-terminal region (CTR) with the ser-rich motif, affecting the translated protein's phosphorylation and polarity. Post-translational modifications (PTM), such as phosphorylation, could impact protein functionality, which regulates morphology and stress response processes (Abolore *et al.* 2020). The CTR region regulates gene transcriptional activation through phosphorylation and ubiquitination. The mutation may have disrupted phosphorylation, thereby affecting the development of lateral spikelets.

4.3. *Vrs1.t1* followed the routes of the Neolithic migrations

We utilised *Vrs1* gene sequences and phylogenetic reconstructions to trace the origin of *Vrs1.t1*. Sakuma *et al.* (2017) believed the A/G mutation in *Vrs1.t1* probably first occurred and became endemic in Ethiopia. However, examining the *Vrs1.t1* sequences among the pan-genome panel suggests that the mutation exists in HOR13954, a landrace from the Arabian Peninsula in Yemen (Fig. 4). The *deficiens* type has also been recorded in Iraq (Milner *et al.* 2019). The *Vrs1.t1* allele in RGT Planet shows close sequence similarity to HOR_13954 (two-rowed, Yemen), HOR13954 (six-rowed, Iran), and HOR13663 (six-rowed, Tuŕkiye) (Fig. 5). The *deficiens* mutation thus was likely present from the very early stages of barley cultivation since its domestication. Indeed, remains of two-rowed barley with the *deficiens* morphology were discovered from the Fayum deposits (*ca*. 4,550-4,350 BCE) in Egypt (Helback 1959). *Vrs1.t1* may have followed the routes of the great Neolithic migrations, as agriculture spread from western Asia southwards to Egypt and further reached Ethiopia, where the *deficiens* barley flourished. Currently, the *deficiens* two-rowed types are a significant spike type of winter barley grown in the UK and Europe (Sakuma *et al.* 2017) and are increasingly cultivated worldwide with the adoption of high-yield *deficiens* barley varieties such as RGT Planet. The pan-genome sequences revealed that the ancient allele *Vrs1.t1* has been one of the critical drivers of the recent success of modern barley improvement through optimising spike architecture.

5. Conclusion

Over the past few decades, the *deficiens* barley, a two-rowed type with extremely suppressed lateral spikelets, has gained dominance in barley-growing regions worldwide. We hypothesised that the absence of lateral spikelets alters spike architecture and spike-related traits, contributing to its superior yield potential of *deficiens* barley cultivation. Therefore, understanding the molecular basis of this phenotype could provide valuable insights for improving cultivated barley breeding strategies. In this study, we identified that an ancient allele *Vrs1.t1* was related to completely degenerated and absent lateral spikelets using two F_2 populations derived from crosses between RGT Planet 'Fathom and RGT Planet' Compass. Phenotypic analysis of both F_2 populations revealed that the *Vrs1.t1* increases the spikelet length, grain number and grain size, demonstrating its high yield potential. Finally, we employed phylogenetic analysis, which suggested that this ancient allele originated during the early stages of barley cultivation in the Fertile Crescent and subsequently spread to Ethiopia and other regions in conjunction with agricultural expansion.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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