Is Tibetan Qingke Barley a Member of Common Barley Family Based on Comparative Genomic Evidence

Jianhui Li 1,2, Jie Zhang 1,2, Renxiang Cai 1,2

1 Institute of Life Science, Jinyang College of Zhejiang A&F University, Zhejiang, China
2 Cuxi Academy of Biotechnology, Zhejiang, China

Corresponding author email: qeren@zju.edu.cn; qerenxiang@zju.edu.cn

Bioscience Evidence, 2020, Vol.10, No.2  doi: 10.5376/be.2020.10.0002

Accepted: 20 May, 2020
Published: 27 June, 2020

Copyright © 2020 Li et al.. This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Abstract Tibetan Qingke barley is the staple food of the Tibetan people. It has been cultivated on the Qinghai-Tibetan Plateau for about 3500 years. Tibetan Qingke barley is a variety of naked barley (Hordeum vulgare linn.var.nudum) belonging to the Hordeum of the family of Gramineae. Unlike other barley, Tibetan Qingke barley has fully adapted to the extreme plateau climate after being domesticated and cultivated on the Qinghai-Tibet plateau for up to 3500–4000 years. The researchers sequenced and mapped the whole genome of a local Tibetan variety-Lasa Garma-guri, and obtained a gene map with a size of 3.89 Gb, containing a total of 36151 protein-coding genes. The genome data with a size of 4.79 Gb was obtained by sequencing the whole genome of a US spring six-row malting barley-Morex and a total of 83105 putative gene loci were identified. The Morex genome was mapped into the genome of Lasa Goumang, with a coverage rate of 92.89%. Compared with 26159 gene sets with high confidence in Morex genome, although these genes in highland barley are greatly similar to barley genes, the length of about 10.97% of the genome in highland barley is significantly longer than that of Morex. The researchers further compared Tibetan Qingke barley genomes with those of other gramineae crops and found that Tibetan Qingke barley was isolated from Aegilops tauschii (Ae. tauschii), Triticum urartu (T. urartu) and Triticum aestivum (T. aestivum) about 17 million years ago. Further analysis by the researchers found that a large number of sequences in the genome of modern Tibetan Qingke barley are still similar to Ae. Tauschii, T.urartu and T. aestivum, and the number of similar gene families is as high as 18849.

Keywords Tibetan Qingke barley; Barley; Genome

Introduction

Barley is the general term of lemma husk barley and hulless barley. In general, barley with outer husk, characterized by the adhesion of outer husk and kernel, is called husk barley. Naked barley where the hull is eased to be removed is called hulless barley, etc.

There are three types of cultivated barley, namely six-rowed barley, two-rowed barley and irregular barley. The flower spikes of six-rowed barley (Hordeum vulgare var.hexastichum) have two opposite grooves, each with 3 spikelets, 1 floret per spikelet and then 1 seed per spikelet. For two-rowed barley (H. distichum), it has a central floret which can set seed and its lateral florets are usually sterile. Irregular barley (H. irregulare) or Abyssinia intermediate barley is rarely cultivated. Its central florets are fertile, and its lateral florets are fertile or sterile. Two subspecies of common barley are economically valuable, that is, two-rowed barley subspecies and multi-rowed barley subspecies. We usually call multi-rowed barley as six-rowed barley.

Tibetan Qingke barley is a type of cereal crops belonging to Hordeum of Gramineae. Because of the separation of inner and outer glumes and naked grains, it is also called naked barley, Yuanmai or rice barley. The Chinese scientific name is Qingke. It is called Ne in Tibetan language, Tibetan hulless barley as its English name and Hordeum vulgare Linn. var. nudum as its Latin name.

Barley is one of the earliest domesticated crops by humans. As a variant of the genus Hordeum, is Tibetan Qingke barley the same as wild or cultivated barley? What is the difference between these two at genome-wide level? Did Tibetan Qingke barley evolve from wild barley? And how does Tibetan Qingke barley adapt to the extreme plateau climate?
A number of research units, including the Academy of Agriculture and Animal Husbandry of Tibet Autonomous Region, Key Laboratory of Barley and Yak Breeding of Tibet Autonomous Region, Chinese Academy of Sciences, Shenzhen Genomics Institute (BGI Shenzhen) and Beijing Genomics Institute (BGI Tech), formally launched the cooperative project of Tibetan Qingke barley genome research in 2012. On Jan. 13, 2015, the first genome map of Tibetan Qingke barley in the world was successfully plotted, and the research results were published online in PNAS (Zeng et al., 2015). The whole genome sequencing and mapping were conducted on the Tibetan local variety of Tibetan Qingke barley, Lasa Garma-guri, to reveal the plateau adaptation mechanism of Tibetan Qingke barley and interpret its origin, domestication, cultivation and breeding processes. This is another milestone for the international wheat family genome research work following wheat genome (A, D) and barley genome physical map, which could provide valuable reference for the improvement of Triticeae crops in the future and the research work of other upland crops.

On April 27, 2017, the latest research results of barley genome entitled “A chromosome conformation capture ordered sequence of the barley genome” were published online in Nature in the form of Article. It was listed as the cover story of the current issue of Nature, along with the news report titled “Genomics: decoding barley genome”. The International Barley Sequencing Consortium, led by Dr. Nils Stein from Leibniz Institute of Plant Genetics and Crop Plant Research, assembled the most complete physical map of barley genome using a variety of the most advanced sequencing and assembling techniques, including chromosome conformation plotting and biology-nano plotting by nearly 10 years. 94.8% of the assembled sequences were located on each chromosome. The perfect genome assembly results provided a good basis for the germplasm resource utilization and genetic improvement of barley.

1 Whole Genome Structure of Tibetan Qingke Barley

Zeng et al. (2015) used the whole-genome shotgun sequencing to comprehensively interpret the Tibetan local variety of Tibetan Qingke barley, Lasa Garma-guri. It was estimated that the genome size of Tibetan Qingke barley was about 4.48 Gb, and the genomic map size of Tibetan Qingke barley constructed in this sequencing was 3.89 Gb, which accounted for 87% of the genome of Tibetan Qingke barley, containing 36 151 protein-coding genes. And the N50 lengths of contig and scaffolds were 18.07 kb and 242 kb, respectively (Table 1). It indicated that the assembly had higher genome coverage and single base accuracy based on the BAC (bacterial artificial chromosomes) sequence and the RNA-seq data. In addition, the researchers used the intact ordered physical and genetic map of the cultivated barley to anchor 28 374 scaffolds (89.4% of the genome) to 7 chromosomes (Figure 1) (Mayer et al., 2012). In combination with evidence-based method and de novo method, about 81.4% of our assembly was identified as duplicate element, similar to Morex (Mayer et al., 2012) and maize (Schnable et al., 2009).

Table 1 Statistics of Tibetan Qingke barley genome sequencing (Adopted from Zeng et al., 2015)

| Genomic statistics | Hordeum vulgare Linn. var. nudum |
|--------------------|---------------------------------|
| Estimated genome size | 4.48 Gb |
| Total size of assembled scaffolds, >200 bp | 3.89 Gb |
| Total sequence length anchored to chromosomes | 3.48 Gb |
| Percent of chromosomal sequences | 89.41% |
| N50 length, scaffolds | 242 kb |
| Longest scaffold | 3.07 Mb |
| Total size of assembled contigs | 3.64 Gb |
| Longest contig | 276.95 kb |
| N50 length, contig | 18.07 kb |
| GC content | 44.00% |
| Repeat content | 81.39% |
| Number of gene models | 36 151 |
Figure 1 Mapping of Tibetan Qingke barley genome (Adopted from Zeng et al., 2015)
Note: Track a: Cultivated barley CV Morex gene region (%)/10 Mb, min: 0; max: 10. Track b: Tibetan Qingke barley gene region (%)/10 Mb, min: 0; max: 10. Track c: LTR retro-transposon (%)/10 Mb, min: 0; max: 100. Track d: Synteny with the *B. distachyon* genome. Track e: Tibetan Qingke barley chromosomes with centromeres marked as black bands. Track f: Syntenic blocks within and between chromosomes

Subsequently, the researchers compared the genomes of Tibetan Qingke barley genome with that of other gramineous crops and found that the Tibetan Qingke barley was isolated from *Ae. Tauschii*, *T. Urartu* and *T. aestivum* about 17 million years ago (Figure 2). Further analysis of researchers showed that there were still a large number of sequences similar to *Ae. Tauschii*, *T. Urartu* and *T. aestivum* in the modern Tibetan Qingke barley genome, and the number of similar gene families was as high as 18849.

Figure 2 Construction of phylogenetic tree by single-copy direct line homologous gene and divergence time

**2 The Genome Structure of Barley**

Barley (*Hordeum vulgare*) is the fourth largest cereal crop in the world. It is also an important model plant for ecological adaptation and distributed in all temperate regions from the Arctic Circle to the tropics. It was one of the first domesticated cereals in Fertile Crescent of Western Asia more than 10000 years ago. About two-thirds of
the world’s barley crops are used for animal feed, while the remaining one-third are used as the basis for the malt production, brewing and distillation industries. Although barley is not primarily used as a diet for humans, it still provides potential health benefits for humans and remains a major source of calories in several regions of the world. Barley is a diploid member of the family Tytonidae, which makes it one of the natural models of Triticaceae Genetics (including polyploid wheat and rye) and genomics. The size of the haploid genome in seven chromosomes of barley is about 5.3 Gb, which is one of the largest diploid genomes sequenced so far.

The International Barley Sequencing Consortium (IBSC) assembled the barley genome using a hierarchical approach (Mascher et al., 2017). Initially, physical, genetic and optical mapping (N50:1.9 Mb) was used to scaffold multiple short reads BAC (bacterial artificial chromosomes) of the BAC contig assemblies (N50:79 KB), and then POPSEQ (population sequencing) genetic mapping was used to assign multiple short reads -to chromosomes (Lam, et al., 2012; Mascher et al., 2013; Ariyadasa et al., 2014). Finally, the idea of conformation capture sequencing (Hi-C) was used to determine the linear sequence and direction of scaffold sequences (Kalhhor et al., 2011; Beier et al., 2017).

The final chromosome-scale assembly consisted of 6 347 ordered super-scaffolds, which were assembled from the combined assembly of a single BAC, accounting for about 95% of the genome sequence content (4.79 Gb), of which 4.54 Gb had been assigned to the exact chromosome positions in the Hi-C map (Mascher et al., 2017) (Table 2).

The researchers mapped transcriptome data and the reference protein sequences of other plant species into the assembly and identified 83 105 putative loci, including protein-coding genes, non-coding RNA, pseudogenes, and retrotransposons. After further screening, these sites were divided into 39 734 high-confidence genes and 41 949 low-confidence genes according to sequence homology. The study predicted 19 908 long non-coding RNA and 792 microRNA precursor sites. Using a set of conserved eukaryotic core genes (BUSCO), it was estimated that the predicted gene model represented 98% of the cv. Morex barley gene complement (Mascher et al., 2017).

The barley chloroplast genome and its gene annotation have also been published (KC912687).

In order to explore how to use the new barley genome combination for genetic breeding, researchers obtained exon sequence data from the 96 European quality barley strain (half spring barley, half winter barley). The extent and classification of molecular variation within and between these groups were studied using 71,285 SNPs and, in a linear sequence (Figure 3a) and according to the physical dimension (Figure 3b) draw diversity value in 100 SNP windows. The results showed that there were significant differences in the level and distribution of diversity within and between gene Banks.

Table 2 Statistics of barley genome sequencing (Adopted from Mascher et al., 2017)

| Number and cumulative length of sequenced BACs | 87 075 (11.3 Gb) |
|-----------------------------------------------|------------------|
| Length of non-redundant sequence               | 4.79 Gb          |
| Number of sequences contigs                    | 466 070          |
| BAC sequence contig N50                        | 79 kb            |
| Number and cumulative length of BAC super-scaffolds | 4 235 (4.58 Gb) |
| Number and cumulative length of singleton BACs | 2 123 (205 Mb)   |
| Super-scaffold N50                             | 1.9 Mb           |
| Sequence anchored to the POPSEQ genetic map    | 4.63 Gb (97%)    |
| Sequence anchored to the Hi-C map              | 4.54 Gb (95%)    |
| Number of annotated high-confidence genes      | 39 734           |
| Annotated coding sequence                      | 65.3 Mb (1.4%)   |
| Annotated transposable elements                | 3.70 Gb (80.8%)  |

In spring type barley, there was almost no diversity in the pericentromeric region of chromosomes 1H, 2H and 7H, and the same was true for chromosome 5H in winter type barley. It led to a single-gene pool specific haplotype across the pericentromeric region. However, 3H, 4H and 6H chromosomes maintained high diversity in these regions, indicating the existence of multiple similar haplotypes (Figure 3a). This was especially more obvious when the diversity was plotted on physical scales (Figure 3b).
Therefore, in the breeding process of barley for different purposes (mainly malting barley and feed barley), it was speculated that the lack of observable variation of high-quality germplasm might be a sign of strong selection, and alleles were not actually recombinant during meiosis due to the restriction of recombination in the pericentromeric region.

![Figure 3 Distribution of genetic diversity in barley genome](image)

Note: Ninety-six elite barley cultivars, including 48 from the winter gene base (blue line) and 48 from the spring gene base (red line), diversity (unbiased heterozygosity, y-axis) is plotted along each rolling average of 100 adjacent SNPs on the chromosome; for better display, all chromosomes have been normalized to standard length; colored dots are the locations of 8 loci identified as distinguishing between winter and spring gene bases; a, the diversity pattern of chromosome 1H-7H (from top to bottom), the distance between each SNP has been normalized (not showing the genetic distance), and the number of SNPs contained on each chromosome is given at the bottom-right of each figure; b, normalize the same diversity value according to the physical scale, the pericentromeric region with very low diversity in the spring barley gene base is highlighted in green, while the diversity in the winter barley gene base is highlighted in purple; Regions with similar levels of diversity in the two gene bases are highlighted in orange.

### 3 Differences and Similarities between Genome of Tibetan Qingke Barley and Barley

As a member of the *Hordeum*, the Tibetan Qingke barley has evolved over a long time, and what is the evolution of its genetic information? What is the difference between the highland barley genome and the barley genome? There is a need for further exploration.
The size of the genome of Tibetan Qingke barley is different from that of barley. It is estimated that the genome size of the former was 4.48 Gb, and the genome data obtained by sequencing was 3.89 Gb. The genome size of the barley was 5.3 Gb, but the genome data obtained by sequencing was 4.79 Gb. It is obvious that the barley genome is larger than the Tibetan Qingke barley genome (Zeng et al., 2015; Mascher et al., 2017). In order to further compare the differences between the two genomes, Zeng et al. (2015) plotted the genome data of barley germplasm Morex sequenced by IBSC in 2012 to the genomes of Tibetan Qingke barley, and its genome coverage was 92.89%, and there was no significant difference among the seven chromosomes. It means that there was no preference for homology on different chromosomes (Mayer et al., 2012).

In addition, the researchers identified specific sequences of Morex and Tibetan Qingke barley with 113 Mb and 288 Mb in length, respectively. The specific sequences of Tibetan Qingke barley contained more than 4 500 genes. The pathways of KEGG (Kyoto Encyclopedia of Genes and Genomes) significantly enriched in Tibetan Qingke barley were flavonoid biosynthesis, stilbenoid, diarylheptanoid and gingerol biosynthesis, and plant hormone signal transduction (Zeng et al., 2015).

By comparing with 26 159 gene sets with high confidence in Morex genome, the researchers identified 22 673 optimum matching gene pairs, of which 7 224 (31.86%) had the same sequence and 17 840 (78.68%) had protein similarity higher than 95%. The length of the coded DNA sequence (CDS) of these gene pairs was basically the same as that of the genome (CDS + intron), but about 10.97% of the genome length was significantly longer than that of Morex in Tibetan Qingke barley (Zeng et al., 2015).

The above results all showed genomic differences between the two species.

As an important member of the Triticeae family, the publication of Tibetan Qingke barley genome not only helps us better understand the different domestication pathways of barley crops, but also enables us to combine barley, wheat and their ancestral varieties to get a glimpse of the evolution history of the Triticeae family. The adaptability of extreme environment, such as cold and hypoxia tolerance, better points out the direction for the improvement of plateau crops for us and helps to solve the food problem in people’s livelihood.

Authors’ contributions
Jianhui Li is responsible for research conception, literature collection, first draft writing, while Zhang Jie is responsible for revision and final draft. Renxiang Cai is responsible for revision and supplement of thesis manuscript. All the authors read and approved the final manuscript.

Acknowledgements
This study was granted by Cuixi Innovative Fund for Research and Development Project Funded by Cuixi Academy of Biotechnology, Zhui. ZHouying Wang, Jia Xu, Mengshao Yu, Chunxia Zhuo, Tianye Zhou and Yan Dong participated in the translation and proofread of this manuscript. In particular, Dr. Xuanjun Fang of Hainan Institute of Tropical Agricultural Resources conducted in-depth and strict review of the manuscript, and gave useful suggestions for writing. The authors would like to express their sincere gratitude here.

References
Ariyadasa R., Mascher M., Nussbaumer T., Schulte D., Frenkel Z., Poursarebani N., Zhou R., Steuernagel B., Gundlach H., Taudien S., Felder M., Platzer M., Himmelbach A., Schmutzer T., Hedley P.E., Muehlbauer G.J., Scholz U., Korol A., Mayer K.F., Waugh R., Langridge P., Graner A., and Stein N., 2014, A sequence-ready physical map of barley anchored genetically by two million single-nucleotide polymorphisms, Plant Physiol., 164(1): 412-423
https://doi.org/10.1104/pp.113.228213
PMid:24243933 PMCID:PMC3875818
Beier S., Himmelbach A., Colmsec C., Zhang X.Q., Barrero R.A., Zhang Q., Li L., Bayer M., Bolser D., Taudien S., Groth M., Felder M., Hastie A., Šimková H., Stašková H., Vrána J., Chan S., Muñoz-Amatriain M., Ounit R., Wanamaker S., Schmutzer T., Aliyeva-Schnorr L., Grasso S., Tanukane J., Sampath D., Heavens D., Cao S.J., Chapman B., Dai F., Han Y., Li H., Li X., Lin C.Y., McCooke J.K., Tan C., Wang S.B., Yin S.Y., Zhou G.F., Poland J.A., Bellgard M.I., Houben A., Doležel J., Aylung S., Lonardi S., Langridge P., Muehlbauer G.J., Kersey P., Clark M.D., Caccamo M., Schulman A.H., Platzer M., Close T.J., Hansson M., Zhang G.P., Braumann I., Li C.D., Waugh R., Scholz U., Stein N., and Mascher M., 2017, Construction of a map-based reference genome sequence for barley, hordeum vulgare I, Sci Data., 4: 170044
https://doi.org/10.1038/sdata.2017.44
PMid:28448065 PMCID:PMC5407242

6
Kalhor R., Tjong H., Jayathilaka N., Alber F., and Chen L., 2011, Genome architectures revealed by tethered chromosome conformation capture and population-based modeling, Nat. Biotechnol., 30: 90-98
https://doi.org/10.1038/nbt.2057
PMid:22198700 PMCid:PMC3782096

Lam E.T., Hastie A., Lin C., Ehrlich D., Das S.K., Austin M.D., Deshpande P., Cao H., Nagarajan N., Xiao M., and Kwoket P.Y., 2012, Genome mapping on nanochannel arrays for structural variation analysis and sequence assembly, Nature Biotechnology, 30(8): 771-776
https://doi.org/10.1038/tpj.2013
PMid:22797562 PMCid:PMC3817024

Mascher M., Gundlach H., Himmelbach A., Beier S., Twardziok S.O., Wicker T., Rachdek V., Dockter C., Hedley P.E., Russell J., Bayer M., Ramsay L., Liu H., Haberer G., Zhang Q., Zhang Q., Barrero R.A., Li L., Taudien S., Groth M., Felder M., Hastie A., Šimková H., Staňková H., Vránov J., Chan S., Muñoz-Amatriain M., Ounit R., Renk M., Bolser D., Colmsee C., Schmutzer T., Alyeova-Schmor L., Grasso S., Tanskanen J., Chaiyan A., Sampath D., Heavens D., Clisold L., Cao S., Chapman B., Duf F., Han Y., Li X., Lin C., McCooke J.K., Tan C., Wang P., Wang S., Yin Q., Zhou G., Poland J.A., Bellgard M.I., Bolisjuk L., Houben A., Doležel J., Aylung S., Lonard S., Kersey P., Langridge P., Muehlbauer G.J., Clark M.D., Caccamo M., Schulman A.H., Moyer K.F.S., Platter M., Close T.J., Scholz U., Hannson M., Zhang G., Braumann I., Spannagl M., Li C., Waugh R., and Stein N., 2017, A chromosome conformation capture ordered sequence of the barley genome, Nature, 544(7651): 427-433
PMid:23998490 PMCid:PMC4298792

Mayer K.F., Waugh R., Brown J.W., Schulman A., Langridge P., Platzer M., Fincher G.B., Muehlbauer G.J., Sato K., Close T.J., Wise R.P., Stein N., Arayaadas R., Schulte D., Poursarebani N., Zhou R., Steueranbel G., Mascher M., Scholz U., Shi B., Landridge P., Madshtety J., Bhat P., Moscow M., Resnik J., Close T.J., Muehlbauer G.J., Hedley P., Liu H., Morris J., Waugh R., Frenkel Z., Korol A., Bergès H., Graner A., Stein N., Steueranbel G., Scholz U., Taudien S., Felder M., Groth M., Platzer M., Stein N., Steueranbel G., Scholz U., Himmelbach A., Taudien S., Felder M., Platzer M., Lonard S., Duma D., Altet M., Cerdos F., Bucotti M., Giard M., Ma Y., Wamamaker S., Close T.J., Stein N., Cattonaro F., Vendramin V., Scalabrin S., Radovic S., Wing R., Schulte D., Steueranbel G., Morgante M., Stein N., Waugh R., Nussbaumer T., Gundlach H., Martis M., Arayaadas R., Poursarebani N., Steueranbel G., Scholz U., Wise R.P., Poland J., Stein N., Mayer K.F., Spannagl M., Pfeifer M., Gundlach H., Mayer K.F., Gundlach H., Moisy C., Tanskanc J., Scalabrin S., Zaccolo A., Vendramin V., Morgante M., Schulman A., Pfeifer M., Spannagl M., Hedley P., Morris J., Russell J., Druka A., Marshall D., Bayer M., Swarbrick D., Sampath D., Aylung S., Feurer M., Caccamo M., Matsumoto T., Tanaka S., Kato S., Wise R.P., Close T.J., Wamamaker S., Muehlbauer G.J., Stein N., Waugh R., Steueranbel G., Schmutzer T., Mascher M., Scholz U., Taudien S., Platzer M., Sato K., Marshall D., Bayer M., Waugh R., and Stein N., 2012, A physical, genetic and functional sequence assembly of the barley genome, Nature, 491(7426): 711-716

Schneible P.S., Ware D., Fulton R.S., Stein J.C., Wei F., Pasternak S., Liang C., Zhang J., Fulton L., Graves TA., Minx P., Reily A.D., Courney L., Krachkowski S.S., Tomlinson C., Strong C., Delehauty K., Fronick C., Courtney B., Rock S.M., Belter E., Du F., Kim K., Abbott R.M., Cotton M., Levy A., Marchetto P., Ochoa K., Jackson S.M., Gillam B., Chen W., Yan L., Wang L., Chang J., Ko M., Chwalina A., Leonard S., Cousse K., Collura K., Kudrna D., Currie J., He R., Angelova A., Rajakser J., Mueller T., Lemoli R., Sca C., Ko A., Delaney K., Wissotzki M., Lopez G., Campos D., Braiddotti M., Ashley E., Golsler W., Kim H., Lee S., Lin J., Dujmic Z., Kim W., Talag J., Zaccolo A., Fan C., Sebastian Kramer A., Spiegel L., Nascimento M., Zutavern T., Miller B., Ambrose C., Muller S., Spooner W., Narechania A., Ren L., Wei S., Kumari S., Faga B., Levy M.J., McManan M., Van Buren P., Vaughan M.W., Yung K., Yeh C.T., Emmrich S.J., Jia Y., Kalyanaraman A., Hsia A.P., Barbazuk W.B., Baucom R.S., Brunnell T.P., Carpita N.C., Parlapo C., Chia J.M., Dergon J.M., Estill J.C., Fu Y., Jeddeloh J.A., Han Y., Lee H., Li P., Lisch D.R., Liu S., Liu Z., Nagel D.H., McCann M.C., Sanmiguel P., Myers A.M., Nettleton D., Nguyen J., Penning W.B., Ponnala L., Schneider K.L., Schwartz D.C., Sharma A., Soderlund C., Springer N.M., Sun Q., Wang H., Waterman M., Westerman R., Wolfgruber T.K., Yang L., Yu Y., Zhang L., Zhou S., Zhu Q., Benetzen J.L., Dawe R.K., Jiang J., Jiang N., Presting G.G., Wessler S.R., Aluru S., Martienssen R.A., Clifton S.W., McCombie W.R., Wing R.A., and Wilson R.K., 2009, The B73 maize genome: Complexity, diversity, and dynamics, Science, 326(5956): 1112-1115
https://doi.org/10.1126/science.1178534
PMid:19965430

Zeng X.Q., Long H., Wang Z., Zhao S.C., Tang Y.W., Huang Z.Y., Wang Y.L., Xu Q.J., Mao L.K., Deng G.B., Yao X.M., Li X.F., Bai L.J., Yuan H.J., Pan Z.F., Liu R.J., Chen X., WangMu Q.M., Chen M., Yu L.L., Liang J.J., DuanZhu D.W., Zheng Y., Yu S.Y., LuoBu Z.X., Guan X.M., Li J., Deng C., Hu W.H., Chen C.H., TaBa X.N., Gao L.Y., Lv X.D., Abu Y.B., Fang X.D., Nevo E., Yu M.Q., Wang J., and Tashi N., 2015, The draft genome of tibetan hulless barley reveals adaptive patterns to the high stress tibetan plateau, Proceedings of the National Academy of Sciences, 112(4): 1095-1100
https://doi.org/10.1073/pnas.1423628112
PMid:25583503 PMCid:PMC4313863