PLANT SCIENCE

Ethylene-gibberellin signaling underlies adaptation of rice to periodic flooding

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Most plants do poorly when flooded. Certain rice varieties, known as deepwater rice, survive periodic flooding and consequent oxygen deficiency by activating internode growth of stems to keep above the water. Here, we identify the gibberellin biosynthesis gene, *SD1* (*SEMIDWARF1*), whose loss-of-function allele catapulted the rice Green Revolution, as being responsible for submergence-induced internode elongation. When submerged, plants carrying the deepwater rice–specific *SD1* haplotype amplify a signaling relay in which the *SD1* gene is transcriptionally activated by an ethylene-responsive transcription factor, OsEIL1a. The SD1 protein directs increased synthesis of gibberellins, largely GA_4, which promote internode elongation. Evolutionary analysis shows that the deepwater rice–specific haplotype was derived from standing variation in wild rice and selected for deepwater rice cultivation in Bangladesh.

Deepwater rice varieties, grown mainly in Asian lowland areas, respond to months-long deep flooding by increasing plant height as water levels rise. The deepwater growth response is due to rapid internode elongation, allowing leaves to remain above the water surface; internode elongation is accomplished by both cell proliferation and elongation (*1*). Only *SNORKEL1* and *SNORKEL2* (*SK1/2*), encoding transcription factors with high similarity to the flash flood–tolerant regulator SUB1A (*2*), have previously been identified as causal genes for the deepwater response (*3*). Although ethylene and gibberellins are thought to trigger this response (*1*, *4*), the molecular mechanism(s) underlying the interaction among these hormones during internode elongation remains elusive.

To identify factors regulating the deepwater response in rice, we carried out a genome-wide association study (GWAS) with a diversity panel of Asian rice and deepwater rice varieties (table S1). We measured nine deepwater traits (Fig. 1A, fig. S1, and table S2) and selected total internode length measured 7 days after submergence at the 10-leaf stage (TILS) as a representative trait (Fig. 1B and figs. S2 and S3). The GWAS with the TILS value as a proxy for the deepwater response (figs. S4 to S6) revealed six quantitative trait loci (QTLs) exceeding the significance threshold (Fig. 1C and table S3). The GWAS peak on chromosome 1 was located within a QTL, $qTIL1^{C9285}$, which we had detected in a previous analysis of the deepwater response (*5*) (fig. S7). To identify the gene(s) responsible for $qTIL1^{C9285}$, we conducted high-resolution linkage analysis by using a mapping population from a cross between near-isogenic lines NIL-12 and NIL-1+12, both containing chromosomal introgressions from deepwater rice (C9285 variety) in a nondeepwater rice (T65 variety) background (figs. S8 to S10). The candidate region was delimited to a 5.5-kb stretch that included the *OsGA20ox2* (*Oryza sativa gibberellin 20–oxidase 2*) gene. Also known as *SD1* (*SEMIDWARF1*), this gene encodes a gibberellin biosynthesis enzyme; its null allele produces a semidwarf phenotype and was selected during the rice Green Revolution (*6*) (Fig. 1D and fig. S11). Introgression of the C9285 *SD1* allele ($SD1^{C9285}$) into NIL-12 increased total internode length in response to submergence (Fig. 1E), and near-constitutive expression of $SD1^{C9285}$ increased internode elongation even without submergence (fig. S12). Furthermore, NIL-12 with a null allele of *SD1* showed shorter total internode length in response to submergence than either NIL-12 or NIL-1+12 (fig. S13). These results suggest that $SD1^{C9285}$ is responsible for $qTIL1^{C9285}$, which contributes to the promotion of internode elongation in response to submergence.

Next, we compared polymorphisms in the GWAS panel across the $qTIL1^{C9285}$ candidate region and identified six *SD1* haplogroups (fig. S14 and table S4). The haplogroup belonging to C9285 (Hap-6) had the highest TILS value in the presence of *SK1/2* (Fig. 2A and fig. S15). Hereafter, we refer to the $SD1^{C9285}$ haplotype, including the 17 specific polymorphisms in the promoter and second intron, as the deepwater rice–specific haplotype (DWH) (fig. S14). In response to submergence, *SD1* transcript accumulation in C9285 was higher than that in T65 (Fig. 2B) and diminished from 6 hours until 12 hours after submergence, consistent with negative feedback of gibberellin suppressing *SD1* transcription (*7*) (fig. S16). Accumulation of *SD1* transcripts was observed in the elongating internode (Fig. 2C). NIL-1 also showed induced *SD1* transcript accumulation (figs. S8A and S17); we found a significant association between the level of *SD1* transcript accumulation and internode elongation in recombinant lines from the linkage analysis (fig. S18). Furthermore, varieties harboring the DWH and Hap-5 showed higher *SD1* transcript accumulation than varieties containing other *SD1* haplotypes, regardless of the presence of *SK1/2* (fig. S19). Our results suggest that the DWH potentiates *SD1* transcript accumulation in response to submergence, independently of *SK1/2*, and that this induction works in synergy with *SK1/2* to enhance internode elongation in response to submergence.

We next tested *SD1* transcription in response to ethylene (*1*, *4*). Ethylene application showed higher *SD1* transcript accumulation in C9285 and NIL-1 than in T65 (Fig. 2D and fig. S20) even in the presence of a protein synthesis inhibitor (fig. S21), suggesting that ethylene-inducible *SD1* transcription is mediated by the DWH and that *SD1* is regulated by the ethylene signaling pathway without de novo protein synthesis. The ethylene response involves stabilization and accumulation of the transcription factor EIN3 (ETHYLENE INSENSITIVE 3) family to activate the transcription of ethylene-responsive genes (*8*), so we investigated the transcriptional regulation of *SD1* by an EIN3 homolog, OsEIL1a protein (fig. S22). Near-constitutive expression of OsEIL1a fused with a repression domain (*9*) resulted in suppression of *SD1* induction in response to ethylene treatment (Fig. 2E and fig. S23). A transactivation assay demonstrated the direct activation of the $SD1^{C9285}$ promoter by OsEIL1a, whereas SK1/2 was not able to transactivate the $SD1^{C9285}$ promoter (fig. S24). Specific binding of OsEIL1a to the $SD1^{C9285}$ promoter is supported by assays using a chemical induction

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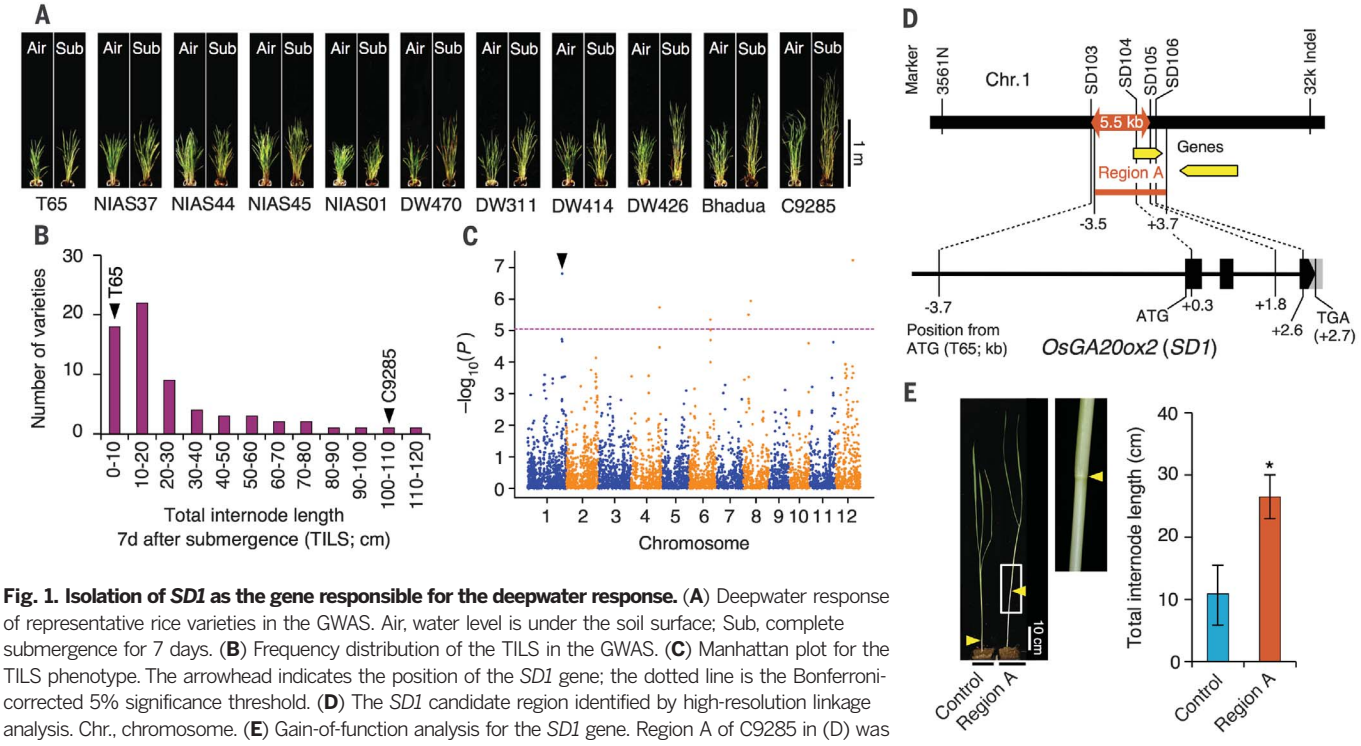

Fig. 1. Isolation of *SD1* as the gene responsible for the deepwater response. (**A**) Deepwater response of representative rice varieties in the GWAS. Air, water level is under the soil surface; Sub, complete submergence for 7 days. (**B**) Frequency distribution of the TILS in the GWAS. (**C**) Manhattan plot for the TILS phenotype. The arrowhead indicates the position of the *SD1* gene; the dotted line is the Bonferroni-corrected 5% significance threshold. (**D**) The *SD1* candidate region identified by high-resolution linkage analysis. Chr., chromosome. (**E**) Gain-of-function analysis for the *SD1* gene. Region A of C9285 in (D) was transformed into NIL-12 (mean ± SD, $n \geq 3$ replicates). *$P < 0.05$ (Student's t test). Arrowheads indicate positions of nodes. The boxed area is shown to the right at greater magnification.

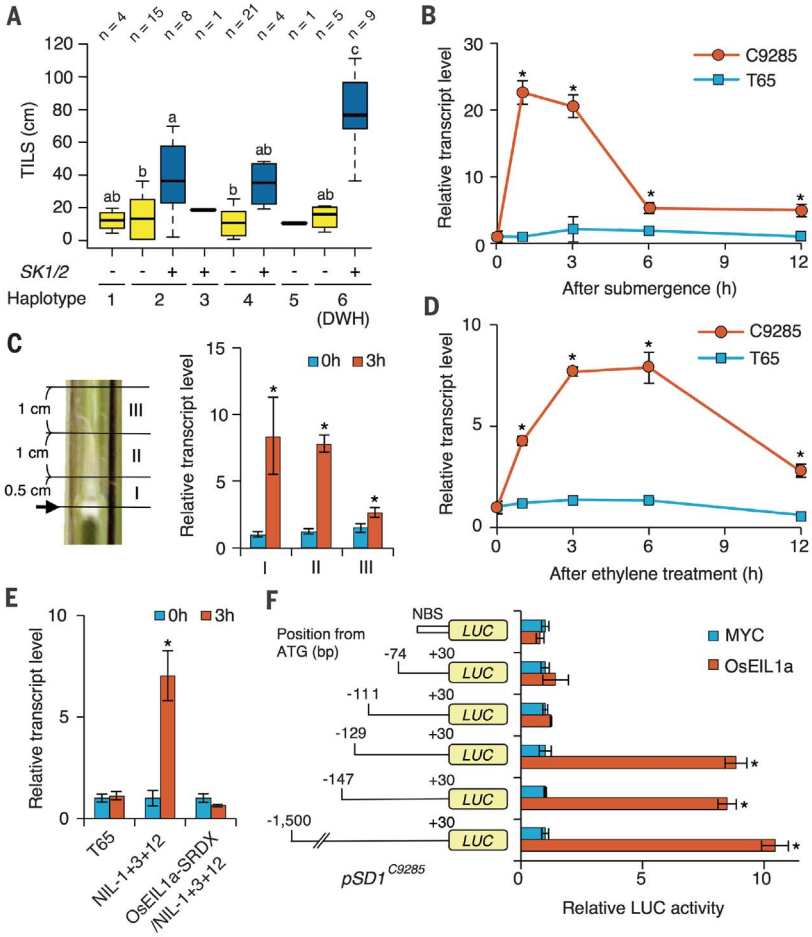

Fig. 2. Contribution of *SD1* to internode elongation in response to submergence via ethylene signaling. (**A**) Box plots of TILS values for six *SD1* haplotypes and absence (−) or presence (+) of *SK1/2*. Box edges represent the 0.25 quantile and 0.75 quantile, with median values shown by bold lines; whiskers indicate 1.5 times the interquartile range. Different letters denote significant differences according to the Tukey-Kramer test ($P < 0.05$). (**B**) Quantitative PCR (qPCR) analysis of *SD1* transcription under submergence treatment. (**C**) qPCR analysis of submergence-induced *SD1* transcription in different tissue regions (I to III) above the top node (arrow). (**D**) qPCR analysis of *SD1* transcription under ethylene treatment. (**E**) qPCR analysis determining the effect of *OsEIL1a-SRDX* near-constitutive expression on the induction of *SD1* transcription by ethylene. Values in (B) to (E) are the mean ± SD ($n = 3$). *$P < 0.05$ (Student's t test) versus 0 hours. (**F**) Transactivation of the *SD1* promoter by OsEIL1a in rice protoplasts (mean ± SD, $n = 3$). *$P < 0.05$ (Student's t test) versus the MYC control. NBS, 35S minimal promoter; LUC, luciferase.

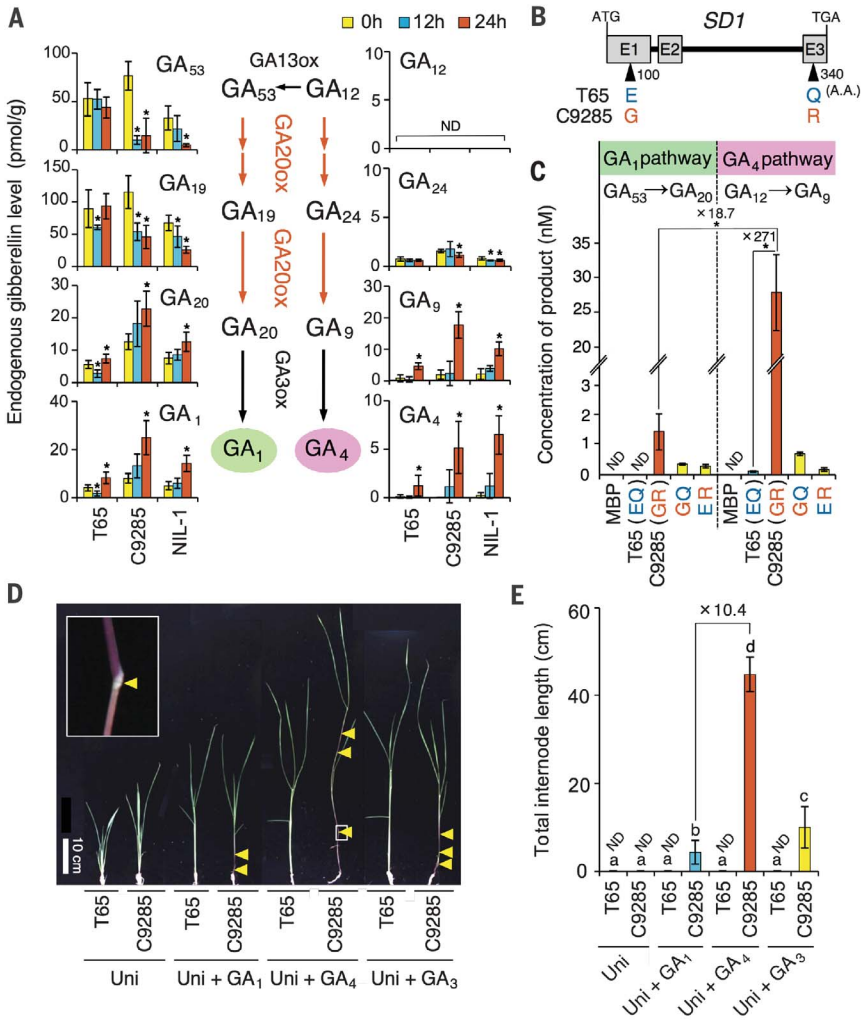

Fig. 3. Contribution of SD1-derived GA_4 for internode elongation. (**A**) Gibberellin levels in elongating internodes under submergence treatment (mean ± SD, $n \geq 3$). ox, -oxidase; ND, not detected. *$P < 0.05$ (Student's t test) versus 0 hours. (**B**) Exonic SNPs of *SD1* between T65 and C9285. E1 to E3, exons 1 to 3; E, Glu; Q, Gln; G, Gly; R, Arg; A.A., amino acid. (**C**) Enzymatic activities of recombinant SD1 proteins for 10-min reactions against GA_{53} or GA_{12} (mean ± SD, $n = 3$). MBP, maltose-binding protein. *$P < 0.05$ (Student's t test). (**D** and **E**) Effects of different active gibberellin species (10^{-5} M) on internode elongation (means ± SD, $n \geq 9$). Uni, 10^{-6} M uniconazole; arrowheads, positions of nodes. Different letters denote significant differences according to the Tukey-Kramer test ($P < 0.05$).

system, the OsEIL1a effector fused with an activation domain, and a mutant form of OsEIL1a (figs. S25 and S26). Promoter deletion, scanning mutagenesis, and synthetic promoter analyses revealed that a 13–base pair (bp) sequence of the $SD1^{C9285}$ promoter region (positions −123 to −111 from the start codon) is required for OsEIL1a transactivation (Fig. 2F and fig. S27, A and B). We confirmed direct binding of the OsEIL1 protein to the $SD1^{C9285}$ promoter region by an in vitro protein-DNA interaction assay (fig. S28). $SD1^{T65}$ and $SD1^{C9285}$ promoters both harbor the 13-bp sequence (table S4) and were each activated by OsEIL1a (fig. S27C), suggesting that the regulatory element(s) for ethylene-induced transcription is conserved in $SD1^{T65}$ and $SD1^{C9285}$ promoters. As *SD1* transcription in T65 was not induced by ethylene treatment (Fig. 2D and fig. S20), these observations imply the existence of an unknown suppressor(s) for the ethylene-inducible transactivation. It has been reported that *GA20-oxidase* transcription is under negative feedback regulation by a transcription factor(s) or transcriptional co-regulators (*10*). In deepwater rice harboring the DWH, this negative feedback may be partially diminished, leading to higher *SD1* transcript accumulation relative to that in other rice in response to submergence.

SD1 encodes a GA20-oxidase for gibberellin biosynthesis (*11*) (Fig. 3A). GA_{20} and GA_9, the products of GA20-oxidases in the early-13-hydroxylation pathway (GA_1 pathway) and non-13-hydroxylation pathway (GA_4 pathway), are converted into bioactive gibberellin species GA_1 and GA_4, respectively (*11*). In rice vegetative tissues, endogenous GA_1 is predominant whereas GA_4 is minor (*12*). Contrastingly, in response to submergence, levels of both GA_1 and GA_4 increased in C9285 but not in T65 (*3*). To test whether this increase is due to the $SD1^{C9285}$ harbored by the DWH, internode gibberellin levels were quantified in T65, C9285, and NIL-1 under submergence treatment (Fig. 3A). Levels of GA_{20}, GA_9, GA_1, and GA_4 increased in a time-dependent fashion in both C9285 and NIL-1, whereas these trends were not observed in T65, suggesting that the DWH contributes to the increase in bioactive gibberellin species GA_1 and GA_4 after submergence.

The *SD1* coding region contains two nonsynonymous single-nucleotide polymorphisms (SNPs) in the first and third exons among rice varieties (*13*) (Fig. 3B and fig. S14). We compared enzymatic activities of recombinant $SD1^{T65}$ and $SD1^{C9285}$ proteins in the GA_1 and GA_4 pathways. $SD1^{C9285}$ showed higher enzymatic activity than $SD1^{T65}$ in both the GA_1 (*13*) and GA_4 pathways (Fig. 3C, fig. S29, and table S5). In the GA_4 pathway, $SD1^{C9285}$ displayed enzymatic activity ~270 times as high as that of $SD1^{T65}$ and ~19 times as high as that in the GA_1 pathway. Moreover, near-constitutive expression of $SD1^{C9285}$ in planta increased GA_9 and GA_4 levels (fig. S30). Further phenotypic analyses revealed that the exonic SNPs and the DWH together contribute to internode elongation in response to submergence (fig. S31). Taken together, our results indicate that the main activity of the $SD1^{C9285}$ protein is the conversion of GA_{12} into GA_9 in the GA_4 pathway rather than of GA_{53} into GA_{20} in the GA_1 pathway and that $SD1^{C9285}$ contributes to the increase of the GA_4 level in response to submergence. The reason GA_1, in addition to GA_4, increases in response to submergence in C9285 can be explained by the existence of GA13-oxidase activity in rice internodes (*14*), involving a metabolic flow from GA_{12} to GA_{53} (Fig. 3A). We further compared physiological activities of gibberellin species for elongation of internodes in T65 and C9285 (Fig. 3, D and E). C9285 showed internode

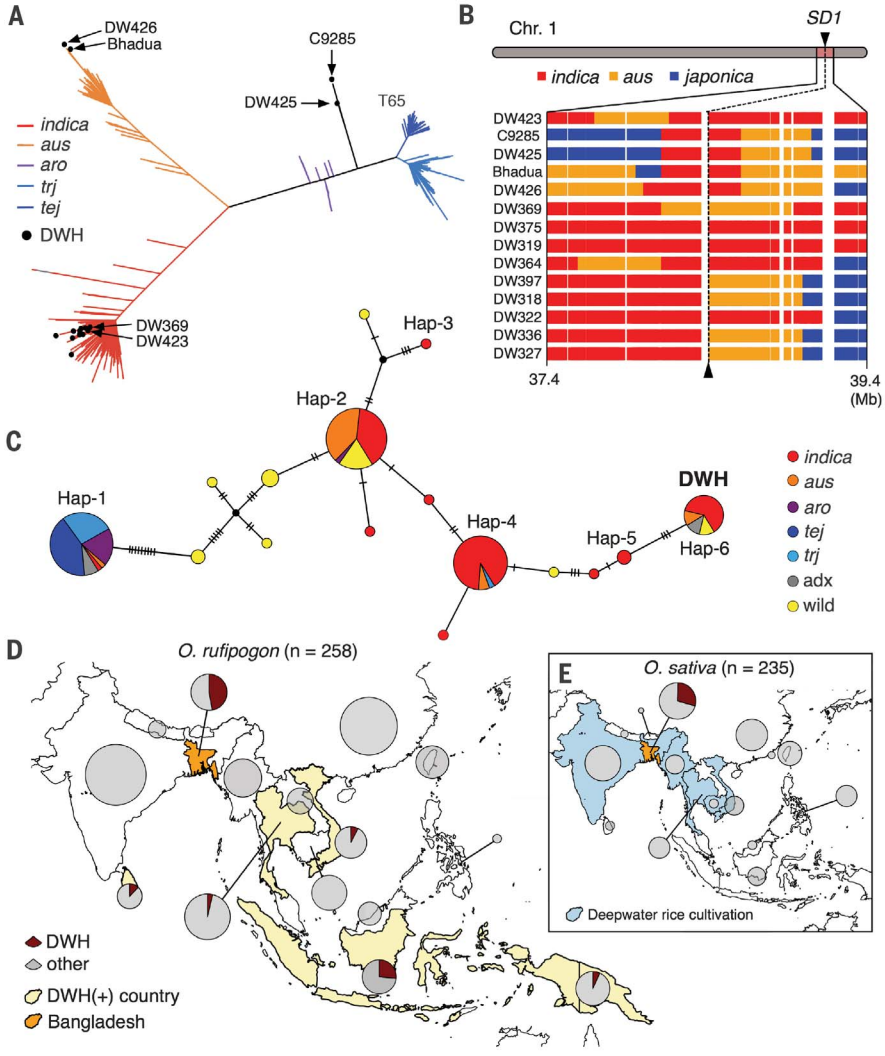

Fig. 4. The DWH was derived from standing variation in *O. rufipogon* and selected in *O. sativa*. (**A**) Distance tree of diverse *O. sativa* varieties in the GWAS panel. Black dots, DWH(+) varieties. Arrows, varieties with accentuated deepwater response. (**B**) Admixture analysis of the 2-Mb region flanking *SD1* in DWH(+) varieties. (**C**) Haplotype network of the *SD1* gene. Each haplotype is separated by mutational changes, with hatches indicating mutational differences between linked haplotypes. *aro*, *aromatic*; *tej*, *temperate japonica*; *trj*, *tropical japonica*; adx, admix; wild, *O. rufipogon*. (**D** and **E**) Geographical distribution of the DWH in *O. rufipogon* and *O. sativa*. The pie chart size is proportional to the number of accessions.

elongation in response to gibberellins, whereas T65 did not (*15*) (Fig. 3, D and E). GA_4 promoted internode elongation 10 times as much as GA_1 did, resulting in the highest increase of total plant height among the gibberellin species (Fig. 3, D and E, and fig. S32). The higher bioactivity of GA_4 than of GA_1, due to differences in binding affinity for the rice gibberellin receptor (*16*), may amplify the effect of gibberellins on cell proliferation and the elongation of the internodes in deepwater rice (*1*). Taken together, our results suggest that the physiological activity of GA_4 impacts internode elongation and that the increase in GA_4 levels under submergence induces rapid internode elongation in deepwater rice.

We next investigated the genetic relationships among deepwater rices. Haplotype analysis of 149 *O. sativa* varieties (*17*) revealed that the DWH is present only in Bangladeshi deepwater rice (tables S6A and S7A). Principal components analysis showed that DWH-positive [DWH(+)] varieties with the most accentuated deepwater responses (table S6A) belonged to *indica*, *aus*, and admixed subpopulations (Fig. 4A and figs. S33 to S35). Other DWH(+) varieties all clustered within *indica* (figs. S33B and S34B); nucleotide diversity analysis suggested that *indica* DWH(+) varieties underwent a population bottleneck via selection for cultivation in Bangladesh (fig. S36). Admixture analysis revealed that the DWH originated in *indica* or *aus* (Fig. 4B). We further investigated DWH presence in *O. sativa*'s wild ancestor, *Oryza rufipogon*. Gene haplotype network analysis showed that wild and cultivated rice shared the DWH (Fig. 4C and tables S6B and S7B). We analyzed wild rice resequencing (fig. S37 and tables S6B and S7B) and indel (table S8) data revealing 16 DWH(+) wild accessions (table S9A). W1 and W4 subpopulations in wild rice have been reported to be likely ancestral populations for *indica* and *aus*, respectively (*18*). All but one DWH(+) wild accession were classified as W1, W4, or W1 admixed (table S9A). Of nine known chloroplast haplotypes (*18*), cpGroup-III had the highest DWH frequency (table S9B). These cpGroup-III DWH(+) accessions originated from Bangladesh (fig. S38A and table S8), suggesting that the DWH emerged in cpGroup-III Bangladeshi wild rice. DWH presence was more broadly distributed in wild rice than in cultivated rice (Fig. 4, D and E); nonetheless, occurrence was more frequent in Bangladesh (table S9C). Comparison of nucleotide diversity of the *SD1* region in DWH(+) accessions versus DWH(−) accessions from the *O. rufipogon* panel (fig. S38A) resulted in a ratio of ~1 (fig. S38B), providing evidence that the DWH evolved first in *O. rufipogon* populations. Three W4 Bangladeshi wild accessions clustering in the same clade (fig. S38A, red circle) shared all 48 polymorphisms in *SD1* with C9285, suggesting that this group may be direct ancestors of Bangladeshi DWH(+) cultivated deepwater rice (table S10). The absence of DWH(+)-diagnostic indels in other wild rice species indicated that the DWH emerged after the speciation of *O. rufipogon* (table S11). Taken together, our results support the hypothesis that DWH emerged in *O. rufipogon* during W1-W4 differentiation; this conditionally functional haplotype was then a target of selection for the cultivation of *O. sativa* under deepwater environments in Bangladesh.

On the basis of our present study, we suggest a model of signaling pathways underlying rice internode elongation in response to submergence via a

direct molecular link between ethylene signaling and gibberellin biosynthesis, ethylene-gibberellin relay (fig. S39). We suggest that the DWH mediates amplification of *SD1* transactivation via direct binding of OsEIL1a, resulting in increased GA_1 and GA_4; this amplification is key to allowing deepwater rice to withstand severe flooding conditions, in combination with *SK1/2*. Finally, we propose a model of evolution and domestication for nondeepwater and deepwater rice whereby the DWH emerged in *O. rufipogon* and was selected for deepwater rice cultivation in Bangladesh (fig. S40).

As contemporary climate change triggers radical shifts in weather patterns, cryptic genetic variation found in wild rice gene pools may offer adaptive solutions to help breeders fine-tune modern rice varieties. Here we reveal that a transcriptional gain-of-function allele of the Green Revolution semidwarf gene triggers rapid stem elongation in deepwater rice, enabling it to survive adverse flooding conditions. Thus, the same gene has been co-opted several times to permit rice cultivation in highly contrasting production systems via different molecular responses—decreasing enzymatic activity in one case and enhancing transactivation in the other. The capacity of *SD1* to function in such diverse roles in cultivated rice highlights the intrinsic complexity and molecular plasticity of plant adaptation strategies.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S40
Tables S1 to S12
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How rice defeats the floodwaters

Deepwater rice varieties grow taller when flooded, in a growth response driven by the plant hormones gibberellin and ethylene. This keeps the leaves above the water. Kuroha *et al.* identified the genes underlying this phenotype, which encode a component of the gibberellin biosynthetic pathway and its regulatory ethylene-responsive transcription factor. This genetic relay drives growth of the plant stem internodes in response to flooding. Modern cultivated deepwater rice, which has been domesticated for adaptation to the monsoon season of Bangladesh, emerged from the genetic variation found in wild rice strains over a broader geographic region.

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