RESEARCH ARTICLE SUMMARY

CROP GENOMICS

Convergent selection of a WD40 protein that enhances grain yield in maize and rice

Wenkang Chen†, Lu Chen†, Xuan Zhang†, Ning Yang†, Jianghua Guo, Min Wang, Shenghui Ji, Xiangyu Zhao, Pengfei Yin, Lichun Cai, Jing Xu, Lili Zhang, Yingjia Han, Yingni Xiao, Gen Xu, Yuebin Wang, Shuhui Wang, Sheng Wu, Fang Yang, David Jackson, Jinkui Cheng, Saihua Chen, Chuanqing Sun, Feng Qin, Feng Tian, Alisdair R. Fernie, Jiansheng Li*, Jianbing Yan*, Xiaohong Yang*

INTRODUCTION: During the independent process of cereal evolution, many trait shifts appear to have been under convergent selection to meet the specific needs of humans. Identification of convergently selected genes across cereals could help to clarify the evolution of crop species and to accelerate breeding programs. In the past several decades, researchers have debated whether convergent phenotypic selection in distinct lineages is driven by conserved molecular changes or by diverse molecular pathways. Two of the most economically important crops, maize and rice, display some conserved phenotypic shifts—including loss of seed dispersal, decreased seed dormancy, and increased grain number during evolution—even though they experienced independent selection. Hence, maize and rice can serve as an excellent system for understanding the extent of convergent selection among cereals.

RATIONALE: Despite the identification of a few convergently selected genes, our understanding of the extent of molecular convergence on a genome-wide scale between maize and rice is very limited. To learn how often selection acts on orthologous genes, we investigated the functions and molecular evolution of the grain yield quantitative trait locus *KRN2* in maize and its rice ortholog *OsKRN2*. We also identified convergently selected genes on a genome-wide scale in maize and rice, using two large datasets.

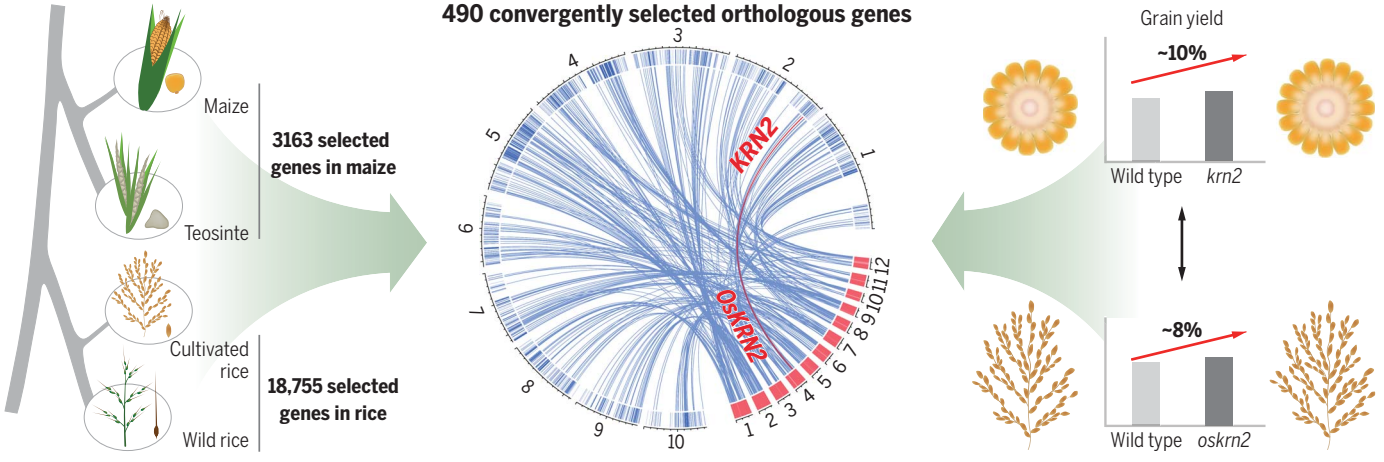
RESULTS: We identified a selected gene, *KRN2* (*kernel row number2*), that differs between domesticated maize and its wild ancestor, teosinte. This gene underlies a major quantitative trait locus for kernel row number in maize. Selection in the noncoding upstream regions resulted in a reduction of *KRN2* expression and an increased grain number through an increase in kernel rows. The rice ortholog, *OsKRN2*, also underwent selection and negatively regulates grain number via control of secondary panicle branches. These orthologs encode WD40 proteins and function synergistically with a gene of unknown function, DUF1644, which suggests that a conserved protein interaction controls grain number in maize and rice. Field tests show that knockout of *KRN2* in maize or *OsKRN2* in rice increased grain yield by ~10% and ~8%, respectively, with no apparent trade-off in other agronomic traits. This suggests potential applications of *KRN2* and its orthologs for crop improvement.

On a genome-wide scale, we identified a set of 490 orthologous genes that underwent convergent selection during maize and rice evolution, including *KRN2/OsKRN2*. We found that the convergently selected orthologous genes appear to be significantly enriched in two specific pathways in both maize and rice: starch and sucrose metabolism, and biosynthesis of cofactors. A deep analysis of convergently selected genes in the starch metabolic pathway indicates that the degree of genetic convergence via convergent selection is related to the conservation and complexity of the gene network for a given selection.

CONCLUSION: Our findings show that common phenotypic shifts during maize and rice evolution acting on conserved genes are driven at least in part by convergent selection, which in maize and rice likely occurred both during and after domestication. We provide evolutionary and functional evidence on the convergent selection of *KRN2/OsKRN2* for grain number between maize and rice. We further found that a complete loss-of-function allele of *KRN2/OsKRN2* increased grain yield without an apparent negative impact on other agronomic traits. Exploring the role of *KRN2/OsKRN2* and other convergently selected genes across the cereals could provide new opportunities to enhance the production of other global crops. ■

The list of author affiliations is available in the full article online.
*Corresponding author. Email: yxiaohong@cau.edu.cn (X.Y.); yjianbing@mail.hzau.edu.cn (J.Y.); lijiansheng@cau.edu.cn (J.L.)
†These authors contributed equally to this work.
Cite this article as W. Chen *et al.*, *Science* **375**, eabg7985 (2022). DOI: 10.1126/science.abg7985

READ THE FULL ARTICLE AT
https://doi.org/10.1126/science.abg7985



Shared selected orthologous genes in maize and rice for convergent phenotypic shifts during domestication and improvement. By comparing 3163 selected genes in maize and 18,755 selected genes in rice, we identified 490 orthologous gene pairs, including *KRN2* and its rice ortholog *OsKRN2*, as having been convergently selected. Knockout of *KRN2* in maize or *OsKRN2* in rice increased grain yield by increasing kernel rows and secondary panicle branches, respectively.

RESEARCH ARTICLE

CROP GENOMICS

Convergent selection of a WD40 protein that enhances grain yield in maize and rice

Wenkang Chen[1]†, Lu Chen[2]†‡, Xuan Zhang[1]†, Ning Yang[2,3]†, Jianghua Guo[1], Min Wang[1], Shenghui Ji[1], Xiangyu Zhao[1], Pengfei Yin[1], Lichun Cai[1], Jing Xu[1], Lili Zhang[1], Yingjia Han[1], Yingni Xiao[1], Gen Xu[1], Yuebin Wang[2], Shuhui Wang[1], Sheng Wu[1], Fang Yang[2,3], David Jackson[2,4], Jinkui Cheng[1,5], Saihua Chen[6], Chuanqing Sun[1], Feng Qin[1,5], Feng Tian[1,5], Alisdair R. Fernie[7], Jiansheng Li[1,5]*, Jianbing Yan[2,3]*, Xiaohong Yang[1,5]*

A better understanding of the extent of convergent selection among crops could greatly improve breeding programs. We found that the quantitative trait locus *KRN2* in maize and its rice ortholog, *OsKRN2*, experienced convergent selection. These orthologs encode WD40 proteins and interact with a gene of unknown function, DUF1644, to negatively regulate grain number in both crops. Knockout of *KRN2* in maize or *OsKRN2* in rice increased grain yield by ~10% and ~8%, respectively, with no apparent trade-offs in other agronomic traits. Furthermore, genome-wide scans identified 490 pairs of orthologous genes that underwent convergent selection during maize and rice evolution, and these were enriched for two shared molecular pathways. *KRN2*, together with other convergently selected genes, provides an excellent target for future crop improvement.

The major cereals, including maize, rice, wheat, barley, and sorghum, were domesticated independently ~10,000 years ago and represent a primary source of human calories (*1*). Genome-wide analyses indicate that domestication and improvement in the cereals were complex and involved numerous genes associated with various biological traits (*2*–*5*). Although the cereals underwent independent domestication and improvement, many morphological and physiological or biochemical traits appear to have been under convergent selection, resulting in an ease of cultivation, high yield, and nutrient richness (*1*). Given the close phylogenetic relationships among cereals, a key question is whether convergent phenotypic selection in distinct lineages was driven by conserved molecular changes. In some cases, selection in independent lineages appears to have acted on conserved genetic loci that control convergent phenotypes (*6*–*8*), whereas in other cases the convergent phenotypic changes appear to have arisen by diverse genetic routes due to homoplasy of selected genetic loci (*9*–*11*).

Two of the most economically important crops, maize (*Zea mays* L. ssp. *mays*) and rice (*Oryza sativa* L.), diverged >50 million years ago (*12*). Although the collinearity of cereal genomes has long been recognized (*12*–*14*), only a few genes—such as those involved in shattering resistance—have been identified as having been convergently selected during the evolution of maize and rice (*7*, *15*). Hence, a genome-wide identification of the genes that have undergone convergent selection in maize and rice could help to clarify the evolution of crop species as well as to accelerate breeding programs.

KRN2 is a selected gene underlying kernel row number variation

We mapped eight quantitative trait loci (QTLs) for kernel row number (KRN) in a maize recombinant inbred line (RIL) population developed from a cross between an inbred line, B73, and an introgression line, MT-6, of which ~25% of its genome is derived from that of teosinte, the wild ancestor of maize (*16*) (Fig. 1A and table S1). *qKRN2*, the QTL with the largest effect, was located within a selective sweep on the short arm of chromosome 2 (*2*), and the maize allele increased KRN relative to the teosinte allele. To identify the gene(s) underlying *qKRN2*, we performed positional cloning using nine markers and 7056 individuals derived from a backcross of MT-6/B73 F_1 plants with B73 (fig. S1). We delimited this QTL to a 5799–base pair (bp) region that contained only one candidate gene (*Zm00001d002641*), which we named *KRN2* (*kernel row number2*; Fig. 1, B and C). Comparisons of the maize and teosinte alleles indicated that the maize (B73) allele increased KRN by ~1.4 rows relative to teosinte (Fig. 1, D and E). To confirm the function of *KRN2*, we identified a loss-of-function allele carrying a *Mutator* (*Mu*) transposon insertion in exon 1. Ears from plants homozygous for the *Mu* insertion produced ~1.8 more rows than wild-type segregants (fig. S2). These results suggest that *KRN2* is the causal gene for KRN variation in *qKRN2* and that loss-of-function alleles can increase KRN in maize.

Genomic sequencing identified 63 single-nucleotide polymorphisms (SNPs) and 37 insertions or deletions (indels) in the promoter and 5′ untranslated region (UTR) of *KRN2*, as well as seven synonymous and seven non-synonymous SNPs in coding exons between the B73 and teosinte alleles (Fig. 1C and fig. S3). Real-time quantitative polymerase chain reaction (qPCR) showed that *KRN2* expression was lower in NIL-*KRN2*^{B73} relative to NIL-*KRN2*^{teosinte} in the early stage of maize inflorescence meristem (IM) development (Fig. 1F and fig. S4). To test whether the sequence polymorphisms in the promoter or 5′UTR might underlie these different expression levels, we performed transient expression assays in maize protoplasts, in which two fragments (~1.2 kb or ~2.0 kb) upstream of the start codon of *KRN2* from maize or teosinte were fused upstream of the luciferase (LUC) gene (Fig. 1G). Both teosinte fragments exhibited higher LUC activity than the maize fragments (Fig. 1H), which suggests that polymorphisms within the ~1.2-kb region of *KRN2* account for expression differences between maize and teosinte alleles. Furthermore, we overexpressed the coding sequences of *KRN2*^{B73} and of *KRN2*^{teosinte} alleles in a maize inbred line and confirmed enhanced expression of *KRN2* by qPCR (fig. S5, A to C). Relative to wild-type plants, all six independent overexpression lines consistently decreased KRN by ~2.0 rows, with no difference between *Ubi*::*KRN2*^{B73} and *Ubi*::*KRN2*^{teosinte} transgenic plants (fig. S5D). These findings indicate that KRN changes are mediated through changes in *KRN2* expression, most likely caused by polymorphisms within the ~1.2-kb promoter and 5′UTR region.

To ascertain whether *KRN2* underwent selection during maize evolution, we calculated nucleotide diversity across its promoter and coding regions. Similar diversity was observed between maize landraces and inbred lines (Fig. 1I). We observed a reduction in nucleotide diversity in maize relative to its ancestor, *Zea mays* ssp. *parviglumis* (hereafter, *parviglumis*; $\pi_{parviglumis} = 2.6 \times 10^{-2}$, $\pi_{landrace} = 6.1 \times 10^{-3}$, $\pi_{inbred} = 2.1 \times 10^{-3}$), and a negative Tajima's D-statistic in maize inbred lines and landraces for a ~700-bp region containing the 5′UTR of *KRN2* (Fig. 1I and fig. S6); these findings suggest that this region underwent selection. This result was further supported by a coalescence simulation (fig. S6). This severe loss of

[1]State Key Laboratory of Plant Physiology and Biochemistry and National Maize Improvement Center of China, China Agricultural University, Beijing 100193, China. [2]National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China. [3]Hubei Hongshan Laboratory, Wuhan 430070, China. [4]Cold Spring Harbor Laboratory, Cold Spring Harbor, NY 11724, USA. [5]Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100193, China. [6]Key Laboratory of Plant Functional Genomics of the Ministry of Education, Yangzhou University, Yangzhou, Jiangsu 225009, China. [7]Department of Molecular Physiology, Max Planck Institute of Molecular Plant Physiology, 14476 Potsdam-Golm, Germany.
*Corresponding author. Email: yxiaohong@cau.edu.cn (X.Y.); yjianbing@mail.hzau.edu.cn (J.Y.); lijiansheng@cau.edu.cn (J.L.)
†These authors contributed equally to this work.
‡Present address: State Key Laboratory of Plant Genomics and National Center for Plant Gene Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China.

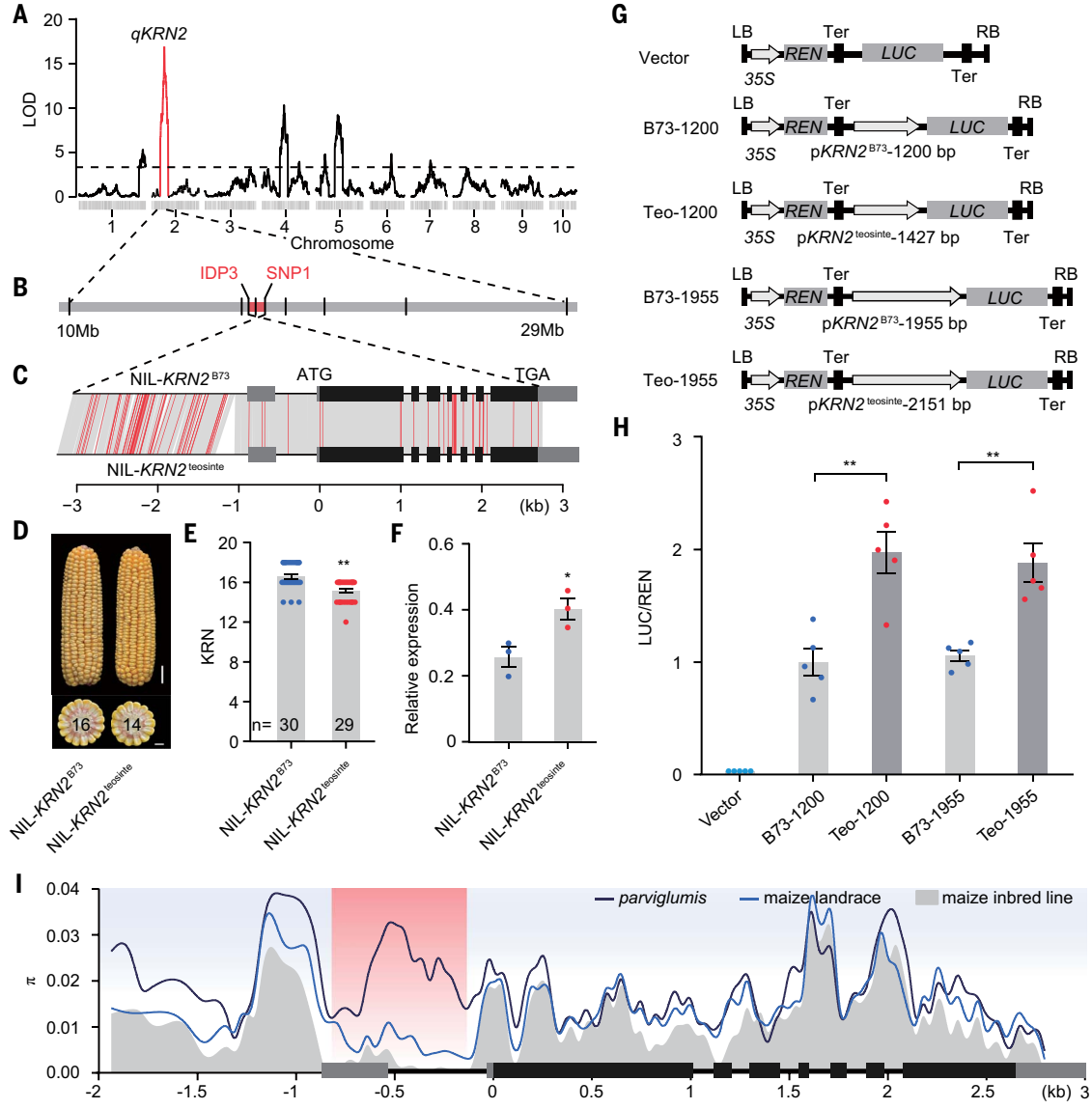


Fig. 1. *KRN2* affects kernel row number and underwent selection during maize domestication. (**A**) Logarithm of odds (LOD) profile of QTLs for KRN in the MT-6/B73 RIL population. The dashed line shows the threshold LOD value (3.3) for putative QTLs. (**B**) *qKRN2* was fine-mapped to a 5799-bp interval (red) flanked by the markers IDP3 and SNP1. (**C**) *KRN2* gene structure and sequence comparison of the target region between NIL-*KRN2*^{B73} and NIL-*KRN2*^{teosinte}. Black, exons; gray, UTRs. The red lines denote SNPs; the white spaces show indels. (**D** to **F**) Ear performance (D), KRN quantification (E), and *KRN2* expression in 0.5-mm IMs (F) of NIL-*KRN2*^{B73} and NIL-*KRN2*^{teosinte}. Scale bars in (D), 2 cm for the ear, 1 cm for ear transverse sections. The expression levels of *KRN2* in (F) were quantified using qPCR and normalized to that of maize *ACTIN*. (**G**) Constructs used to test the effect of polymorphisms in the promoter and 5′UTR on *KRN2* expression in transient expression assays in maize leaf protoplasts. B73-1200, Teo-1200, B73-1955, and Teo-1955 constructs harbor the promoter and 5′UTR of different *KRN2* alleles, including 1200 bp from B73, 1427 bp from teosinte, 1955 bp from B73, and 2151 bp from teosinte. (**H**) The teosinte sequences drive increased LUC activity relative to the B73 alleles. The data were normalized with respect to the average values of the B73-1200 construct. (**I**) Nucleotide diversity across the *KRN2* locus. A 150-bp sliding window with a 35-bp step size was used to calculate nucleotide diversity (π). The selected region (−800 to −100 bp) is shaded in red. In (E), (F), and (H), data are means ± SEM, $n = 3$ in (F) and $n = 5$ in (H). *$P < 0.05$, **$P < 0.01$ (two-tailed Student's t test).

diversity could not be explained by a domestication bottleneck or modern improvement in maize alone. Our selection analyses seem to suggest that human selection was likely involved in the evolution of *KRN2* between initial domestication and modern improvement. Taken together, both our transgenic studies and surveys of nucleotide diversity suggest that selection in the noncoding upstream regions resulted in a reduction in *KRN2* expression and, in turn, an increased KRN in maize.

KRN2 negatively regulates KRN by interacting with DUF1644, a protein of unknown function

Sequence analysis of *KRN2* predicted that it encodes a cytoplasmic WD40 protein containing seven WD40 repeats (figs. S7 and S8, A and B). Members of the WD40 family act as scaffolds for protein-protein interactions (*17*, *18*) and have diverse functions in plants, including in development, metabolite biosynthesis, and immune responses (*19*–*21*). To illuminate the molecular mechanism of KRN2, we identified six potential interaction partners using a yeast two-hybrid (Y2H) screen (table S2). Among them, we focused on the gene *DUF1644*, which encodes a DUF1644-containing protein that

localized to both the cytoplasm and the nucleus (fig. S8, A and C). We confirmed a direct interaction between KRN2 and DUF1644 by Y2H assays as well as split firefly LUC complementation assays (Fig. 2, A and B). Next, to further elucidate the relationship between *KRN2* and *DUF1644*, we generated *krn2* and *duf1644* null mutants by CRISPR-Cas9 technology as well as a *krn2 duf1644* double mutant (fig. S9). Neither of the two single *duf1644* mutants had an obvious phenotype, but the *krn2 duf1644* double mutant had a significantly higher KRN relative to the *krn2* single mutant (16.3 ± 1.2 versus 15.9 ± 1.1; unpaired *t* test, $t = 2.0$, df = 124, $P = 4.6 \times 10^{-2}$; Fig. 2C and fig. S9). This result suggests that DUF1644 acts with KRN2, although it remains unknown how this affects KRN and the underlying molecular function of DUF1644.

To better understand the cause of the increase in KRN, we measured IM size. The NIL-*KRN2*^{B73} IMs (345.5 ± 25.2 μm) were wider than those of NIL-*KRN2*^{teosinte} (313.0 ± 19.6 μm), and *KRN2* overexpression decreased IM diameter by ~56 μm (fig. S10). Consistently, both the *krn2* single mutant and *krn2 duf1644* double mutant significantly increased their IM size relative to the wild-type plants (unpaired *t* test; 446.3 ± 33.0 μm versus 422.4 ± 23.8 μm, $t = 3.3$, df = 61, $P = 1.7 \times 10^{-3}$ for the single mutant; 465.9 ± 27.4 μm versus 422.4 ± 23.8 μm, $t = 6.5$, df = 56, $P = 2.6 \times 10^{-8}$ for the double mutant; Fig. 2, D and E). We hypothesize that these increases in IM size provided additional space for initiation of spikelet pair meristems, and hence a higher KRN (Fig. 2F).

Convergent selection of the *KRN2* ortholog in rice

A single ortholog of *KRN2* containing conserved WD40 domains was identified in most major cereal crops (Fig. 3A and fig. S7). The rice *KRN2* ortholog, *Os04 g0568400* (hereafter, *OsKRN2*), mapped to a region that underwent a selective sweep (27.5 to 29.0 Mb) on rice chromosome 4 (*3*) that is syntenic with the short arm of chromosome 2 in maize (Fig. 3B) and is within a QTL for rice grain number (*22*, *23*). These observations suggest that *OsKRN2* may have also experienced selection on rice grain number. Consistent with this, nucleotide diversity was reduced in an ~1100-bp region upstream of the *OsKRN2* start codon in cultivated rice (fig. S11). As expected, a minimum-spanning tree of 27 haplotypes in the ~1100-bp region separated wild rice *Oryza rufipogon* (hereafter, *rufipogon*; 59 accessions) from cultivated rice (109 accessions) according to the sequenced accessions (Fig. 3C).

Like the *KRN2* expression profile in maize, *OsKRN2* was expressed in all rice tissues, with high levels in panicle primordia (fig. S12). Rice panicle branches are initiated by branch meristems, which are analogous to spikelet pair meristems in maize (*24*). We made *OsKRN2* null mutants using CRISPR-Cas9 technology,

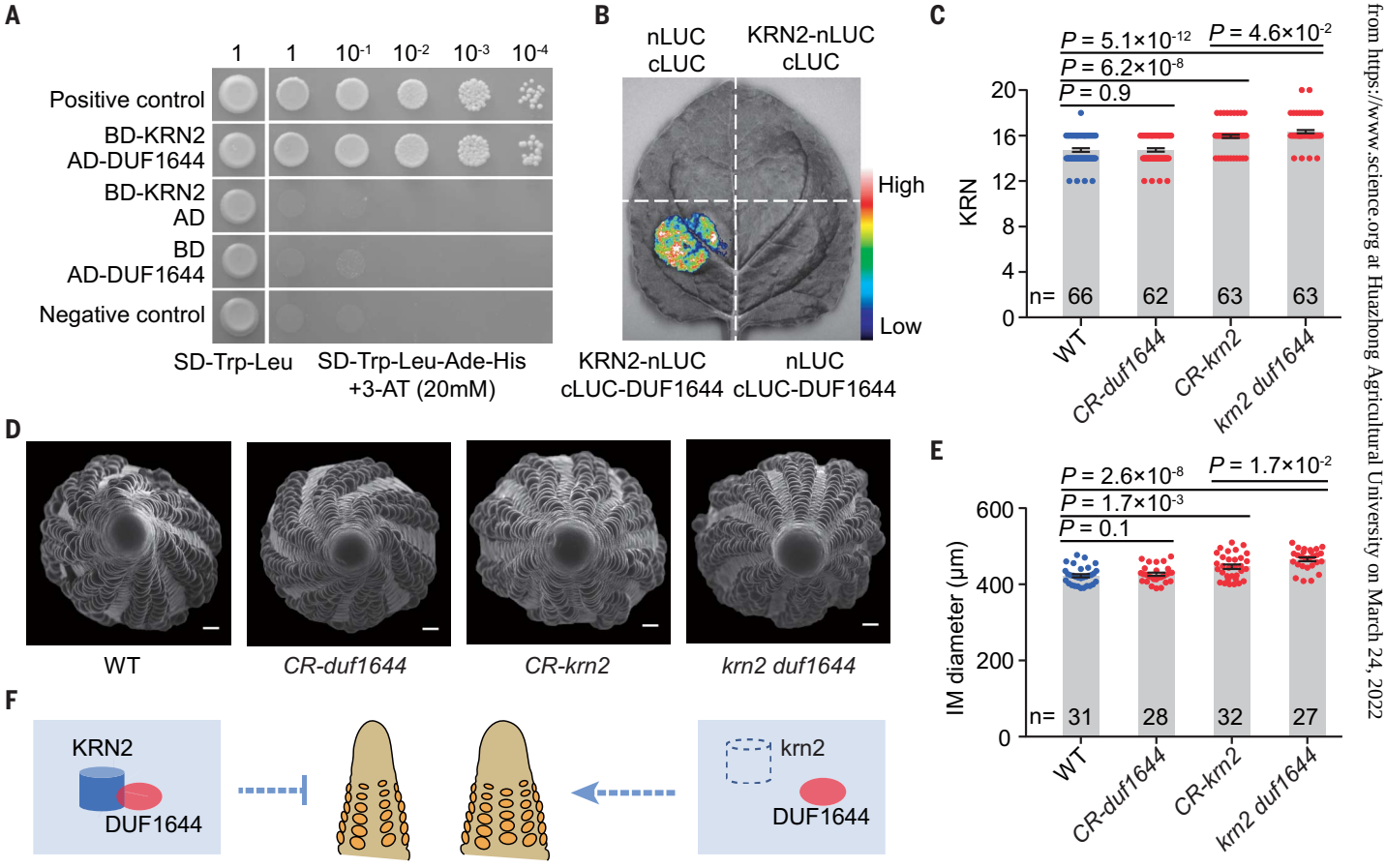


Fig. 2. KRN2 and its interactor, DUF1644, regulate KRN in a synergistic pathway. (**A** and **B**) Interaction between KRN2 and DUF1644 confirmed by Y2H assays (A) and the split firefly LUC complementation assay in tobacco (B). BD, binding domain; AD, activation domain; Ade, adenine; 3-AT, 3-aminotriazole. Fluorescence intensity represents the strength of the interaction. (**C** to **E**) KRN quantification (C), top-down scanning electron microscopy views of ear primordia (D), and IM diameter quantification (E) from wild type (WT) and single and double mutants of *krn2* and *duf1644*. In (C) and (E), data are means ± SEM. *P* values were calculated from two-tailed Student's *t* test. Scale bars in (D), 100 μm. (**F**) A hypothetical working model for *KRN2* in controlling KRN in maize. When KRN2 function is lost, DUF1644 cannot interact with it, resulting in an increase in IM diameter and, consequently, KRN. Otherwise, DUF1644 interacts with KRN2 to synergistically and negatively regulate IM diameter and KRN.

and, similar to the results in maize, we observed an increase in secondary branches from an average of 16.0 (±2.5) branches in the wild-type plants to as many as 18.9 (±3.5) in the null mutants (Fig. 3, D and E, and fig. S13). Consequently, an increase in grain number in the mutant panicles (up to 118.1 ± 11.9 grains) was observed relative to wild-type panicles (107.7 ± 9.5 grains) (Fig. 3F). In contrast, lines overexpressing *OsKRN2* had fewer secondary branches with fewer grains (Fig. 3, G to I, and fig. S13). These findings indicate that *OsKRN2* likely controls grain production in rice by affecting the number of secondary branches. In addition, Y2H and split firefly LUC complementation assays

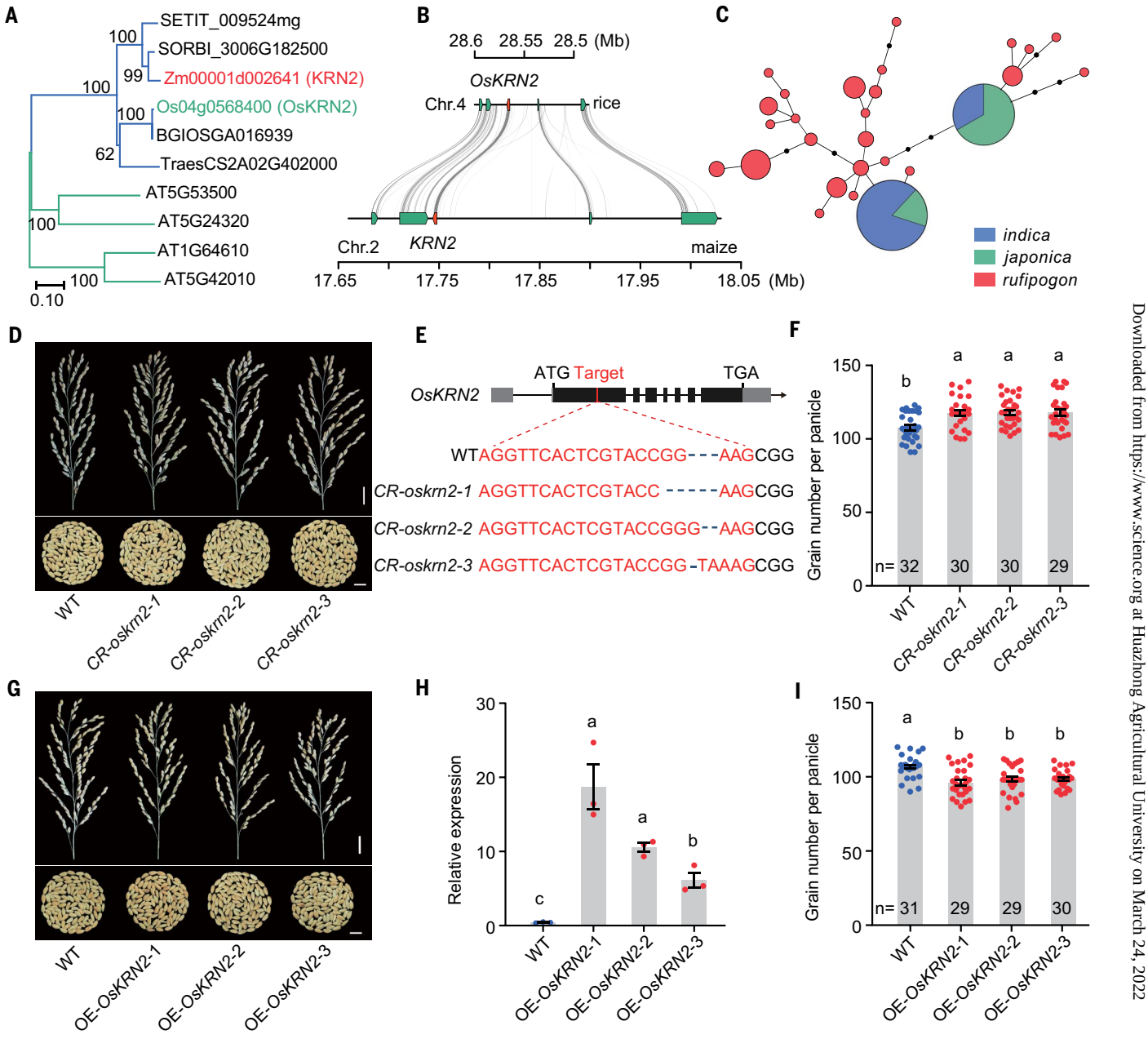


Fig. 3. *OsKRN2* is a selected gene in rice and contributes to grain number. (**A**) The neighbor-joining phylogenetic tree of *KRN2* and its orthologs from major cereal crops and *Arabidopsis*. Bootstrap values from 1000 replicates are indicated at each node; the scale represents branch length. (**B**) Comparative genomic analysis of syntenic and conserved sequences in the 0.4/0.1-Mb region around *KRN2*/*OsKRN2* (red) from maize (B73) and rice (Nipponbare). The aligned orthologs (from left to right, in green) are *Zm00001d002639*, *Zm00001d002640*, *Zm00001d002642*, and *Zm00001d002644* in maize and *Os04 g0568900*, *Os04 g0568800*, *Os04 g0567800*, and *Os04 g0566900* in rice. (**C**) A minimum-spanning tree for the ~1100-bp *OsKRN2* promoter and 5′UTR region. Each haplotype group is represented by a circle whose size is proportional to the individual number of the haplotype. (**D**) *CR-oskrn2* mutants increase panicle branching and grain number. (**E**) Null coding sequences of *CR-oskrn2* mutants. Gene diagram is shown. Black, exons; gray, UTRs. The red line indicates the guide RNA site. (**F**) Quantification of grain number per panicle from WT and *CR-oskrn2* mutants. (**G** to **I**) Panicle morphologies and grains per panicle (G), *OsKRN2* expression level (H), and grain number per panicle (I) of WT and *OsKRN2*-overexpressing transgenic lines. The expression levels of *OsKRN2* in (H) were quantified using qPCR and normalized to that of rice *ACTIN*. Scale bars in (D) and (G), 2 cm for panicle morphologies, 1 cm for grains. In (F), (H), and (I), data are means ± SEM, $n = 3$ in (H); different letters indicate significant differences at $P < 0.05$ (one-way analysis of variance followed by Tukey's multiple-comparison test).

confirmed a direct interaction between OsKRN2 and OsDUF1644 (fig. S14), suggesting that a conserved protein interaction controls KRN in maize and the number of secondary branches in rice.

Gene editing of *KRN2* and *OsKRN2* enhances grain yield in maize and rice field trials

We next asked whether gene editing of *KRN2/OsKRN2* could increase yield in the field, which serves as a proxy for applicability in breeding programs. Thus, we planted maize *KRN2* and rice *OsKRN2* gene-edited lines in multiple environments for yield testing (Fig. 4). For maize, field tests across three environments showed that two *KRN2*-edited lines (*CR-krn2-1* and *CR-krn2-2*) stably increased KRN by ~1.6 to 2.0 rows and kernel numbers per ear by ~27 to 53 kernels, resulting in an increase in grain yield of 9.0 to 10.5% (Fig. 4B, figs. S9B and S15, and table S3). Remarkably, these *krn2* knockouts did not alter plant architecture, flowering time, or ear length, although kernel width was slightly reduced (Fig. 4A and table S3). In rice, *OsKRN2*-edited lines (*CR-oskrn2-1* and *CR-oskrn2-2*) showed a similar increase in the number of grains per panicle (average increase of 9.8 to 10.3 grains per panicle) and grain yield per plant (7.9 to 8.2%), again with no obvious changes in other agronomic traits (Fig. 4, C and D, and fig. S16). These findings indicate that a complete loss-of-function allele of *KRN2/OsKRN2* increased grain yield without an apparent negative impact on other agronomic traits in tested environments. Whether the performance is consistent in diverse environments remains to be resolved. We neither identified any natural loss-of-function mutations of *KRN2/OsKRN2* nor detected association signals for grain number–related traits in natural populations, including hundreds of diverse lines in maize (table S4) and rice (*25*); this suggests that gene editing of *KRN2/OsKRN2* could provide a unique way to modify grain number in breeding lines.

Genome-wide convergent selection between maize and rice

Morphologically, cultivated maize and rice differ substantially from their ancestors and display a "domestication syndrome"—a common suite of traits that have changed in domesticated crops (*26*). These include loss of seed dispersal, decreased seed dormancy, and increased grain number, size, and weight (*1*) (Fig. 5A). In addition to *KRN2/OsKRN2* for grain number, two additional orthologous gene pairs—*ZmSh1/OsSh1* for seed shattering (*7*) and *ZmSWEET4c/OsSWEET4* for grain filling (*27*)—have also experienced convergent selection during maize and rice evolution. Hence, it is worth exploring the extent of molecular convergence on a genome-wide scale between maize and rice, which could reveal how often selection acts on orthologous gene pairs. We therefore reanalyzed selected genes using two large new datasets, including ~65 million SNPs in 507 maize inbred lines and 70 *parviglumis* accessions, as well as ~71 million SNPs in 461 cultivated rice and 257 wild rice accessions (fig. S17 and table S5). Using phylogenetic information (*3*, *28*), we estimated cross-population composite likelihood ratios (XP-CLRs) (*29*) followed by cross-validation on the basis of permutation tests for nucleotide diversity in the regions with the top 10% of XP-CLR scores

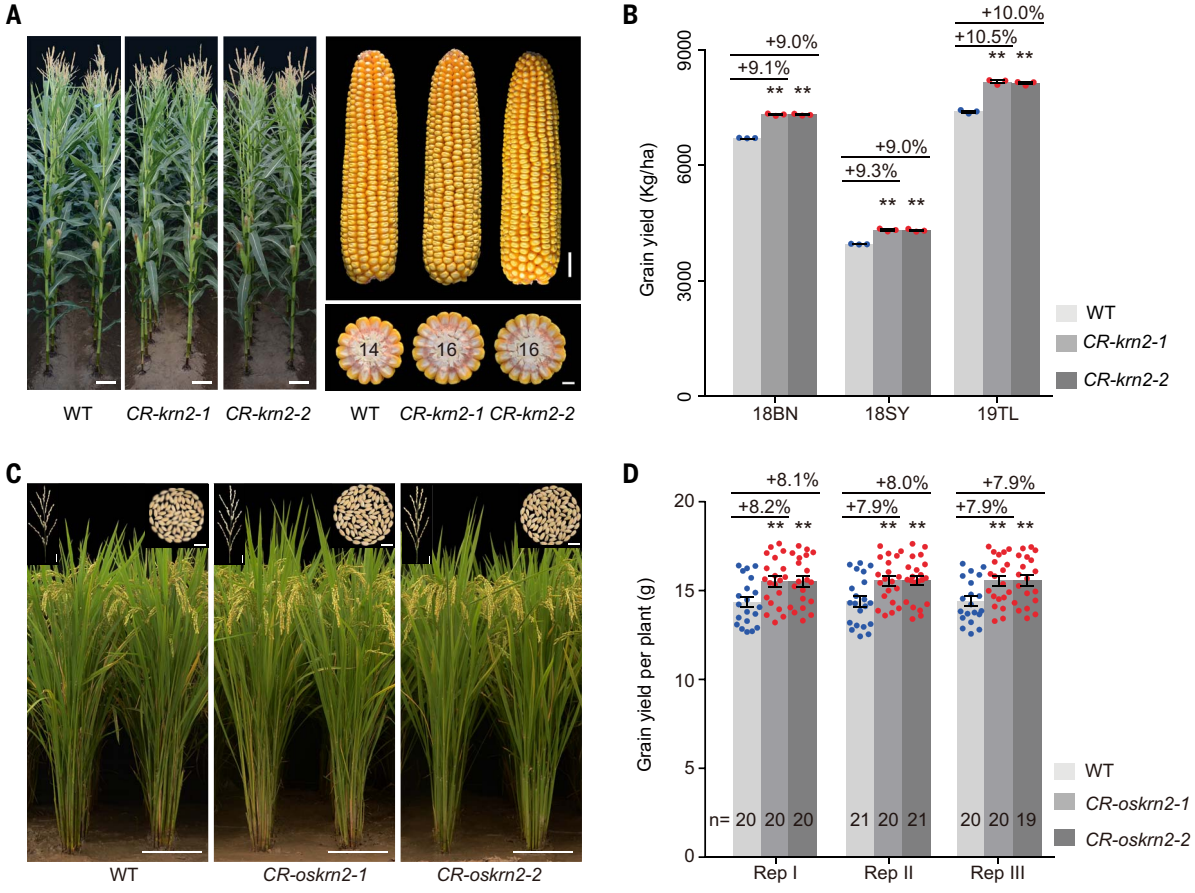


Fig. 4. Yield performance of *KRN2* and *OsKRN2* gene-edited lines under field conditions. (**A**) Plant and ear morphologies of WT, *CR-krn2-1*, and *CR-krn2-2*. (**B**) Grain yield of WT, *CR-krn2-1*, and *CR-krn2-2* in three locations. At each location, 26 to 38 ears for each replicate were quantified; data are means ± SEM from three replicates (shown as dots) in each location. 18BN, 18SY, and 19TL indicates the field trials performed in Bayan Nur in 2018, Sanya in 2018, and Tieling in 2019, respectively. (**C**) Plants, panicle, and grain morphologies of WT, *CR-oskrn2-1*, and *CR-oskrn2-2*. (**D**) Grain yield of WT, *CR-oskrn2-1*, and *CR-oskrn2-2* in one location with three replicates (Rep I to Rep III). For each replicate, 19 to 21 plants were quantified; data are means ± SEM. Scale bars in (A) and (C), 20 cm for plants, 2 cm for ears and panicles, 1 cm for ear transections and grains. In (B) and (D), $^{**}P < 0.01$ (two-tailed Student's *t* test).

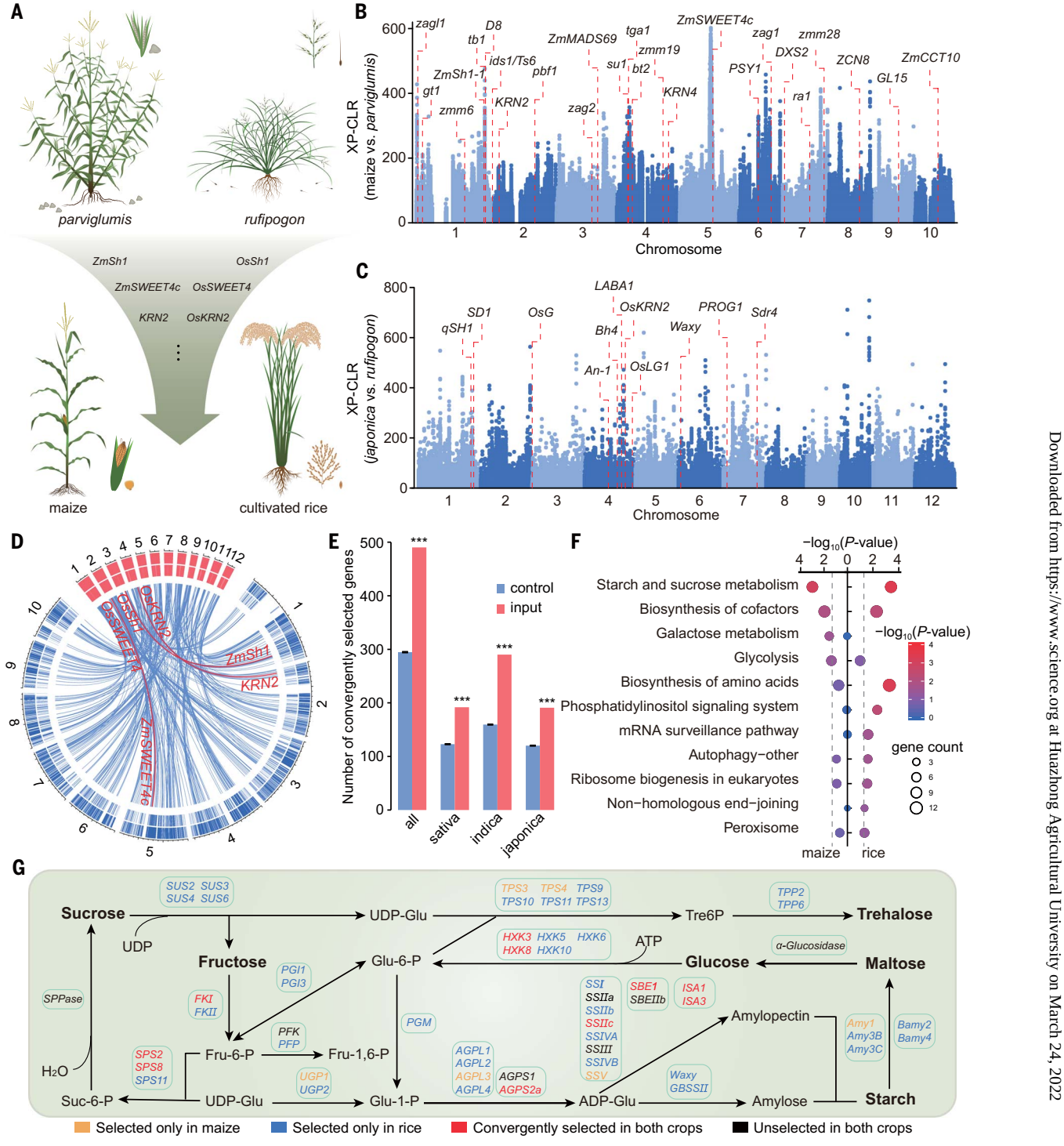


Fig. 5. Overview of convergent selection in maize and rice. (**A**) Convergence of traits in domesticated species versus wild ancestors, likely driven by genes with conserved functions. Three pairs of known orthologous genes under convergent selection are shown: *ZmSh1/OsSh1* for seed shattering (*7*), *ZmSWEET4c/OsSWEET4* for grain filling (*27*), and *KRN2/OsKRN2* for grain number. (**B** and **C**) Genome-wide XP-CLR values between maize and *parviglumis* (B) and between *japonica* and *rufipogon* (C). Regions of 1 kb and 300 bp were used to calculate the XP-CLR values for maize and rice, respectively; each point represents a value in a region. The red dashed lines indicate the positions of known selected genes detected in our study (table S7). (**D**) The distribution of selected regions (outer) and genes (inner) in maize (blue) and rice (red). The blue lines in the inner rings show the convergently selected genes that were syntenic in the maize and rice genomes. The red lines highlight the positions of genes that are known to have undergone convergent selection. (**E**) Convergent selection acts on the identified orthologs more often than expected by chance between maize and different rice datasets. ***$P < 0.001$ (pairwise comparison via permutation test). (**F**) Enriched pathways in maize or rice identified using g:Profiler (adjusted $P < 0.05$, multiple-testing correction via the g:SCS algorithm) among the 490 orthologous gene pairs under convergent selection. Circle size indicates the number of genes from the common gene hit list included in each pathway; circle color and *x*-axis position indicate the $-\log_{10}$-transformed *P* value. The vertical dashed lines indicate the significant threshold $P < 0.05$. (**G**) Detailed molecular representation of genes implicated in the starch and sucrose metabolism pathway during selection. Detailed information for these genes is listed in table S9.

(2). By comparing maize and *parviglumis*, we identified a total of 69.6 Mb of selected genomic regions that covered 3.3% of the maize B73 reference genome (30) and contained 3163 genes (Fig. 5B and tables S6 to S8). In this analysis, we identified two canonical domestication genes: *tb1*, which controls branching (31), and *tga1*, which controls the formation of the stony fruitcase (32) (Fig. 5B and table S7). In rice, we identified a total of 27.6, 25.8, and 26.3 Mb of selected genomic regions, including 7709, 10,196, and 7864 genes, respectively, by comparing *rufipogon* with *Oryza sativa* subsp. *japonica*, *O. sativa* subsp. *indica*, and *O. sativa*, respectively (hereafter, *japonica*, *indica*, and *sativa*; Fig. 5C, fig. S18, and tables S6 to S8). Collectively, these selected regions covered 17.2% (64.0 Mb) of the Nipponbare reference genome (33) and encompassed 18,755 genes (tables S6 to S8). Notably, 16 genes that are known to have undergone selection were detected, such as *PROG1* for growth habit (34, 35) and *OsLG1* for inflorescence architecture (36, 37) (Fig. 5C, fig. S18, and table S7).

By comparing these datasets, we identified 490 pairs of orthologous genes that had an apparent history of convergent selection in maize and rice (Fig. 5D and table S7), which is significantly greater than expected by chance (permutation test, $P < 0.001$; Fig. 5E), indicating that we observed an excess of shared selected genes in maize and rice on the basis of comparative genomics results. However, because the time period during which traits of common interest to humans were selected is far less than the time necessary for the evolutionary divergence between maize and rice (12), it is not surprising that only a limited number of selected genes in maize (15.5%) and rice (2.6%) experienced convergent selection during evolution. Of the 490 orthologous gene pairs, 67.8% were localized to syntenic blocks between the maize and rice genomes (Fig. 5D and table S7). In addition to the three known orthologous gene pairs that have undergone convergent selection mentioned above, the functions of an additional 13 orthologous gene pairs have been experimentally verified. These include *KN1/OSH1*, regulators of shoot meristem development (38, 39), and *SBE1*, which controls starch biosynthesis (40, 41) (table S7). The prevalence of shared selected genes with conserved functions supports the idea that common phenotypic shifts during maize and rice evolution acting on conserved genes are driven at least in part by convergent selection, which in maize and rice likely occurred both during and after domestication. Further characterization of these orthologs could provide insight into the processes driving human selection on cereal traits and, in turn, enhance knowledge-driven crop breeding.

Interestingly, the convergently selected orthologous genes appear to be significantly enriched in specific pathways in maize and rice (multiple-testing correction via the g:Profiler g:SCS algorithm, adjusted $P < 0.05$), including two commonly enriched pathways (starch and sucrose metabolism, biosynthesis of cofactors; Fig. 5F). Starch is the main component of cereal seeds and contributes substantially to grain yield, so it is reasonable that starch and sucrose metabolism is a primary pathway of convergent selection when human selection targeted high cereal productivity. Of 25 maize and 93 rice selected genes that are known contributors to the starch metabolic pathway (42, 43), we found that 11 orthologous gene pairs showed convergence at the genic level (Fig. 5G and table S9). The types and functions of starch synthesis–related enzymes are highly conserved, although their copy number and isoenzyme number differ between maize and rice (43). Hence, different functionally redundant paralogs could be differentially selected. For example, *UGP1* was selected in maize, whereas its homolog, *UGP2*, was selected in rice (Fig. 5G). In addition to whether a gene contributes to selected traits, whether a gene is selected is also affected by the levels of genetic diversity and the frequency of the preexisting desirable alleles in the ancestral population (1, 10, 44). For example, *TPS4* was selected in maize but not in rice (Fig. 5G). The various levels of genetic diversity in wild ancestors (e.g., there is less nucleotide diversity in maize than in its *parviglumis* ancestor, but there is more in cultivated rice than in its *rufipogon* ancestor; fig. S19) indicate that it may be difficult to target *TPS4* for selection in rice. These findings suggest that some orthologous genes function in the same metabolic or regulatory pathway for the same selected traits but have distinct selection routes among crops. Indeed, the degree of genetic convergence via convergent selection is related to the conservation and complexity of the gene network for a given selection (11).

Discussion

Collectively, we found a set of 490 orthologous genes that underwent convergent selection during maize and rice evolution, including *KRN2/OsKRN2*, which affect grain number. Because grain number is a common domestication syndrome trait as well as a key grain yield component in cereal crops, exploring the role of *KRN2/OsKRN2* across the cereals could provide new opportunities for enhancing production of other global crops, such as wheat. These findings suggest that the identification of genes that have undergone convergent selection could further inform breeding efforts of cereals. A deep understanding of the conservation of selection-driven genetic elements will not only enable more rapid innovation of the maize and rice germplasm but also inform knowledge-driven de novo domestication of new crops to meet the diverse needs of food production worldwide (45).

Methods summary

QTL mapping for KRN in the MT-6/B73 RIL population was performed using composite interval mapping (46). *qKRN2* was positionally cloned using a recombinant-derived progeny testing strategy (47). The functions of *KRN2*, *DUF1644*, and *OsKRN2* were investigated via mutant analysis, transgenic overexpression or CRISPR-Cas9 gene editing. The constructed overexpression and gene-editing vectors were transformed into maize inbred line LH244 or rice cultivar Nipponbare through an *Agrobacterium*-mediated transformation system. *KRN2*-based association mapping was performed using a mixed linear model (48) in a subset of 379 maize inbred lines (49). The yield tests of *KRN2/OsKRN2* gene-edited lines were carried out in a randomized block design with three replicates.

The expression levels of *KRN2* and *OsKRN2* in tested samples were detected via qPCR. The expression differences caused by the sequence polymorphisms in *KRN2* promoter or 5′UTR were tested by transient expression assays in maize protoplasts (50). The candidate interaction partners of KRN2 were identified using a Y2H screen by Hybrigenics Services. The interaction between KRN2/OsKRN2 and DUF1644/OsDUF1644 was validated by Y2H assays and split firefly LUC complementation assays in tobacco (51). The fresh IM was imaged with a scanning electron microscope, and then the IM diameter was measured with an EZ4 HD stereo microscope and corresponding LAS EZ software.

To determine the molecular evolution of the *KRN2* or *OsKRN2* locus, we sequenced their target regions in a set of cultivar or landrace, and wild relatives in maize or rice. Nucleotide diversity (π) and Tajima's D were calculated using DnaSP software (52). Coalescent simulations were performed for *KRN2* using the MS program (53). A minimum spanning tree was constructed for *OsKRN2* using Arlequin software (54).

To explore the extent of molecular convergence on a genome-wide scale between maize and rice, we collected or generated two high-depth SNP datasets in 507 maize inbred lines and 70 *parviglumis* accessions, and 461 cultivated rice and 257 wild rice accessions. The genetic relationship of rice accessions was estimated using ADMIXTURE software (55) and confirmed by principal components analysis using GCTA software (56). The SNP alignment (57) and phylogenetic tree construction in maize and rice were performed using SNPhylo software (58). The genome-wide scans for selection signals were performed via an XP-CLR method (29) followed by cross-validation on the basis of permutation tests for the nucleotide diversity ratio between wild and cultivar

accessions (*2*, *57*). The genes that are located within the selected regions were regarded as having undergone selection. The maize and rice orthologs were identified by reciprocal blastp with protein sequence coverage of ≥0.7. Collinearity was analyzed using MCScanX software (*59*). A permutation test was performed for the enrichment of the orthologous genes under convergent selection (*57*). Finally, the g:Profiler program (*60*) was used for KEGG pathway enrichment analysis of genes under convergent selection.

All details of the materials and methods, including those summarized above, are provided in the supplementary materials.

REFERENCES AND NOTES

1. J. F. Doebley, B. S. Gaut, B. D. Smith, The molecular genetics of crop domestication. *Cell* **127**, 1309–1321 (2006). doi: 10.1016/j.cell.2006.12.006; pmid: 17190597
2. M. B. Hufford *et al*., Comparative population genomics of maize domestication and improvement. *Nat. Genet.* **44**, 808–811 (2012). doi: 10.1038/ng.2309; pmid: 22660546
3. X. Huang *et al*., A map of rice genome variation reveals the origin of cultivated rice. *Nature* **490**, 497–501 (2012). doi: 10.1038/nature11532; pmid: 23034647
4. A. Pankin, M. von Korff, Co-evolution of methods and thoughts in cereal domestication studies: A tale of barley (*Hordeum vulgare*). *Curr. Opin. Plant Biol.* **36**, 15–21 (2017). doi: 10.1016/j.pbi.2016.12.001; pmid: 28011443
5. Y. Liang, H. J. Liu, J. Yan, F. Tian, Natural variation in crops: Realized understanding, continuing promise. *Annu. Rev. Plant Biol.* **72**, 357–385 (2021). doi: 10.1146/annurev-arplant-080720-090632; pmid: 33481630
6. A. H. Paterson *et al*., Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. *Science* **269**, 1714–1718 (1995). doi: 10.1126/science.269.5231.1714; pmid: 17821643
7. Z. Lin *et al*., Parallel domestication of the *Shattering1* genes in cereals. *Nat. Genet.* **44**, 720–724 (2012). doi: 10.1038/ng.2281; pmid: 22581231
8. M. Wang *et al*., Parallel selection on a dormancy gene during domestication of crops from multiple families. *Nat. Genet.* **50**, 1435–1441 (2018). doi: 10.1038/s41588-018-0229-2; pmid: 30250128
9. H. Tang *et al*., Seed shattering in a wild sorghum is conferred by a locus unrelated to domestication. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 15824–15829 (2013). doi: 10.1073/pnas.1305213110; pmid: 24019506
10. B. S. Gaut, Evolution is an experiment: Assessing parallelism in crop domestication and experimental evolution. *Mol. Biol. Evol.* **32**, 1661–1671 (2015). doi: 10.1093/molbev/msv105; pmid: 26012904
11. Q. Chen, W. Li, L. Tan, F. Tian, Harnessing knowledge from maize and rice domestication for new crop breeding. *Mol. Plant* **14**, 9–26 (2021). doi: 10.1016/j.molp.2020.12.006; pmid: 33316465
12. B. S. Gaut, Evolutionary dynamics of grass genomes. *New Phytol.* **154**, 15–28 (2002). doi: 10.1046/j.1469-8137.2002.00352.x
13. M. D. Gale, K. M. Devos, Comparative genetics in the grasses. *Proc. Natl. Acad. Sci. U.S.A.* **95**, 1971–1974 (1998). doi: 10.1073/pnas.95.5.1971; pmid: 9482816
14. A. H. Paterson, J. E. Bowers, B. A. Chapman, Ancient polyploidization predating divergence of the cereals, and its consequences for comparative genomics. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 9903–9908 (2004). doi: 10.1073/pnas.0307901101; pmid: 15161969
15. M. R. Woodhouse, M. B. Hufford, Parallelism and convergence in post-domestication adaptation in cereal grasses. *Philos. Trans. R. Soc. London Ser. B* **374**, 20180245 (2019). doi: 10.1098/rstb.2018.0245; pmid: 31154975
16. L. Cai, K. Li, X. Yang, J. Li, Identification of large-effect QTL for kernel row number has potential for maize yield improvement. *Mol. Breed.* **34**, 1087–1096 (2014). doi: 10.1007/s11032-014-0101-8
17. C. U. Stirnimann, E. Petsalaki, R. B. Russell, C. W. Müller, WD40 proteins propel cellular networks. *Trends Biochem. Sci.* **35**, 565–574 (2010). doi: 10.1016/j.tibs.2010.04.003; pmid: 20451393
18. B. P. Jain, S. Pandey, WD40 repeat proteins: Signalling scaffold with diverse functions. *Protein J.* **37**, 391–406 (2018). doi: 10.1007/s10930-018-9785-7; pmid: 30069656
19. K. A. Lease *et al*., A mutant Arabidopsis heterotrimeric G-protein β subunit affects leaf, flower, and fruit development. *Plant Cell* **13**, 2631–2641 (2001). doi: 10.1105/tpc.010315; pmid: 11752377
20. Y. Wu *et al*., Presence of tannins in sorghum grains is conditioned by different natural alleles of *Tannin1*. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 10281–10286 (2012). doi: 10.1073/pnas.1201700109; pmid: 22699509
21. Q. Wu *et al*., The maize heterotrimeric G protein β subunit controls shoot meristem development and immune responses. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 1799–1805 (2020). doi: 10.1073/pnas.1917577116; pmid: 31852823
22. M. J. Thomson *et al*., Mapping quantitative trait loci for yield, yield components and morphological traits in an advanced backcross population between *Oryza rufipogon* and the *Oryza sativa* cultivar Jefferson. *Theor. Appl. Genet.* **107**, 479–493 (2003). doi: 10.1007/s00122-003-1270-8; pmid: 12736777
23. C. Li, A. Zhou, T. Sang, Genetic analysis of rice domestication syndrome with the wild annual species, *Oryza nivara*. *New Phytol.* **170**, 185–193 (2006). doi: 10.1111/j.1469-8137.2005.01647.x; pmid: 16539615
24. P. Bommert, N. Satoh-Nagasawa, D. Jackson, H. Y. Hirano, Genetics and evolution of inflorescence and flower development in grasses. *Plant Cell Physiol.* **46**, 69–78 (2005). doi: 10.1093/pcp/pci504; pmid: 15659432
25. X. Bai *et al*., Genome-wide association analysis reveals different genetic control in panicle architecture between *indica* and *japonica* rice. *Plant Genome* **9**, (2016). doi: 10.3835/plantgenome2015.11.0115
26. K. Hammer, Das Domestikationssyndrom. *Kulturpflanze* **32**, 11–34 (1984). doi: 10.1007/BF02098682
27. D. Sosso *et al*., Seed filling in domesticated maize and rice depends on SWEET-mediated hexose transport. *Nat. Genet.* **47**, 1489–1493 (2015). doi: 10.1038/ng.3422; pmid: 26523777
28. Y. Matsuoka *et al*., A single domestication for maize shown by multilocus microsatellite genotyping. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 6080–6084 (2002). doi: 10.1073/pnas.052125199; pmid: 11983901
29. H. Chen, N. Patterson, D. Reich, Population differentiation as a test for selective sweeps. *Genome Res.* **20**, 393–402 (2010). doi: 10.1101/gr.100545.109; pmid: 20086244
30. Y. Jiao *et al*., Improved maize reference genome with single-molecule technologies. *Nature* **546**, 524–527 (2017). doi: 10.1038/nature22971; pmid: 28605751
31. A. Studer, Q. Zhao, J. Ross-Ibarra, J. Doebley, Identification of a functional transposon insertion in the maize domestication gene *tb1*. *Nat. Genet.* **43**, 1160–1163 (2011). doi: 10.1038/ng.942; pmid: 21946354
32. H. Wang *et al*., The origin of the naked grains of maize. *Nature* **436**, 714–719 (2005). doi: 10.1038/nature03863; pmid: 16079849
33. S. A. Goff *et al*., A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). *Science* **296**, 92–100 (2002). doi: 10.1126/science.1068275; pmid: 11935018
34. L. Tan *et al*., Control of a key transition from prostrate to erect growth in rice domestication. *Nat. Genet.* **40**, 1360–1364 (2008). doi: 10.1038/ng.197; pmid: 18820699
35. J. Jin *et al*., Genetic control of rice plant architecture under domestication. *Nat. Genet.* **40**, 1365–1369 (2008). doi: 10.1038/ng.247; pmid: 18820696
36. T. Ishii *et al*., *OsLG1* regulates a closed panicle trait in domesticated rice. *Nat. Genet.* **45**, 462–465 (2013). doi: 10.1038/ng.2567; pmid: 23435087
37. Z. Zhu *et al*., Genetic control of inflorescence architecture during rice domestication. *Nat. Commun.* **4**, 2200 (2013). doi: 10.1038/ncomms3200; pmid: 23884108
38. R. A. Kerstetter, D. Laudencia-Chingcuanco, L. G. Smith, S. Hake, Loss-of-function mutations in the maize homeobox gene, *knotted1*, are defective in shoot meristem maintenance. *Development* **124**, 3045–3054 (1997). doi: 10.1242/dev.124.16.3045; pmid: 9272946
39. K. Tsuda, Y. Ito, Y. Sato, N. Kurata, Positive autoregulation of a *KNOX* gene is essential for shoot apical meristem maintenance in rice. *Plant Cell* **23**, 4368–4381 (2011). doi: 10.1105/tpc.111.090050; pmid: 22207572
40. S. L. Blauth *et al*., Identification of *Mutator* insertional mutants of starch-branching enzyme 1 (*sbe1*) in *Zea mays* L. *Plant Mol. Biol.* **48**, 287–297 (2002). doi: 10.1023/A:1013335217744; pmid: 11855730
41. H. Satoh *et al*., Starch-branching enzyme I-deficient mutation specifically affects the structure and properties of starch in rice endosperm. *Plant Physiol.* **133**, 1111–1121 (2003). doi: 10.1104/pp.103.021527; pmid: 14526120
42. F. Fichtner, J. E. Lunn, The role of trehalose 6-phosphate (Tre6P) in plant metabolism and development. *Annu. Rev. Plant Biol.* **72**, 737–760 (2021). doi: 10.1146/annurev-arplant-050718-095929; pmid: 33428475
43. L. Huang, H. Tan, C. Zhang, Q. Li, Q. Liu, Starch biosynthesis in cereal endosperms: An updated review over the last decade. *Plant Commun.* **2**, 100237 (2021). doi: 10.1016/j.xplc.2021.100237; pmid: 34746765
44. L. Wang *et al*., Molecular parallelism underlies convergent highland adaptation of maize landraces. *Mol. Biol. Evol.* **38**, 3567–3580 (2021). doi: 10.1093/molbev/msab119; pmid: 33905497
45. A. R. Fernie, J. Yan, *De novo* domestication: An alternative route toward new crops for the future. *Mol. Plant* **12**, 615–631 (2019). doi: 10.1016/j.molp.2019.03.016; pmid: 30999078
46. Z. B. Zeng, Precision mapping of quantitative trait loci. *Genetics* **136**, 1457–1468 (1994). doi: 10.1093/genetics/136.4.1457; pmid: 8013918
47. J. Tian *et al*., Teosinte ligule allele narrows plant architecture and enhances high-density maize yields. *Science* **365**, 658–664 (2019). doi: 10.1126/science.aax5482; pmid: 31416957
48. J. Yu *et al*., A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. *Nat. Genet.* **38**, 203–208 (2006). doi: 10.1038/ng1702; pmid: 16380716
49. X. Yang *et al*., Characterization of a global germplasm collection and its potential utilization for analysis of complex quantitative traits in maize. *Mol. Breed.* **28**, 511–526 (2011). doi: 10.1007/s11032-010-9500-7
50. C. Huang *et al*., *ZmCCT9* enhances maize adaptation to higher latitudes. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E334–E341 (2018). doi: 10.1073/pnas.1718058115; pmid: 29279404
51. Z. Zhang, J. Yang, Y. Wu, Transcriptional regulation of zein gene expression in maize through the additive and synergistic action of opaque2, prolamine-box binding factor, and O2 heterodimerizing proteins. *Plant Cell* **27**, 1162–1172 (2015). doi: 10.1105/tpc.15.00035; pmid: 25901087
52. P. Librado, J. Rozas, DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**, 1451–1452 (2009). doi: 10.1093/bioinformatics/btp187; pmid: 19346325
53. R. R. Hudson, Generating samples under a Wright-Fisher neutral model of genetic variation. *Bioinformatics* **18**, 337–338 (2002). doi: 10.1093/bioinformatics/18.2.337; pmid: 11847089
54. L. Excoffier, H. E. Lischer, Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**, 564–567 (2010). doi: 10.1111/j.1755-0998.2010.02847.x; pmid: 21565059
55. D. H. Alexander, J. Novembre, K. Lange, Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**, 1655–1664 (2009). doi: 10.1101/gr.094052.109; pmid: 19648217
56. J. Yang, S. H. Lee, M. E. Goddard, P. M. Visscher, GCTA: A tool for genome-wide complex trait analysis. *Am. J. Hum. Genet.* **88**, 76–82 (2011). doi: 10.1016/j.ajhg.2010.11.011; pmid: 21167468
57. W. Chen *et al*., Code and processed data for "Convergent selection of a WD40 protein that enhances grain yield in maize and rice." Figshare (2022). doi: 10.6084/m9.figshare.18104336
58. T. H. Lee, H. Guo, X. Wang, C. Kim, A. H. Paterson, SNPhylo: A pipeline to construct a phylogenetic tree from huge SNP data. *BMC Genomics* **15**, 162 (2014). doi: 10.1186/1471-2164-15-162; pmid: 24571581
59. Y. Wang *et al*., *MCScanX*: A toolkit for detection and evolutionary analysis of gene synteny and collinearity. *Nucleic Acids Res.* **40**, e49 (2012). doi: 10.1093/nar/gkr1293; pmid: 22217600

60. U. Raudvere *et al*., g:Profiler: a web server for functional enrichment analysis and conversions of gene lists (2019 update). *Nucleic Acids Res.* **47**, W191–W198 (2019). doi: 10.1093/nar/gkz369; pmid: 31066453

ACKNOWLEDGMENTS

We thank L. Tan and H. Chen for help growing rice, G. Wang for sharing the wild rice leaves, and J. Ross-Ibarra for constructive suggestions on manuscript revision. **Funding:** Supported by the National Natural Science Foundation of China (91935302, 31421005, 31961133002, and 91435205), the National Key Research and Development Program of China (2020YFE0202300), Beijing Outstanding Young Scientist Program (BJJWZYJH01201910019026), Young Elite Scientists Sponsorship Program by CAST (2019QNRC001), and NSF (IOS-2129189). **Author contributions:** X.Y., J.Y., and J.L. conceived and designed this study. W.C., X.Z., J.G., S.J., X-Y.Z., L-C.C., J.X., L.Z., Y.H., Y.X., G.X., Y.W., S-H.W., S.W., J.C., and S.C. performed experiments. L.C., X.Z., W.C., N.Y., M.W., and P.Y. analyzed data. F.Y., D.J., C.S., F.Q., F.T., and A.R.F. contributed valuable suggestions on this study. W.C., L.C., X.Z., N.Y., J.Y., and X.Y. wrote the manuscript. All the authors edited and proofed the manuscript. **Competing interests:** D.J. serves as a consultant for Inari Agriculture, and the authors declare no competing interests. A patent with application no. PCT/CN2018/117844 is pending. **Data and materials availability:** All data are available in the main text, supplementary materials, public databases, or referenced permanent online repositories. Sequence data were deposited in NCBI GenBank under accession number MW238854-MW239029 for *KRN2*, MW219821-MW219975 and OK655843-OK655881 for *OsKRN2*, PRJNA771523 for all CRISPR knockouts in maize and rice, and PRJNA771230 for our resequenced rice data. The alignments used for phylogenetic tree and all codes are provided online at Figshare (*57*).

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abg7985
Materials and Methods
Figs. S1 to S19
Tables S1 to S12
References (*61*–*86*)
MDAR Reproducibility Checklist

View/request a protocol for this paper from *Bio-protocol*.

1 February 2021; resubmitted 27 November 2021
Accepted 24 February 2022
10.1126/science.abg7985

Science

Convergent selection of a WD40 protein that enhances grain yield in maize and rice

Wenkang ChenLu ChenXuan ZhangNing YangJianghua GuoMin WangShenghui JiXiangyu ZhaoPengfei YinLichun CaiJing XuLili ZhangYingjia HanYingni XiaoGen XuYuebin WangShuhui WangSheng WuFang YangDavid JacksonJinkui ChengSaihua ChenChuanqing SunFeng QinFeng TianAlisdair R. FernieJiansheng LiJianbing YanXiaohong Yang

Science, 375 (6587), eabg7985. • DOI: 10.1126/science.abg7985

Amazing grains

Maize and rice are important sources of human calories and have been, mostly independently, subject to human selection for thousands of years, often for similar traits such as grain yield. W. Chen *et al*. examined the genomes of accessions of domestic maize and its wild relative, teosinte, for evolutionary signals of selection. From these sequences, the authors identified a quantitative trait locus in maize that increased kernel row number. Fine mapping determined that this locus contains a candidate gene, *KRN2*. Gene-editing experiments of *KRN2* and its homolog in rice determined that a similar phenotype increasing grain number per plant could be recapitulated. Thus, identifying genes under selection in one cereal provides useful fodder for crop improvements. —LMZ

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.