Genome-wide identification of Gramineae histone modification genes and their potential roles in regulating wheat and maize growth and stress responses

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Abstract

Background: In plants, histone modification (HM) genes participate in various developmental and defense processes. Gramineae plants (e.g., Triticum aestivum, Hordeum vulgare, Sorghum bicolor, Setaria italica, Setaria viridis, and Zea mays) are important crop species worldwide. However, little information on HM genes is in Gramineae species.

Results: Here, we identified 245 TaHMs, 72 HvHMs, 84 SbHMs, 93 SvHMs, 90 SiHMs, and 90 ZmHMs in the above six Gramineae species, respectively. Detailed information on their chromosome locations, conserved domains, phylogenetic trees, synteny, promoter elements, and gene structures were determined. Among the HMs, most motifs were conserved, but several unique motifs were also identified. Our results also suggested that gene and genome duplications potentially impacted the evolution and expansion of HMs in wheat. The number of orthologous gene pairs between rice (Oryza sativa) and each Gramineae species was much greater than that between Arabidopsis and each Gramineae species, indicating that the dicotyledons shared common ancestors. Moreover, all identified HM gene pairs likely underwent purifying selection based on their non-synonymous (Ka)/synonymous (Ks) nucleotide substitutions. Using published transcriptome data, changes in TaHM gene expression in developing wheat grains treated with brassinosteroid, brassinazole, or activated charcoal were investigated. In addition, the transcription models of ZmHMs in developing maize seeds and after gibberellin treatment were also identified. We also examined plant stress responses and found that heat, drought, salt, insect feeding, nitrogen, and cadmium stress influenced many TaHMs, and drought altered the expression of several ZmHMs. Thus, these findings indicate their important functions in plant growth and stress adaptations.

Conclusions: Based on a comprehensive analysis of Gramineae HMs, we found that TaHMs play potential roles in grain development, brassinosteroid- and brassinazole-mediated root growth, activated charcoal-mediated root and leaf growth, and biotic and abiotic adaptations. Furthermore, ZmHMs likely participate in seed development, gibberellin-mediated leaf growth, and drought adaptation.

Keywords: Histone modification, Wheat and maize, Growth and development, Stress

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Background

In plants, epigenetic histone modification (HM) can activate or silence gene expression. HM genes play essential functions in various growth and development processes and stress responses, such as carotenoid biosynthesis, floral organ development, and fungal pathogen resistance [1–3]. In plants, HM depends on four kinds of enzymes, including histone methyltransferases (HMTs), histone demethylases (HDMs), histone acetylases (HATs), and histone deacetylases (HDACs) [4–7].

HMTs are mainly encoded by the SET DOMAIN GROUP (SDG) and protein arginine methyltransferases (PRMTs) genes [8]. Plant HMT genes are involved in shoot and root branching, hormone regulation, morphogenesis, circadian cycle, fungal pathogen resistance, and abscisic acid (ABA) and salt stress [9, 10]. Furthermore, in plants, HMT-mediated processes can be reversed by activation of HDM genes. The HDM gene family contains two gene subfamilies, i.e., SWIRM and C-terminal domain (HDMA) and JmjC domain-containing proteins (JMF) [11]. Studies on HDMs in plants have revealed their functions in chromatin regulation, brassinosteroid (BR) signaling, floral induction, pollen development, floral organ formation, and circadian cycle [12, 13]. Four types of genes (HAGs, HAMs, HACs, and HAFs) are recognized in the HAT gene family [14]. HAT genes participate in the transition from vegetative to reproductive growth, abiotic and biotic responses, and stress-related hormone signaling [15–18]. The HDAC family contains the RPD3/HDA1 (HDA), Silent Information Regulator 2 (SRT), and HD2 (HDT) subfamilies [19]. HDAC genes participate in vegetative and reproductive growth, stress adaptations, gene silencing, cell growth, and regeneration [20, 21].

Gramineous grain crops, including *Triticum aestivum*, *Hordeum vulgare*, *Sorghum bicolor*, *Setaria italica*, *Setaria viridis*, and *Zea mays*, are widely cultivated and provide important caloric intake for humans [22]. In Gramineae species, growth and development are closely related to grain yield and quality [23, 24]. Biotic and abiotic stresses markedly affect crop development and yield [25–30]. Although the functions of HMs in plant growth and environmental adaptations have been identified in some plant species [8, 18, 20], their characteristics and functions in *T. aestivum*, *H. vulgare*, *S. bicolor*, *S. viridis*, *S. italica*, and *Z. mays* remain unclear. The publication of the genomes of these species allows for the systematic characterization of HM genes via bioinformatics analysis.

In this study, 245, 72, 84, 93, 90, and 90 HMs were identified in the *T. aestivum*, *H. vulgare*, *S. bicolor*, *S. viridis*, *S. italica*, and *Z. mays* genomes, respectively. Their location on chromosomes, conserved domains, evolution, synteny, promoter sequences, and gene structures were analyzed. The expression patterns of *TaHMs* and *ZmHMs* in developing wheat grain and maize seed were investigated. Moreover, the responses of *TaHMs* to growth regulators (BR, brassinazole (BRZ), and activated charcoal (AC)) and to biotic and abiotic stresses (heat, drought, salt, insect feeding, nitrogen (N), and cadmium (Cd)) were explored, and changes in the expression profiles of *ZmHMs* after gibberellin (GA3) and drought treatment were also analyzed.

Results

Identification and characterization of HM genes in *T. aestivum*, *H. vulgare*, *S. bicolor*, *S. viridis*, *S. italica*, and *Z. mays*

*Arabidopsis* and rice (*Oryza sativa*) contain 102 and 92 HMs, including 48 and 42 HMTs, 24 and 24 HDMs, 12 and eight HATs, and 18 and 18 HDACs, respectively (Fig. 1a). In total, 245, 72, 84, 93, 90, and 90 HMs were identified in *T. aestivum*, *H. vulgare*, *S. bicolor*, *S. viridis*, *S. italica*, and *Z. mays*, respectively (Fig. 1a and b). The number of HMTs, HDMs, HATs and HDACs were broadly equal among the Gramineae species, except for *T. aestivum* (Fig. 1a). There were 2.4- and 2.7-fold as many wheat HMs (HMTs, HDMs, HATs, and HDACs) than *Arabidopsis* and rice HMs, respectively (Fig. 1a). There were 30–117 SDGs, 1–7 PRMTs, 3–12 HDMs, 11–48 JMIs, 1–6 HAGs, 1–3 HAMs, 3–10 HACs, 1–6 HAFs, 11–32 HADs, 1–6 SRTs, and 1–5 HDTs among all species (Fig. 1b). Furthermore, there were 3–8 *T. aestivum* SDGs (TaSDGs), 0–1 TaPRMT-TaHAG-TaHAM-TaSRT-TaHDT, 0–2 TaHDMAs-TaHACs-TaHAFs, 1–4 TaJMs, and 0–3 TaHADs on chromosome 1A-7D (Fig. 1c). One TaHAG and one TaSRT were located on an unknown chromosome (Fig. 1c).

The identified Gramineae HMs were named based on their chromosomal location (Fig. S1). For example, wheat chromosome 5A (Ta5A) contained the most HMs, followed by Ta2D (Fig. 1c and S1–1). Most barley HMs (HvHMs) were found on the longest chromosome 2 (chr2H), and HvSDG29, HvSDG30, and HvHDA14 were located on an unknown chromosome (Fig. S1–2). Sorghum SDGs (SbSDGs) were the most numerous among all HM genes, with 38 SbSDGs distributed on nine chromosomes, and chromosome 2 containing the most SbHMs (Fig. S1–3). Details on the Gramineae HMs are listed in Table S1. Their coding region (CDS) lengths ranged from 195 (HvHDT3) to 7008 (AtSADG2) bp, with the deduced polypeptides ranging from 64 to 2335 amino acids (aa).

Conserved domain and phylogenetic analyses of HM genes

Conserved HM domains were investigated, with various domains identified in the different HMs (Fig. S2). A total of 35 conserved motifs were identified in all *Arabidopsis*
and rice HMs (Fig. S2–1, Fig. S2–8, Fig. S2–9, Fig. S2–10, Fig. S2–17, Fig. S2–18, Fig. S2–19, Fig. S2–20, Fig. S2–21, Fig. S2–28, and Fig. S2–29). For example, one to seven domains were found in the AtSDG and OsSDG proteins (Fig. S2–1) and six conserved motifs were identified in all AtPRMTs and OsPRMTs (Fig. S2–8). Most conserved domains identified in *T. aestivum*, *H. vulgare*, *S. bicolor*, *S. italica*, *S. viridis*, and *Z. mays* were the same as those in AtHMs and OsHMs, but several distinct domains were found in the Gramineae HMs (Fig. S2–2, Fig. S2–3, Fig. S2–4, Fig. S2–5, Fig. S2–6, Fig. S2–7, Fig. S2–8, Fig. S2–9, Fig. S2–10, Fig. S2–11, Fig. S2–12, Fig. S2–13, Fig. S2–14, Fig. S2–15, and Fig. S2–16). For example, 51 elements were identified in TaSDGs, most of which were the same as those found in AtSDGs and OsSDGs (Fig. S2–2). Almost all JMJ proteins included JmjC or JmjN, and specific motifs were found in the Gramineae JMJs (Fig. S2–11, Fig. S2–12, Fig. S2–13, Fig. S2–14, Fig. S2–15, and Fig. S2–16).

To clarify the evolutionary relationships among HM genes, unrooted phylogenetic trees were constructed (Fig. S3). All AtHMTs (except AtSDG41), OsHMTs, and TaHMTs were classed into groups A–E, which were further subdivided (Fig. S3–1). All SDGs were clustered together in classes A–D and F–H, and PRMTs were divided into group E subgroups e1 and e2 (Fig. S3–2). In Fig. S3–3, AtPRMTs, OsPRMTs, and SbPRMTs were clustered together in group A, which could be divided into subgroups a1 and a2, and all SDGs (except for AtSDG41) were identified in groups B–G. AtPRMTs, OsPRMTs, and SbPRMTs were grouped in either class A or B, and the other HMTs were in classes C–H (Fig. S3–4). All *Arabidopsis*, rice, and *S. italica* SDGs were clustered together in groups B–E, with the exception of OsSDG738, SiSDG17, and SiSDG34, and PRMTs were all clustered in group A (Fig. S3–5). AtPRMTs-OsPRMTs-ZmPRMTs and AtSDGs-OsSDGs-ZmSDGs were clustered together in groups A and B–G (Fig. S3–6). In classes A, B, and D, the model and Gramineae JMJs were closely clustered, and HDMAs were divided into subclasses c1 and c2 in group C (Fig. S3–7). The evolutionary relationships among HATs were investigated (Fig. S3–8). HAGs were classified into groups B, C, and E, and HAFs, HAMs, and HACs were separately
divided into groups A, D, and F. HDTs and SRTs were clustered into groups A and B, while HDAs were found in groups C and D (Fig. S3–9).

**Synteny analysis of HM genes**
To identify expansion patterns in HM genes, duplicated blocks in each Gramineae genome were investigated, within which gene pairs were identified (Fig. S4). For example, 144 pairs of TaHMs were identified from 21 chromosomes (Fig. 2a and Fig. S4–1). Only four SbHM gene pairs (SbSDG16-SbSDG37, SbSDG22-SbSDG26, SbMJ1-SbMJ10, and SbHDA11-SbHDA5) were identified in the S. bicolor genome (Fig. 2a, b, and Fig. S4–2). A total of four types of SvHM gene pairs (i.e., four SvSDGs, two SvJMJs, one SvHAC, and two SvHDAs) were found (Fig. 2a, b, and Fig. S4–3). However, no HvHM gene pairs were identified (Fig. 2a and b).

We investigated the syntenic relationships among Gramineae and Arabidopsis HMs (Fig. 2c and Fig. S5). For example, one HMT gene pair (AtSDG24 and TaSDG97), four HDM gene pairs (AtMJ13 and TaMJ3, AtMJ13 and TaMJ7, AtMJ13 and TaMJ11, and AtMJ13 and TaMJ42), and one HDAC gene pair (AtHDA9 and TaHDA12) were identified between Arabidopsis and wheat (Fig. 2c and Fig. S5–1). Only AtSDG24 and SbSDG19 were found in the same Arabidopsis and S. bicolor gene pair (Fig. 2c and Fig. S5–2). No HM gene pairs were identified in Arabidopsis-barley and Arabidopsis-maize.

Various HM gene pairs were found between the rice and wheat genomes, including 62 pairs of HMTs (59 pairs of SDGs and three pairs of PRMTs), 25 pairs of HDMs (nine pairs of HDMAs and 16 pairs of JMJs), eight pairs of HATs (one pair of HAGs, three pairs of HAMS, three pairs of HACs, and three pairs of HAFs), and 16 pairs of HDACs (12 pairs of HDAs, two pairs of SRTs, and two pairs of HDTs) (Fig. 2d, e, and Fig. S6–1). Gene pairs between rice and other Gramineae species were also found (Fig. 2d, e, Fig. S6–2, Fig. S6–3, Fig. S6–4, Fig. S6–5, and Fig. S6–6). For example, a total of 27 pairs of OsHMs-HvHMs were
identified (Fig. 2d, e, and Fig. S6–2); different HM gene pairs were found between S. bicolor and rice, including 21 pairs of SDGs, three pairs of HDMAs, 10 pairs of JMs, two pairs of HAGs, one pair of HACs, PRMTs, and HAFs, six pairs of HDAzs, and two pairs of HDTs (Fig. 2d, e, and Fig. S6–3).

To evaluate selection pressure during duplication of the above gene pairs, their non-synonymous (Ka), synonymous (Ks), and Ka/Ks values were calculated. Data showed that the Ka/Ks values were all less than or generally equal to 1 (Tables S2, S3, S4). However, several gene pairs, such as SiJMJ5-SiJMJ19, AtJMJ13-TaJMJ3, and AtJMJ13-TaJMJ7, shared no non-synonymous mutations based on their Ks values.

Promoter and structural analyses of HM genes
HM genes play important roles in plant stress and defense responses [31, 32]. Various stress-related elements were identified in Gramineae HM genes (Fig. S7). For example, in the TaHMT, TaHDM, and TaHDAC genes, at least one absicic acid-, methyl jasmonate (MeJA)-, defense-, drought-, low temperature-, or salt-related element was uncovered (Fig. S7–1, 2, and 4). Furthermore, 2–13 stress-related motifs (defense/stress, absicic acid, and MeJA-responsiveness elements) were identified in the HvHMT genes. SbSDG3, SbSDG13, SbPRMT1, and SbJMJ16 only contained one defense/stress, absicic acid, or MeJA-responsiveness motif, whereas all other SbHMs included at least two stress-related elements (Fig. S7–6).

We next identified HM gene structures. In general, homologous HM genes, especially those in the same pair, shared similar structures, although gene lengths differed (Fig. S8). For example, most homologous TaHMT genes contained more than one CDS and were more than 3000 bp in length (Fig. S8–1). All HvHMTs, except for HvSDG4, shared a short non-coding sequence, and most were 2000–5000 bp in length (Fig. S8–3). Many SbHMTs (SbSDGs and SbPRMTs), SbHDAs (SbHDMAs and SbJMJs), SbHATS (SbHAGs, SbHAMs, SbHACs, and SbHAFs), and SbHDACs (SbHDAs, SbSRTs, and SbHDTs) consisted of short CDSs, but several genes contained one to two long CDSs (Fig. S8–9, 8–10, 8–11, and 8–12).

Expression patterns of TaHMs in developing wheat grain in response to BR and AC
To investigate the potential roles of HMs in wheat grain growth and development, we examined their expression profiles in the endosperm, inner pericarp, and outer pericarp (Fig. 3). Based on these expression patterns, TaHMs were divided into various clusters (Fig. 3a–d). In cluster 1, TaSDG53, TaSDG29, TaSDG56, and TaSDG61 were highly expressed in all tissues, especially in the inner pericarp. In cluster 2, several TaSDGs, such as TaSDG15, TaSDG103, and TaSDG21, were also highly expressed in the inner pericarp. In cluster 3, seven TaSDGs were found at relatively low levels in the outer pericarp. In clusters 4 and 5, TaSDGs showed lower expression levels than in the other clusters. In cluster 6, most genes were highly expressed in the inner and outer pericarps (Fig. 3a). The expression levels of TaHDMAs and TaJMs were generally low compared with other genes (Fig. 3b).

TaHATS were classified into two classes according to their expression patterns. Genes in cluster 1 were more highly expressed in all tissues than genes in cluster 2 (Fig. 3c). In clusters 3 and 4, TaHDAs, TaSRT3, and TaSRT5 were highly expressed in the pericarps (Fig. 3d).

In Arabidopsis, rice, wheat, and maize, BR plays an important role in root growth, including lateral root initiation and hair formation [33–36]. BR treatment significantly increases the number of lateral roots in wheat, but inhibits root length and diameter, whereas the BR synthesis inhibitor BRZ shows the opposite roles on lateral root number and root diameter [33]. Although HM genes are known to regulate various developmental processes, information on their roles in regulating wheat root is scarce. In this study, we analyzed HM gene expression profiles during BR- and BRZ-mediated root growth (Fig. 4). In cluster 2, TaSDG4, TaSDG23, TaSDG55, and TaSDG112 showed a 2-fold increase after BR treatment, whereas, in cluster 1, BRZ treatment repressed TaSDG26, TaSDG68, TaSDG89, TaSDG92, TaSDG95, TaSDG103, and TaJM5 expression (Fig. 4a). BR treatment increased the expression of more than 10 TaHMs (especially TaJM5 and TaSDG28), while BR1 and BR2 exposure inhibited the expression of several other TaHMs (Fig. 4b and c). For example, TaSDG26, TaSDG28, and TaJM5 were induced by BR1 and BR2 treatment; TaSDG92 and TaSDG101 were up-regulated by BR2 treatment; and TaJM21, TaSDG53, and TaHDA18 were repressed by both BR1 and BR2 treatment.

In plant culture, AC is widely used to promote seedling growth [37]. Notably, AC treatment promotes wheat seedling growth, accompanied by an increase in soluble protein, root activity, and total phenol and sugar content [37]. Here, we found that 26 and 31 TaHMs were differentially expressed in roots and leaves after AC treatment, respectively (Fig. 5), with an almost equal number down-regulated and up-regulated by AC treatment. For example, after AC treatment, TaSDG68 and TaSDG84 showed a 4- and 8-fold decrease in the roots and leaves, respectively; TaSDG55 was increased in the roots; and TaJM21 was up-regulated in the leaves (Fig. 5a and b).

Responses of TaHMs to abiotic and biotic stresses
To explore whether TaHMs respond to abiotic stresses, we analyzed their expression levels after heat stress
(HS), drought stress (DS), and heat stress (HD) treatment using previously published RNA-seq data [38]. In total, 86 TaHMT genes (83 TaSDGs and three TaPRMTs) were differentially expressed at 1 or 6h after the different treatments (Fig. 6a). These TaHMT genes could be divided into six clusters based on their transcription patterns. In cluster 1, almost all TaSDGs were induced and repressed by DS at 1 and 6h, respectively, and were up-regulated by HD at 6h. In cluster 2, 20 TaSDGs were obviously increased at 6h after HS and HD treatment, but were decreased at 1h, and several TaSDGs were clearly induced or inhibited by DS. In cluster 3, TaSDGs were generally induced by both HS and HD at 6h but were suppressed at 1h in the HS and HD groups, and increased at 1 and 6h in the DS group. All TaHDMs were divided into four clusters (Fig. 6b). In cluster 1, TaMJ21 was highly expressed after HS and HD treatment, and increased at 1h following DS treatment. In cluster 2, TaJM7, TaMJ11, and TaMJ3 were generally up-regulated by DS and HD at 1h, whereas other genes were generally up-regulated at 6h after HS and HD treatment. TaHATs were clustered into two classes (Fig. 6c). In cluster 1, TaHAG1, TaHAG2, and TaHAG5 were increased after HS and HD treatment. In cluster 2, TaHAM2 and TaHAM3 were obviously up-regulated at 6h in the HS and HD groups, and other genes were induced by HS, DS, or HD at least at one time point. As shown in Fig. 6d, TaHDA4, TaHDA17, and TaSRT2 were induced by DS in cluster 1, and TaHDA4 was also increased in the HS group. DS treatment increased the expression levels of 10
Fig. 4 Expression analysis of TaHMs in response to BR and BRZ. 

- **a** Differentially expressed TaHMs between BRZ-treated and control groups.
- **b** Differentially expressed TaHMs between BR1-treated and control groups.
- **c** Differentially expressed TaHMs between BR2-treated and control groups.

BR1, 50 nM EpiBL; BR2, 1 mM EpiBL; BRZ, 1 mM BRZ. FC: fold-change

Fig. 5 Expression pattern analysis of TaHMs in response to AC.

- **a** Differentially expressed TaHMs between AC (R10AC) and control (R10) groups in roots of 10-day-old seedlings.
- **b** Differentially expressed TaHMs between AC (L10) and control (L10AC) groups in leaves of 10-day-old seedlings. FC: fold-change
In cluster 1, TaHAC8 were mainly regulated (Fig. 7b). Six genes were obviously induced by SS treatment at least one time point (Table 1). In both the CS and QM, TaJMJ38 were induced by SS treatment at most time points. The SS treatment most significantly induced TaHMs at least one time point in both the CS and QM groups after SS treatment. Most TaHDM genes were up-regulated by SS from 6 to 24h in cluster 1. Genes in cluster 2 were induced by SS treatment at most time points. The transcripts of TaJMJ18, TaJMJ27, TaJMJ23, TaJMJ25, TaJMJ28, TaJMJ44, and TaJMJ48 increased from 12 to 48h after SS treatment in cluster 3. In both CS and QM, six TaHMs were obviously induced by SS in cluster 4 (Fig. 7b). TaHATs were divided into two clusters (Fig. 7c). In cluster 1, TaHAC8 and TaHAC10 were mainly regulated by SS in CS, and TaHAF4, TaHAG3, and TaHAC6 were induced by SS in both the CS and QM cultivars. In cluster 2, SS treatment increased the expression levels of TaHACs and TaHAGs, especially TaHAC1 and TaHAC2, at every time point (Fig. 7c). The expression levels of TaHDACs, especially genes in cluster 3, were also markedly increased at least one time point after SS treatment (Fig. 7d).

Wheat pests Sitobion avenae and Schizaphis graminum can increase yield losses [39]. Compared with the non-phytotoxic aphid S. avenae, feeding by phytotoxic aphid S. graminum causes more severe damage in wheat leaves [40]. N is an essential macronutrient for plant growth and development, and low N stress can repress wheat leaf and root growth [40]. In addition, Cd can inhibit leaf photosynthesis, carbon and N metabolism, and wheat growth and yield [41]. To clarify how TaHMs respond to biotic, nutritional, and heavy metal stress, their expression patterns were obtained from previous transcriptome research [39–41]. In our study, TaJMJ7 increased 3.4- and 4-fold after S. avenae and S. graminum feeding, respectively; TaJMJ11 was induced by S. avenae infection; TaJMJ40 and TaJMJ42 increased in the S. graminum feeding group compared with the control; and TaHDA17, TaSDG73, TaHDA20, TaSDG81, TaHDA22, and TaSDG89 were distinctly controlled following S. graminum feeding (Table 1). In addition, N stress suppressed TaSDG73 and TaHDA20 expression in the leaves, but up-regulated TaJMJ11 and TaJMJ3 in the roots (Table 1). Furthermore, Cd treatment induced a 2.2- to 6.4-fold increase in the expression levels of 12 TaHMs (e.g., TaSDG13, TaJMJ28, and TaHDT1) in the roots but decreased the expression of TaSDG102 (Table 1).

Diverse responses of TaHMs to growth and stress signaling
To investigate the multiple functions of TaHMs in wheat growth and stress adaptations, a Venn diagram was constructed with the above identified DEGs (Fig. 8). The DEGs were clustered into six sets, including the BR or BRZ (BR-BRZ) class, AC class, heat or drought (heat-drought) class, salt class, S. avenae or S. graminum (Sa-Sg) class, and N or Cd (N-Cd) class (Fig. 8 and Table S5). Some TaHMs were simultaneously respond to various signals, while several ones were only regulated by single clue. For example, two TaHMs (TaSDG68 and TaJMJ5) were concurrently in response to BR-BRZ and AC; the expression patterns of TaSDG95 and TaSDG103 were altered by both BR-BRZ and salt treatment; and 72 TaHMs simultaneously responded to heat, drought, and salt stress. We found that TaSDG13 and TaJMJ28 were common DEGs after AC, heat-drought, salt, and N-Cd treatment. TaJMJ34 was commonly induced or repressed by BR-BRZ, AC, heat-drought, salt, and N-Cd treatment. In total, 55, 23, five, and two TaHMs responded to heat-drought, salt, AC, and BR-BRZ, stress, respectively (Fig. 8 and Table S5).

Expression analysis of ZmhMs in developing seed and response to GA treatment
To investigate the functions of ZmhMs in maize growth and development, we analyzed the expression profiles of ZmhMs in different seed growth stages of B73 and SWL01 cultivars (Fig. 9a and b). The SWL01 cultivar is a mutant of B73 and shows higher viscosity [42]. From 0 to 24days (d) after pollination (DAP), 80 ZmhM genes were clustered into five classes (Fig. 9a). During the whole experimental period (especially at 2 DAP), ZmSDG36 in cluster 1 showed higher expression than...
Fig. 6 (See legend on previous page.)
genes in other classes. In cluster 2, ZmHMs showed higher expression at the early stages (from 0 to 8 DAP) than during the later periods (from 16 to 24 DAP). In cluster 3, 11 ZmHMs were highly expressed at all stages, especially from 0 to 4 DAP. There were 81 ZmHM genes detected during SWL01 seed development (Fig. 9b). Like genes in B73, these ZmHMs were distributed into five clusters in SWL01. For example, ZmHMs in clusters 1 and 2 (especially cluster 2) were mainly expressed at 0, 2, and 4 DAP. ZmHMs, such as ZmSDG29, ZmSDG36, ZmSDG40, and ZmHDA1, showed higher expression levels in cluster 3 than genes in other clusters. A total of 79 ZmHMs were commonly expressed in both B73 and SWL01 seeds, but most showed different expression patterns between the two cultivars. A total of 79 ZmHMs were commonly expressed in both B73 and SWL01 seeds, but most showed different expression patterns between the two cultivars. For example, ZmSDG41 expression was higher in B73 than in SWL01; ZmHAF1 gradually decreased over time in B73 but showed almost no change in SWL01 (Fig. 9c). GA3 application significantly promoted leaf sheath growth of D11 [43]. Seven ZmHM genes were differentially expressed between the GA and control groups (Fig. 9d). In cluster 1, ZmH-DMA3, ZmHDA10, ZmMJM10, and ZmSDG10 were down-regulated by GA, whereas ZmHDA12, ZmHDA3, and ZmSDG33 were up-regulated.

Expression analysis of ZmHMs in response to drought stress
To identify the potential roles of ZmHMs in drought adaptation, their expression patterns were analyzed in drought-tolerant cultivars (ND476 and H082183), drought-sensitive cultivars (ZX978 and Lv28), and C7–2 (Table 2). In total, 10 ZmHMs were identified as DEGs in response to drought stress. After drought treatment, the transcription level of ZmMJM2 showed a 6-fold increase in ND476 compared with ZX978, whereas ZmHDA11 was repressed in ND476. ZmSDG5, ZmMJF4, and ZmSDG24 were induced by drought treatment in C7–2, but ZmSDG33 and ZmMJM17 were controlled. In Lv28 and H082183, ZmMJM5 was up-regulated under both moderate and severe drought treatment. The expression level of ZmSDG1 increased in H082183 after moderate drought treatment, whereas ZmHDA2 was markedly down-regulated after severe drought treatment.

Discussion
Although HM genes are known to play essential roles in plant growth and biotic and abiotic stress in model plants [8, 18, 20], little information has been reported for Gramineae species. Here, we systematically characterized
TaHMs, HvHMs, SbHMs, SvHMs, SiHMs, and ZmHMs, including information on their gene location, conserved domains, gene phylogeny, gene expansion, synteny, promoter cis-elements, and gene structure. Moreover, we analyzed their expression levels in wheat and maize in regard to growth and stress adaptations. These findings will provide a basis for further functional analyses of HM genes.

Comparison of HM genes between Gramineae and model plants

Based on previous research, there are 48 AtHMTs, 24 AtHDMs, 12 AtHATs, and 18 AtHDACs in Arabidopsis [17, 19] and 92 OsHMs, including 42 OsHMTs, 24 OsHDMs, eight OsHATs, and 18 OsHDACs in O. sativa [44].

In the six Gramineae plants, we identified 245 TaHMs (120 TaHMTs, 60 TaHDMs, 24 TaHATs, and 41 TaHDACs), 72 HvHMs (31 HvHMTs, 15 HvHDMs, seven HvHATs, and 19 HvHDACs), 84 SbHMs (39 SbHMTs, 21 SbHDMs, seven SbHATs, 17 SbHDACs), 93 SvHMs (41 SvHMTs, 22 SvHDMs, 12 SvHATs, and 18 SvHDACs), 90 SiHMs (43 SiHMTs, 24 SiHDMs, seven SiHATs, and 16 SiHDACs), and 90 ZmHMs (42 ZmHMTs, 20 ZmHDMs, 10 ZmHATs, and 18 ZmHDACs) (Fig. 1). In terms of gene number, we found 2.4- and 2.6-fold greater number of TaHMs than AtHMs and OsHMs, respectively. TaSDGs, TaHDMAs, TaJMJs, TaHAGs, TaHMs, TaHACs, TaHAFs, TaHDAs, and TaSRTs were increased 1.5–3-fold. However, the number HM genes in other species varied slightly compared with those in the model plants (Fig. 1a and b). In wheat, a total of 144 gene pairs were identified in 10 kinds of HM genes, but there were 4–14 HM gene pairs among S. bicolor, S. viridis, S. italica, and Z. mays, and no gene duplication in H. vulgare. Genome duplication occurs during species evolution [45], and the wheat genome contains three homologous subgenomes [22]. Therefore, the expansions in wheat HM genes may be associated with gene and genome duplications during evolution.

In general, Gramineae, Arabidopsis, and rice HM genes shared similar domains (Fig. S2), although there were several exceptions. For example, TaSDGs, HvSDGs, ZmSDGs, TaJMJs, and ShJMJs contained 15, two, 10, 14, and eight special motifs, respectively (Fig. S2–2, 2–3, 2–7, 2–11, and 2–13). As new functions can be predicted from unique domains, greater attention should be paid to those

**Table 1** Expression analysis of TaHMs during different biotic and abiotic stresses

| Gene          | Sa/C       | Sg/C       | N/C_leaf | N/C_root | Cd/C |
|---------------|------------|------------|----------|----------|------|
| TaJMJ7        | 3.46054762 | 4.06182894 | Nan      | Nan      | Nan  |
| TaJMJ11       | 4.25128801 | Nan        | Nan      | 3.242752801 | Nan |
| TaJMJ40       | Nan        | 176.8521564| Nan      | Nan      | Nan  |
| TaJMJ42       | Nan        | 12.76303914| Nan      | Nan      | Nan  |
| TaHDA17       | Nan        | 0.19218931 | Nan      | Nan      | Nan  |
| TaSDG73       | Nan        | 0.095377977| 0.1224898| Nan      | Nan  |
| TaHDA20       | Nan        | 0.198773867| 0.114219114| Nan | Nan |
| TaSDG81       | Nan        | 0.109196612| Nan      | Nan      | Nan  |
| TaHDA22       | Nan        | 0.161925264| Nan      | Nan      | Nan  |
| TaSDG89       | Nan        | 0.06737233 | Nan      | 3.68753184 | Nan |
| TaJM3         | Nan        | Nan        | Nan      | 6.470609988| Nan |
| TaSDG13       | Nan        | Nan        | Nan      | 4.03956068 | Nan |
| TaSDG100      | Nan        | Nan        | Nan      | 0.265806191| Nan |
| TaSDG102      | Nan        | Nan        | Nan      | 4.300055702| Nan |
| TaSDG66       | Nan        | Nan        | Nan      | 3.36746059| Nan |
| TaSDG74       | Nan        | Nan        | Nan      | 3.12760118| Nan |
| TaSDG112      | Nan        | Nan        | Nan      | 3.248304936| Nan |
| TaSDG82       | Nan        | Nan        | Nan      | 2.966738703| Nan |
| TaSDG106      | Nan        | Nan        | Nan      | 2.971222851| Nan |
| TaSDG62       | Nan        | Nan        | Nan      | 2.453364919| Nan |
| TaJM34        | Nan        | Nan        | Nan      | 2.228164872| Nan |
| TaSDG87       | Nan        | Nan        | Nan      | 2.353792646| Nan |
| Sa S. avenae, Sg S. graminum, N nitrogen stress, Cd cadmium stress, Control |
genes sharing special elements in the future. According to phylogenetic analysis, each type of HM gene was clustered together (Fig. S3), although there were exceptions. For example, AtSDG41, HvSDG4, SiSDG17, SiSDG34, and OsSDG738 shared a close relationship with PRMTs other than SDGs (Fig. S3–1, 3–2, and 3–5). This may be due to their incompletely matching protein sequences.

To better understand Gramineae HMs, duplicated blocks between model plants and Gramineae were determined. In this study, 13 orthologous genes were identified between Arabidopsis and the six Gramineae species (Fig. S5 and Table S3), and 389 rice-Gramineae gene pairs were found (Fig. S6 and Table S4), indicating that these gene pairs shared common ancestors. Gene pairs showed considerable differences between Arabidopsis-Gramineae and rice-Gramineae in terms of number, which may be due to the diversity in evolutionary history between monocotyledons and dicotyledons. Several AtHMs and OsHMs are involved in plant growth and stress responses [9, 10, 12, 15–17, 20, 21, 46–48]. Although many unknown Gramineae HMs could be inferred from the orthologous genes of model plants, these predictions must be confirmed in future experiments. Gene evolution mode can be determined through Ka/Ks values. Here, the Ka/Ks ratios of all gene pairs were less than 1, indicating purifying selection [49].

Potential functions of TaHMs and ZmHMs in plant growth and stress responses

Like transcription factors, HMs are important regulators of many biological processes, including plant growth and development [1–3]. We proposed that TaHMs and ZmHMs share similar roles with known HMs. Candidate TaHMs involved in wheat grain development and ZmHMs involved in maize seed development were characterized in this study. Expression patterns showed that almost all TaHMs (especially TaSDGs in cluster 1 (Fig. 3a), TaHDMs in cluster 3 (Fig. 3b), TaHATs in cluster 1 (Fig. 3c) and TaHDACs in cluster 4 (Fig. 3d)) were expressed in developing wheat grains, and many genes were highly expressed in specific grain tissue layers (Fig. 3). About 80% ZmHMs showed different expression
Fig. 9 Expression profiles of ZmHMs in developing seeds and in response to GA signaling. 

- **a** Expression profiles of ZmHMs in developing B73 seeds. 
- **b** Expression profiles of ZmHMs in developing SWL01 seeds. 
- **c** Venn analysis of genes expressed in B73 and SWL01 seeds. 
- **d** Differentially expressed TaHMs between GA-treated and control groups. FPKM: fragments per kilobase per million. FC: fold-change.

Table 2 Expression analysis of ZmHMs during different drought stresses

| Gene_id     | TD/SD | CD/CC | LMD/LMC | LSD/LSC | HMD/HMC | HSD/HSD |
|-------------|-------|-------|---------|---------|---------|---------|
| ZmJMJ2      | 6.086 | Nan   | Nan     | Nan     | Nan     | Nan     |
| ZmHDA11     | 0.249 | Nan   | Nan     | Nan     | Nan     | Nan     |
| ZmSDG5      | Nan   | 9.388824371 | Nan     | Nan     | Nan     | Nan     |
| ZmJMJ4      | Nan   | 3.074936123 | Nan     | Nan     | Nan     | Nan     |
| ZmSDG24     | Nan   | 2.363578856 | Nan     | Nan     | Nan     | Nan     |
| ZmSDG33     | Nan   | 0.457540122 | Nan     | Nan     | Nan     | Nan     |
| ZmJMJ17     | Nan   | 0.390122323 | Nan     | Nan     | Nan     | Nan     |
| ZmJMJ5      | Nan   | Nan   | Nan     | Up      | Nan     | Up      |
| ZmSDG1      | Nan   | Nan   | Nan     | Up      | Nan     | Up      |
| ZmHDA2      | Nan   | Nan   | Nan     | Nan     | Nan     | Down    |

TD tolerant cultivar ND476 drought treatment, SD sensitive cultivar ZX978 drought treatment, CD C7–2 drought treatment, CC C7–2 control, LMD Lv28 moderate drought treatment, LMC Lv28 control, LSD Lv28 severe drought treatment, LSC Lv28 control, HMD H082183 moderate drought treatment, HMC H082183 control, HSD H082183 severe drought treatment, HSC H082183 control.
patterns in developing maize seeds (Fig. 9a and b). Several ZmHMs genes specifically expressed in B73 (ZmSDG23) or SWL01 (ZmSDG14 and ZmJMJ4) were found (Fig. 9c). In addition, several commonly expressed ZmHMs between B73 and SWL01 were found but showed varied expression patterns (Fig. 9c). Moreover, seed-specific motifs of ZmHMs were identified. These findings suggest that TaHM genes affect grain growth and development, most ZmHMs genes play roles in wax and regular maize seed development, and several ZmHMs genes specifically participate in regulating seed viscosity.

BR is an essential plant hormone and stimulates wheat root hair formation and lateral root initiation [33]. However, responses of TaHMs to BR and BRZ are not known. In this study, four TaSDGs were induced by BRZ, but six TaSDGs as well as TaJMJ5 and TaHDA14 were repressed (Fig. 4a). In addition, BR respectively increased or decreased the expression of 11 TaHMs (Fig. 4b). We also found that GA treatment stimulated leaf sheath elongation of maize seedlings and altered the expression of seven ZmHMs (Fig. 9d). The above results indicate that these TaSDGs and ZmSDGs are likely involved in BR-mediated root growth and GA-mediated leaf development. AC is a positive growth regulator in wheat culture [37]. However, the relationship between TaHMs and AC is unclear. Here, 26 TaHMs were differentially expressed between the control and AC-treated roots, with about half repressed or induced by AC, respectively (Fig. 5a). In leaves, 16 TaHMs were regulated by AC, with 15 found to be highly expressed (Fig. 5b). Thus, these up- and down-regulated TaHMs are speculated to play important roles in AC-promoted wheat seedling growth.

In addition to their important functions in growth, HM genes also play essential roles in plant defenses [9, 17, 21, 46]. Here, TaHM-mediated stress responses were explored (Figs. 6–7 and Table 1). In total, 86 TaHMTs were differentially expressed after HS, DS, or HD treatment (Fig. 6a), and 45 TaHDMs, 20 TaHDAs, and 27 TaHDTs were induced by stress treatment (Fig. 6b-d). In response to SS, almost all TaHMs were increased, especially TaSDGs in cluster 3 (Fig. 7a), TaJMJ5 in cluster 4 (Fig. 7b), TaHADs in cluster 2 (Fig. 7c), and TaHDACs in cluster 3 (Fig. 7d). The expression patterns of 10 TaHMs, including TaSDG73, TaSDG81, TaSDG89, TaJMJ7, TaJMJ11, TaJMJ40, TaJMJ42, TaHDA17, TaHDA20, and TaHDA22, were affected by S. avenae or S. graminum feeding (Table 1). Furthermore, N stress regulated the expression of four TaHMs (TaSDG73, TaJMJ3, TaJMJ11, and TaHDA20) (Table 1). Transcriptions of 13 TaHMs were influenced by Cd treatment, with most found to be increased (Table 1). Several ZmHMs were up-regulated or down-regulated by drought treatment (Table 2). A number of stress-related elements were identified in TaHMs and ZmHMs, which may partly explain their responses to stress. The above findings suggest the occurrence of methylation when wheat and maize experience biotic or abiotic stresses.

The multiple functions of TaHMs are discussed in Fig. 8 and Table S5. In total, 85 TaHMs were simultaneously regulated by two signals; 25 TaHMs were simultaneously regulated by three treatments; nine TaHMs were up-regulated or down-regulated by four signals; and one wheat gene was simultaneously regulated by five treatments. The diverse functions of these TaHMs indicate that they are essential for wheat growth and stress adaptations, and thus warrant further study. Moreover, all ZmHMs, except for ZmJMJ2 and ZmJMJ4, that responded to drought stress were also identified in developing seeds, indicating their roles in maize growth and stress adaptations.

Conclusions
TaHMs, HvHMs, SbHMs, SvHMs, SiHMs, and ZmHMs were systematically explored in our study to clarify their chromosome locations, protein structures, gene duplications, promoters, and gene structures. Phylogenetic and synteny comparisons between model plant and Gramineae HMs were performed and the potential roles of Gramineae HMs were posited through their known homologs. The unique characteristics of the HM genes were investigated based on their domains and expansions. Specific domains were identified in several Gramineae species, e.g., SDGs, PRMTs, JMJ5s, HDAs, and HDTs, which may exhibit unique functions. The expansion patterns of Gramineae HMs were analyzed to elucidate differences in gene number and function among Gramineae species. Using previously published RNA-seq data, we also investigated the potential roles of TaHMs in developing grain, as well as BR-mediated root growth and AC-regulated seedling development and explored the functions of ZmHMs in seed development and GA-mediated leaf growth. Candidate wheat HMs involved in high temperature, drought, salt, insect feeding, nutrition and heavy metal stress were analyzed. In addition, the ZmHMs involved in drought response were examined, and their responses to the above-mentioned stresses were inferred through promoter analysis. In summary, based on bioinformatics analysis, we predicted the functions of the Gramineae HMs, with the potential functions of wheat and maize in growth and stress adaptations verified based on expression profile analysis. The results of this study will lay the foundation for future research.

Methods
Identification and naming of HMs
The HMM files of each type of HM gene were downloaded from the Pfam database (http://pfam.sanger.ac
anthesis and sampled for library construction and RNA sequencing (RNA-seq). RNA-seq expression data [fragments per kilobase per million (FPKM)] in the above tissues were uploaded to the WheatExp database (https://wheat.pw.usda.gov/WheatExp/about.html). For regular field-grown maize (B73), seeds were sampled at each growth phase. The waxy maize inbred line (SWL01) was grown and sampled in the same way. We downloaded transcriptome data from a previous study [42].

**BR treatment**

Three-day-old wheat seedlings were treated with 50 nM epibrassinolide (EpiBL, Sigma, USA) (BR1-treated group), 1 mM EpiBL (BR2-treated group), or 1 mM BRZ (BR synthesis inhibitor, Sigma) (BRZ-treated group). After 12 d of treatment, wheat roots were sampled and used for RNA-seq analysis [33]. Differentially expressed genes (DEGs) were provided by the corresponding author of a previously published study [33].

**GA₃ treatment**

Dwarf D11 is a GA-sensitive maize mutant. Seedlings in the control and GA-treated groups were treated daily with distilled water or 10⁻⁴ M GA₃ (Sigma), respectively. The second leaf sheaths of D11 were collected at the three fully-expanded-leaves (V3) stage for RNA-seq, as described previously [43]. The RNA-seq data were obtained from a previously published study [43].

**AC treatment**

After sterilization, immature wheat (T. aestivum) embryos were used to investigate the effects of AC (a widely used growth regulator in plant tissue culture) on wheat seedling growth in medium. The roots and leaves were used for RNA isolation and library construction, respectively. The DEGs were obtained from the supplementary data of a previously published paper [37].

**Heat, drought, and salt treatment**

In the control group, seven-day-old TAM 107 seedlings were grown in hydroponic solution under 16 h day (22 °C) and 8 h night (18 °C) conditions. Seedlings were treated with 40 °C in the HS group, with 20% (m/V) PEG-6000 in the DS group, and with combined heat (40 °C) and drought stress (40 °C and 20% PEG-6000) in the HD group [38]. Seedling leaves were sampled for RNA-seq after 1 and 6 h of stress treatment. DEG analysis was performed by Liu et al. (2015), and DEGs were downloaded from the WheatExp database (https://wheat.pw.usda.gov/WheatExp/about.html) [38].

In terms of drought treatment for maize, three published studies were cited [59–61]. Firstly, drought-sensitive ZX978 and drought-tolerant ND476 cultivars were used in early study. Maize seedlings planted in soil with...
70–80% and 15–20% water content were set as the control and drought-treated groups, respectively. After 12 d of treatment, flag leaves of ND476 and ZX978 under both control and drought conditions were sampled for RNA-seq [60]. Secondly, maize ChangC7–2 (C7–2) seedlings were used for identifying drought-tolerant mechanisms. After 7 d of drought treatment, the expanded third leaves of seven-day-old C7–2 seedlings were sampled for RNA-seq analysis. The DEGs detected between the control and drought-treated groups were obtained from the additional files of a previously published study [59]. Thirdly, two maize inbred lines (drought-sensitive inbred line Lx28 and drought-tolerant inbred line H082183) were used for maize drought tolerance analysis. In the control group, Lx28 and H082183 seedlings were well-watered. In the moderate drought (MD) and severe drought (SD) treatment groups, maize seedlings were subjected to 27 and 46 d of drought treatment, respectively. The roots of Lx28 and H082183 were sampled for RNA-seq, as described in Zhang et al. (2017) [61]. DEGs between the drought (moderate and severe drought) and control groups were obtained from Zhang et al. (2017) [61].

Salt-tolerant cultivar QM and salt-sensitive cultivar CS were used to detect responses of wheat to salt [62]. The growth conditions of the QM and CS seedlings were the same as for TAM 107. For salt treatment, 150 mmol L\(^{-1}\) NaCl was added to solution. The roots of QM and CS were collected at 6, 12, 24, and 48 h after salt treatment [62]. Salt-related DEGs were obtained from previous study [62].

**Insect feeding and N and cd treatment**

Two-leaf stage Zhongmai 175 wheat seedlings were used for adult aphid (non-phytotoxic S. avenae and phytotoxic S. graminum) infestation [40]. Leaf samples (~2.5 × 2.5 cm) from aphid feeding sites were used for RNA-seq. Information on DEGs between control and treated samples were obtained from the additional files of a previously published study [40].

Two-leaf stage Wanmai No. 52 seedlings were used for N stress treatment. The roots and leaves were sampled for transcriptome analysis at 10 d after treatment [63]. We downloaded the DEGs related to N stress from a previous study [63].

For cadmium (Cd) stress treatment, 50 μM CdCl\(_2\) was applied to Zhengmai 379 seedlings. The roots of seedlings were harvested at 12 d after Cd treatment and used for transcriptome sequencing [41]. The identified DEGs were obtained from a previous study [41].

For the various wheat and maize genome versions, we converted gene IDs of the above wheat genes in the website (http://202.194.139.32/idConvert/) and maize gene IDs in the MaizeGDB database (https://chinese.maizegdb.org/gene_center/gene).

**Abbreviations**

HTs: Histone acetylases; HDACs: Histone deacetylases; HDMs: Histone methylases; HM: Histone modification; HMTs: Histone methyltransferases; FPKM: Fragments per kilobase per million; HS: Heat stress; DS: Drought stress; MD: Moderate drought; SD: Severe drought; S. avenae: Sitobion avenae; S. graminum: Schizaphis graminum; IWGSC: International Wheat Genome Sequencing Consortium.

**Supplementary Information**

The online version contains supplementary material available at https://doi.org/10.1186/s12870-021-03332-8.

**Additional file 1: Figure S1.** Chromosome location analysis of HM genes.

**Additional file 2: Figure S2.** Conserved domain analysis of HM proteins.

**Additional file 3: Figure S3.** Phylogenetic analysis of HM genes.

**Additional file 4: Figure S4.** Synteny analysis of Gramineae HM gene.

**Additional file 5: Figure S5.** Synteny analysis of HM genes between each Gramineae species and Arabidopsis.

**Additional file 6: Figure S6.** Synteny analysis of HM genes between each Gramineae species and rice.

**Additional file 7: Figure S7.** Promoter analysis of T. aestivum, H. vulgare, S. bicolor, S. viridis, S. italica, and Z. mays HM genes.

**Additional file 8: Figure S8.** Gene structure analysis of HM genes.

**Additional file 9: Table S1.** List of HM gene families in Arabidopsis, O. sativa (rice), T. aestivum, H. vulgare, S. bicolor, S. viridis, S. italica, and Z. mays genomes. Table S2. Ka, Ks, and Ka/Ks values of each Gramineae duplication gene pair. Table S3. Ka, Ks, and Ka/Ks values of duplication gene pairs between Arabidopsis and each Gramineae species. Table S4. Ka, Ks, and Ka/Ks values of duplication gene pairs between rice and each Gramineae species. Table S5. Common DEGs among different classes.

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**Authors’ contributions**

JH conceived and designed the experiment; LZ, SM, DS, YW, HF, and CY performed the experiments; LZ drafted the manuscript and analyzed the data; JH revised the final version of the manuscript. All authors read and approved the final manuscript.

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**Availability of data and materials**

All RNA-seq data mentioned here can be found in previous studies [33, 37, 38, 40–43, 58–62]. The datasets used and/or analyzed during the current study are also available from the corresponding author on reasonable request.

**Declarations**

**Ethics approval and consent to participate**

Not applicable.
Consent for publication
Not applicable.

Competing interests
The authors declare there are no conflicts of interest.

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