

# Abscisic Acid Signaling Shapes Rice Adaptation to Tropical Climates

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## Article

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# Abstract

Improving the tropical adaptation of temperate cereal germplasms with high-yield is a promising strategy to enhance tropical food productivity and increase their resilience to warming climate. However, the mechanisms that restrict crop adaptation to tropical climates remain largely unknown. Here, we found that the poor adaptation of temperate-cultivated *japonica* rice to tropics, characterized by early flowering and yield penalties, is linked to abscisic acid (ABA)-dependent stress-escape response. Tropical conditions robustly activated ABA pathway in *japonica* rice with a significant induction of florigen genes, whereas such responses were largely suppressed in the tropic-adapted *indica* cultivars harboring weak ABA responsiveness. Repressing ABA signaling by introducing *PYL1/4/6* mutations dramatically improved the tropical adaptability of various *japonica* cultivars, including our developed variety *Ganwan Jing 21* (GWJ21), with delayed-heading and boosted-yield (+ 26 ~ 51%). By contrast, *indica* cultivars derived no benefit from the identical mutations, and instead, the further ABA suppression impaired their tropical fitness with early heading and sharply reduced productivity (-10 ~ 15%). Consistently, *PYL1/4/6* mutations enhanced yield stability of *japonica* rice but reduced the viability of *indica* rice under heat stresses. Given that both excessive and overly suppressed ABA signaling incur yield penalties, our results establish a balance relationship between ABA signaling strength and latitudinal adaptation, which provides practical strategies for crop latitude-range spreading as well as climate-resilient breeding.

## Introduction

Latitudinal adaptation shapes the geographic distribution of staple crops, which is pivotal to global food security<sup>1-3</sup>, especially under global warming with the shift of climate zones<sup>4-7</sup>. Low-latitude tropical regions accommodate nearly half of the global population, where rapid population growth coincides with severe malnutrition prevalence<sup>8-10</sup>. The grain crops exhibit 35%–50% lower average yields in tropical zones relative to temperate regions, largely due to the scarcity of high-yield crop varieties optimized for tropical climatic conditions<sup>10-12</sup>. Consistently, temperate-adapted cultivars of cereal crops, including rice, maize, and soybean, generally display higher yield potential than those varieties in tropical countries<sup>11, 13-15</sup>, making the introduction of elite temperate varieties a promising strategy to enhance tropical crop productivity. However, temperate crop varieties suffer from poor adaptability to tropical climates with precocious flowering and substantial yield losses. This limitation not only restricts their cultivation in low-latitude tropics, but also drives their migration to higher latitude regions as the tropical expansion under global warming<sup>1, 4, 14, 16, 17</sup>, presenting substantial challenges to global food security.

Current research on crop tropical adaptation predominantly centers on the precise modulation of photoperiodic flowering pathways<sup>1, 18</sup>. In temperate *japonica* rice, mutations in *Heading date 1* (*HD1*, a homolog of *CONSTANS*) or *Early heading date 1* (*Ehd1*) facilitate tropical adaptation by disrupting the short-day-induced activation of florigen genes *Hd3a/RFT1*<sup>16, 19-21</sup>. In soybean, retrotransposon insertion or frameshift mutations in *J/E6*, a long-juvenile trait governor encoding an ELF3 ortholog, abolish its

repression of the legume-specific flowering repressors *E1/E1Ls*, thus suppressing the expression of florigen genes and prolonging vegetative growth under tropical conditions<sup>22–24</sup>. Additionally, phytochromes are involved in this pathway by destabilizing the evening complex (ELF3, ELF4 and LUX) to reinforce flowering repression<sup>25, 26</sup>. Multiple genes regulating photoperiodic flowering, including *LHYs*, *SOC1*, *TOE4b*, *REVEILLE 1*, and *GmNF-YC4*, have been functionally validated as key determinants of soybean tropical adaptation<sup>27–32</sup>. In maize, the absence of retrotransposon/transposon insertions at the promoter region of *ZmELF3.1* and *ZmCCT9/10* suppresses their expression for delayed-flowering under a tropical climate<sup>33, 34</sup>, and two *cis*-regulatory variants located upstream of the florigen gene *ZCN8* contribute to latitudinal flowering in maize<sup>35</sup>. Despite these advances, tropical ecosystems represent a complex combination of short photoperiods, elevated temperatures, high light intensity, infertile soils, and multiple concurrent stressors, leaving the mechanisms underlying plant adaptation to low-latitude tropical regions still mysteries.

Phytohormones act as core regulators that mediate plant adaptation to fluctuating environmental conditions, among which abscisic acid (ABA) serves as an indispensable modulator<sup>36, 37</sup>. In response to environmental stresses, such as extreme temperatures, drought, salinity, light stresses, and nutrient deficiency, plants biosynthesize ABA from  $\beta$ -carotenoids via enzymes including NCEDs<sup>38, 39</sup>. The endogenous ABA is further perceived by PYLs/PYRs receptors to recruit and inactivate PP2Cs, thereby releasing the downstream SnRK2s to phosphorylate targets for a series of ABA-dependent adaptive responses<sup>37, 40, 41</sup>. These responses facilitate plant dormancy maintenance and stress tolerance to survive harsh growth conditions<sup>38, 40, 42</sup>. Notably, ABA also mediates drought escape responses by initiating floral transition under water-deficit conditions, which is achieved by upregulating the transcription of florigen genes, including *Arabidopsis FT* and rice *RFT1/Hd3a*<sup>43–45</sup>.

Here, we find that the maladaptation of *japonica* rice varieties to tropical climates is attributed to an ABA-mediated stress escape response, and the suppressed-ABA pathway is tightly associated with enhanced-tropical adaptation in rice. Mutations in the ABA receptor genes *PYL1*, *PYL4*, and *PYL6* (*PYL1/4/6*) substantially improve the tropical adaptability of temperate- and subtropical- *japonica* rice cultivars, as evidenced by an obviously delayed heading date and significantly elevated grain yield (26%–51%) under field tropical conditions. Furthermore, *PYL1/4/6* mutations facilitate tropical adaptation of *japonica* rice by rescuing heat-induced impairments in vegetative and reproductive growth. In contrast, likely due to the excessive repression of ABA signaling, these mutations compromise the tropical adaptability of *indica* rice, leading to pronounced yield reduction and decreased viability to tropical heat stress. Collectively, our findings establish a balance correlation between the ABA pathway and plant latitudinal adaptation, offering a novel genetic strategy for breeding elite crop varieties with enhanced cross-latitude adaptability and climate- resilience.

## Results

## Poor adaptation of japonica rice to tropics is associated with an ABA-dependent stress-escape response

Using an “*indica-japonica* bridging technique” with our self-developed *indica*-compatible *japonica* variety BP39, *indica* variety Ganzao Xian 15 (GZX15), super *indica*-introgressive *japonica* variety Shengnong 9816 and *japonica* variety Wuyu Jing 33 (WYJ33), we developed a stable subtropic-adapted variety designated Ganwan Jing 21 (GWJ21) (Fig. 1a). Regional variety trials conducted in Gao'an (28.45°N) demonstrated that GWJ21 achieved a theoretical grain yield of 9344.0 kg/ha. Although its theoretical yield decreased by 16.2% to 7834.5 kg/ha in tropical field trials at Sanya (18.25°N), GWJ21 exhibited substantially improved tropical adaptability relative to the control subtropical *japonica* variety Ganning Jing 1 (GNJ1). Under tropical field conditions in Sanya, GWJ21 displayed superior agronomic performance compared with GNJ1, including a prolonged reproductive period (approximately 103 days), increased plant height (~ 62.3 cm), higher tiller number (12 tillers per plant), longer leaf blades (~ 17.9 cm), larger panicles with more grains per panicle (126 grains), and heavier 1000-grain weight (~ 32.5 g) (Fig. 1b,c). Consistent with the phenotypic alterations, tropical conditions significantly upregulated the expression of the florigen genes *RFT1* and *Hd3a* relative to temperate conditions in GNJ1, while this transcriptional induction was markedly suppressed in GWJ21 (Fig. 1d). Collectively, these results suggest that the newly developed *indica*-introgressed *japonica* variety GWJ21 displays robust adaptability to low-latitude subtropical and tropical environments.

Short-day photoperiods, elevated ambient temperatures, high light intensity, and nutrient deficiency are well-established triggers for ABA biosynthesis, and ABA signaling is functionally implicated in stress-induced floral transition during drought escape responses<sup>38, 39, 42, 43</sup>. On this basis, we hypothesized that the poor tropical adaptability of *japonica* rice is attributed to an ABA-mediated stress escape response. Quantitative real-time PCR analyses revealed that the transcript levels of the ABA biosynthesis gene *NCED3* and the ABA receptor gene *PYL4* were markedly upregulated under tropical conditions (characterized by short-day photoperiods, high temperatures, intense light, and low nitrogen supply) in the GNJ1, relative to growth under temperate conditions. In contrast, such tropical-induced transcriptional activation of ABA-related genes was substantially attenuated in the tropical-adapted *japonica* cultivar GWJ21 (Fig. 1e). Seed germination assays further validated the differential ABA responsiveness between the two varieties: GWJ21 exhibited a significantly higher germination rate than GNJ1 under both normal conditions and exogenous ABA treatment, indicating attenuated ABA signaling activity in GWJ21 (Fig. 1f,g). In line with the gene expression profiles of *NCED3*, tropical cultivation conditions substantially increased endogenous ABA accumulation in both GNJ1 and GWJ21 compared with temperate conditions, with GNJ1 accumulating drastically higher ABA levels than GWJ21 under tropical climates (Fig. 1h).

To verify the conserved association between ABA signaling and latitudinal adaptation in rice, we extended our analysis to additional representative cultivars. Consistent with the observations in GNJ1 and GWJ21, tropical conditions markedly induced the expression of *NCED3*, *PYL4*, and the florigen genes *RFT1*/*Hd3a* in the temperate *japonica* cultivar Huaidao 5 (HD5), whereas such inductive effects were

eliminated in the tropics-adapted *indica* cultivar *Huanghua Zhan* (HHZ) (Fig. 1i,j). Physiological assessment of ABA sensitivity via germination assays revealed that HD5 had a significantly lower germination rate than HHZ under both control and ABA-treated conditions. Across a broader panel, temperate *japonica* varieties generally exhibited a greater ABA-mediated reduction in germination than low latitude-adapted *indica* cultivars (Fig. 1k–m; Table S1). These results indicated an association between greater ABA responsiveness and temperate *japonica* ancestry.

Taken together, these results demonstrate that enhanced tropical adaptability in rice is correlated with repressed ABA signaling. By contrast, the poor adaptability of temperate *japonica* rice to tropical low-latitude environments is likely attributed to hyperactive ABA-mediated stress escape responses.

### **Suppression of ABA signaling via *PYL1/4/6* mutation improves the tropical adaptation of GWJ21**

Considering that GWJ21 exhibited a penalty under tropical regions, and that the ABA pathway is activated by tropical conditions in GWJ21 (Fig. 1e,h), we therefore asked whether repressing ABA signaling in GWJ21 would further improve its adaptive capacity to tropical climate. Our previous work showed that mutation of ABA receptor genes *PYL1/4/6* is an efficient strategy to reduce ABA sensitivity and promote rice vegetative/reproductive growth<sup>46</sup>. We thereby constructed a CRISPR/Cas9 vector to edit *PYL1*, *PYL4* and *PYL6* in the background of GWJ21 and identified a triple mutant with frame-shifts in all of three *PYL* genes in the T2 generation (Fig. S1). ABA sensitivity assays based on seed germination, seedling shoot growth, and primary root length revealed that the *pyl1/4/6* triple mutant exhibited substantially reduced sensitivity to exogenous ABA at multiple concentrations relative to wild-type GWJ21 (Fig. 2a–c), confirming the successful generation of viable and ABA-hyposensitive triple mutant materials.

Heading date is a core phenotypic indicator of rice tropical adaptability. We therefore evaluated the heading performance of the *pyl1/4/6* mutant and GWJ21 under both potted and field conditions in Sanya. The *pyl1/4/6* mutant exhibited pronouncedly delayed heading in potted plants (Fig. S2). Consistent with the potted results, field-grown *pyl1/4/6* plants flowered approximately 18 days later than GWJ21, with a remarkably extended reproductive period (125 days versus 103 days in GWJ21) (Fig. 2d,e). Transcriptional analysis further showed that the tropical condition-induced upregulation of key heading regulators, including *Hd3a*, *RFT1*, *Ehd1*, and *Hd1*, as well as the ABA biosynthesis gene *NCED3*, was significantly repressed in the *pyl1/4/6* mutant compared with GWJ21 (Fig. 2f). These results indicate that reducing ABA sensitivity via *PYL1/4/6* mutagenesis serves as a robust strategy to delay precocious heading of *japonica* rice under tropical climates.

Improving grain yield is the ultimate target for optimizing crop tropical adaptability. We further quantified the agronomic and yield-related traits of the *pyl1/4/6* mutant under tropical field conditions. Relative to GWJ21, the *pyl1/4/6* mutant displayed significant improvements in multiple vegetative traits, including increased plant height (+ 27.2%), tiller number (12 to 16 tillers per plant, + 31.4%), and leaf blade length in tropical fields (Fig. 2g–i, S3), consistent with phenotypic changes observed in potted cultivation (Fig. S4). In addition, the mutant produced longer panicles with significantly elevated numbers of primary and

secondary panicle branches (Fig. 2j–n, S4). These architectural improvements contributed to a marked increase in filled grain number per panicle, with a 39.7% enhancement in field-grown plants and a 35.7% increase in potted plants (Fig. 2q, S4). Moreover, the *pyl1/4/6* mutant exhibited enlarged grain size, which was primarily attributed to increased grain length rather than altered grain width (Fig. S5), ultimately resulting in a 7.1% higher 1000-grain weight than GWJ21 (Fig. 2p,q). Given that the three core yield components (tiller number per plant, filled grain number per panicle, and grain weight) were all significantly enhanced, *PYL1/4/6* mutagenesis increased plot yield by 38.5% under field conditions and individual plant yield by 55.3% under potted conditions compared with wild-type GWJ21 (Fig. 2r,s, S4).

Collectively, these findings demonstrate that *PYL1/4/6* triple mutations comprehensively improve tropical adaptability and grain yield of *japonica* rice, providing a promising genetic strategy for breeding high-yield *japonica* varieties suitable for tropical cultivation.

### ***PYL1/4/6* disruptions enhance the tropical adaptation of multiple temperate *japonica* varieties**

Since introducing *PYL1/4/6* mutations comprehensively improved the tropical adaptation of subtropical *japonica* rice GWJ21, we further explored the effect of the *PYL1/4/6* mutant allele on the adaptability and agronomic performance of *japonica* rice in tropical environments. Via CRISPR/Cas9-mediated gene editing, we obtained *pyl1/4/6* mutants in the background of three temperate *japonica* varieties, including HD5, *Yanfeng 47* (YF47), and *Nan Jing 9108* (NJ9108) (Fig. S6). We then conducted field trials in Sanya using these mutants, with their corresponding wild-type (WT) plants as controls. Consistent with the later heading observed in the *pyl1/4/6* mutant of GWJ21, the *pyl1/4/6* mutants in the background of these *japonica* cultivars exhibited obviously delayed-heading phenotypes when compared with their WT plants, showing delays of approximately 7 days at the heading date stage across all three genetic backgrounds (Fig. 3a,b).

At the mature stage, the *pyl1/4/6* mutants displayed superior reproductive growth compared to the WT controls, and they were visibly taller and produced more tillers than the WT plants (Fig. 3a,c–e). Further characterization of yield-related traits demonstrated that the *pyl1/4/6* mutants developed more panicles per plant, with more primary branches and a greater number of filled grains per panicle, fewer unfilled grains compared to WT (Fig. 3f). Quantitative validation confirmed that the number of filled grains per panicle was significantly elevated in the mutants, due to the increased primary branch number and total grain number per panicle, as well as a higher seed-setting rate (Fig. 3g, S7). The 1000-grain weight was also significantly higher in the *pyl1/4/6* mutants, with obviously larger and longer grains in comparison to the WT controls (Fig. 3h,i). Consequently, the plot yield evaluation (1 m<sup>2</sup> per plot) showed that the mutants outperformed the WT controls by 26.6%, 37.8%, and 51.2% in HD5, YF47, and NJ9108 backgrounds, respectively (Fig. 3j,k).

Taken together, these results demonstrate that the *PYL1/4/6* mutations substantially improve the adaptability of temperate *japonica* rice to tropical regions, leading to delayed heading date, enhanced reproductive performance, and significantly increased grain yield.

## The beneficial effects of *PYL1/4/6* disruptions are not observed in *indica* cultivars with weak ABA responsiveness

Given that suppressed ABA signaling is tightly associated with rice tropical adaptation and naturally tropical/subtropical *indica* cultivars inherently exhibit weak ABA signaling (Fig. 1), we investigated whether *PYL1/4/6* mutations could further improve the agronomic performance of *indica* rice. We thereby introduced *PYL1/4/6* mutations via CRISPR/cas9 system in the background of three *indica* varieties, including HHZ, *Wushan Simiao* (WSSM), and *Xiangya Zhan* (XYZ), and homozygous *pyl1/4/6* mutant lines were successfully identified for subsequent phenotyping (Fig. S8). Parallel field trials were conducted in Sanya with paired WT plants serving as isogenic controls. Contrary to the beneficial effects observed in *japonica* rice, *PYL1/4/6* mutations failed to delay heading date in *indica* cultivars. Instead, the mutant lines exhibited approximately two days of earlier heading relative to WT plants across all three *indica* genetic backgrounds (Fig. 4a,b).

At the maturing stage, the *pyl1/4/6* mutant plants showed no visible differences in overall plant architecture relative to WT (Fig. 4a,c), and statistical analysis revealed that plant height as well as tiller number were indistinguishable between the *pyl1/4/6* mutants and WT in all three *indica* cultivars (Fig. 4c-f). Further characterization of yield components demonstrated that, despite the absence of changes in primary branches and total grains per panicle, the mutants produced significantly fewer filled grains per panicle than WT plants, mainly due to the decreased grain setting with more blighted grains (Fig. 4g,h, S9). The 1000-grain weight was also markedly reduced in the *pyl1/4/6* mutants, as validated by both quantitative measurement and the observation of smaller, shorter grains in the mutant lines (Fig. 4i,j). Consequently, the *pyl1/4/6* mutants exhibited significant reductions of plot yield relative to WT controls, with yield losses of 10.0%, 15.0%, and 12.6% in the HHZ, WSSM, and XYZ backgrounds, respectively (Fig. 4k, l).

Collectively, these results demonstrate that *PYL1/4/6* mutations compromise the tropical adaptability of *indica* rice. Considering the inherently repressed ABA signaling in tropic-adapted *indica* cultivars (Fig. 1m), the contradictory effects of *PYL1/4/6* mutations between *indica* and *japonica* rice are likely caused by excessive repression of ABA signaling beyond the optimal threshold required for tropical adaptation.

## ABA signaling balances growth and viability during tropical heat adaptation

Consistent with the impaired tropical adaptability, the *pyl1/4/6* mutants of *indica* cultivars also exhibited compromised field viability under tropical summer environments (Fig. S10). Given that high temperature represents a dominant tropical stressor that constrains plant survival and growth, we asked whether the opposite genetic effects of *PYL1/4/6* mutations in *indica* versus *japonica* rice are attributed to an intensity effect of ABA signaling on heat stress responses. To test this hypothesis, we evaluated the seedling performance of wild-type (WT) and *pyl1/4/6* mutant plants across three *japonica* cultivars (HD5,

YF47, NJ9108) and three *indica* cultivars (HHZ, WSSM, XYZ) under natural tropical field conditions with frequent heat waves, in which 9 out of 21 consecutive days recorded maximum temperatures exceeding 35°C (Fig. S11). Under such heat waves, *PYL1/4/6* mutation-mediated attenuation of ABA signaling promoted seedling growth in *japonica* rice, as manifested by improved leaf greenness and increased plant height compared with WT plants (Fig. 5a). In sharp contrast, the same triple mutations in *indica* rice, which possesses inherently weak basal ABA signaling, resulted in pronounced heat hypersensitivity, with mutant seedlings exhibiting severe leaf chlorosis, stunted growth, and reduced survival rates under identical heat stress conditions (Fig. 5a). These observations suggest that hyperactive ABA signaling in temperate *japonica* rice restricts vegetative growth under tropical heat stress, whereas further repression of the already weakened ABA pathway in *indica* rice severely compromises plant heat tolerance and survival.

To further validate the intensity effect of ABA signaling on balancing rice growth and heat stress viability, we selected three rice cultivars with distinct endogenous ABA sensitivity (ranked as HD5 > GWJ21 > HHZ) and their corresponding *pyl1/4/6* mutants for controlled short-day heat stress assays (Fig. 5b). Under severe heat stress, WT seedlings of HD5, GWJ21, and HHZ exhibited a gradual reduction in chlorophyll content accompanied by enhanced shoot growth, consistent with their progressive decrease in ABA sensitivity (Fig. 5c–e). In the strong ABA-signaling *japonica* cultivar HD5, *pyl1/4/6* mutagenesis exerted no adverse effects on plant viability but significantly promoted seedling growth relative to WT. In contrast, in GWJ21 and HHZ with moderate and weak ABA signaling, respectively, *PYL1/4/6* mutations markedly reduced thermotolerance and even caused seedling lethality (Fig. 5c–e), confirming that ABA pathway repression facilitates vegetative growth at the cost of heat stress survival.

Exogenous ABA application further verified this intensity-dependent regulatory pattern. In rice lines with intrinsically weak ABA signaling, including HHZ and *pyl1/4/6* mutants, exogenous ABA supplementation effectively rescued heat-induced seedling lethality and restored chlorophyll accumulation, with the magnitude of growth inhibition negatively correlated with endogenous ABA signaling strength. Conversely, in ABA-sensitive cultivars HD5 and GWJ21, exogenous ABA treatment reduced chlorophyll content and suppressed seedling growth under heat stress relative to untreated controls (Fig. 5c–e), indicating that excessive ABA signaling triggers leaf damage and restricts plant growth under thermal stress.

Beyond vegetative-stage regulation, ABA signaling also modulates reproductive growth performance under tropical heat conditions. Heat stress severely impaired the reproductive development of GWJ21 WT plants, causing a 41.3% reduction in seed-setting rate and a 46.2% loss of grain yield (Fig. 5f–h). Notably, the *pyl1/4/6* mutant of GWJ21 maintained stable filled grain number and single-plant yield under both normal and heat-stressed conditions. Although a 22.2% reduction in seed-setting rate was still detected in heat-treated mutants, this phenotypic penalty resulted from prolonged panicle development and a slight increase in sterile grain proportion (Fig. 5f–h). These findings are consistent with field observations across multiple genetic backgrounds: WT temperate *japonica* cultivars (HD5, YF47, NJ9108) exhibited low seed-setting rates under tropical summer conditions, while their corresponding

*pyl1/4/6* mutants displayed superior reproductive performance and higher grain setting (Fig. 5i). By comparison, *pyl1/4/6* mutants in all three *indica* backgrounds showed substantially lower seed-setting rates than their WT counterparts (Fig. 5J).

Taken together, these results demonstrate that the intensity of ABA signaling shapes rice tropical adaptation via balancing rice growth and heat stress viability. Moderately repressed ABA signaling improves rice thermotolerance and agronomic performance during both vegetative and reproductive stages, whereas either excessive ABA signaling or extreme ABA pathway repression disrupts this balance and impairs overall tropical heat adaptability.

## Discussion

Tropical adaptation is a complex and poorly understood biological process that governs the latitudinal distribution of staple crops and underpins global food security. In this study, we systematically elucidated a novel regulatory role of ABA on controlling rice tropical adaptation, which resolves the long-standing puzzle of why temperate cereals suffers from precocious flowering and severe yield loss under tropical environments: The tropical maladaptation observed in temperate varieties is triggered by excessive ABA-dependent stress escape response. Tropical climatic cues (short-day photoperiod, high temperature, intense light, and nutrient deficiency) constitutively activate ABA biosynthesis and signaling in temperate *japonica* rice, which further induces the transcription of florigen genes and causes premature reproductive transition. Therefore, moderately attenuating ABA signaling by *PYL1/4/6* mutations in strong-signaling *japonica* rice effectively delays heading, improves performance under heats, and drastically boosts grain yield. Consistently, the beneficial effects of *PYL1/4/6* disruptions are not observed in *indica* cultivars as they harbored inherently weak ABA responsiveness with low stress-escape response, and instead, such excessive repression of the already weak ABA pathway disrupts the optimal signaling threshold required for tropical fitness, leading to heat hypersensitivity and significant yield penalties.

Our ABA-dependent latitudinal adaptation model is also supported by previous studies across plant species. Accumulated evidence showed that robust ABA signaling is indispensable for perennial tree survival in high-latitude boreal regions, where it promotes bud dormancy and leaf abscission to resist freezing and drought stresses in harsh winters<sup>42, 47, 48</sup>. Consistent with our results that the temperate *japonica* rice maintains stronger ABA sensitivity than low latitude-adapted *indica* rice, numerous natural favorable variants that enhance ABA biosynthesis or signaling have been selected during the domestication of temperate *japonica* rice, including *OsNCED3/5*<sup>49, 50</sup>, *bZIP73*<sup>51</sup>, *GF14h*<sup>52</sup>, *COG4-OsbZIP23* module<sup>53</sup>, *OsWRKY115*<sup>54</sup>, *CTB5*<sup>55</sup>, *OsUBC12*<sup>56</sup>, and *ROAD1*<sup>57</sup>. Conversely, the moderately repressed ABA signaling observed in tropical-adapted rice facilitates continuous vegetative growth and enhances thermotolerance under hot tropical climates, likely by promoting stomatal opening and alleviating ABA-mediated growth inhibition<sup>37, 40, 41</sup>. Integrating our results with previous studies, we propose a unified regulatory paradigm: the intensity of ABA signaling acts as a switch that shapes crop

latitudinal adaptation, with enhanced ABA signaling favoring high-latitude boreal winter survival and moderate ABA repression optimizing low-latitude tropical growth for competitive advantage (Fig. 5k).

Ongoing global warming drives both the expansion of the tropical belt and widespread increases in ambient temperature, and these shifting conditions have already caused substantial yield reductions in major staple crops grown in temperate zones<sup>4–7, 58</sup>. In temperate cereals, excessive ABA signaling aggravates heat-induced pollen abortion, suppresses post-stress seedling recovery, and exacerbates heat-triggered yield loss<sup>59, 60</sup>. Given a stronger ABA pathway in temperate *japonica* rice and a better yield performance in *pyl1/4/6 japonica* mutants under tropical heat conditions, we propose that climate change-associated yield penalties in temperate crops are likely attributed to hyperactive ABA-mediated stress responses activated by elevated temperature. Therefore, partial attenuation of ABA signaling offers a practical strategy to bolster heat-stress tolerance for temperate crops, and generate climate-resilient cultivars that offset global warming-driven yield losses.

## Methods

### Plant materials and growth conditions

GWJ21 was bred via an “*indica-japonica*” bridging technique (Fig. 1a), and the *pyl1/4/6* mutants in the background of different varieties were obtained via the CRISPR/Cas9 system. Rice plants were sown in the fields at Sanya County (18°N) of Hainan Province (China). For the phenotypic observation, at least 20 m<sup>2</sup> of paddy field was used for each line.

#### CRISPR/Cas9 system-based *PYL1/4/6* mutation

As described previously<sup>46</sup>, A rice multi-gene editing vector, with maize ubiquitin promoter-driven Cas9 and *OsU3/6* promoters-directed sgRNA (targeting *PYL1/4/6*) in the backbone of PCAMBIA1300, was constructed (Fig. S1). The recombined vector for *PYL1/4/6* editing was then transformed into the calli of different rice varieties via *Agrobacterium*-mediated transformation, and frameshift mutants of *pyl1/4/6* were identified from transgenic plants through genotyping using primer pairs described in Table S2.

### RNA extraction and real-time RT-PCR

Total RNA was extracted from 14-day old seedlings grown under temperate conditions (16h light & 28°C/8 h dark & 25°C, 70% humidity, 75  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photon density, 114.36 mg/L  $\text{NH}_4\text{NO}_3$ ) or tropical conditions (12h light & 30°C/12 h dark & 28°C, 80% humidity, 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photon density, 57.18 mg/L  $\text{NH}_4\text{NO}_3$ ) by using *TransZol Up Plus* RNA Kit, (TransGen). The first-strand cDNA was synthesized from total RNA (2  $\mu\text{g}$ ) via *TransScript® II One-Step gDNA Removal and cDNA Synthesis SuperMix* (TransGen), and real-time RT-PCR analyses were performed in a qTOWER<sup>3</sup> G real-time PCR instrument

(Analytik Jena) by using SYBR Green PCR mix (Applied Biosystems) with the primer sets shown in Table S2.

## Quantification of endogenous level of ABA

Approximately 200 mg (fresh weight) of 14-day old seedlings grown under temperate conditions or tropical conditions was homogenized under liquid nitrogen, weighed, and extracted for 24 h with methanol and  $^2\text{H}_6$ -ABA. Endogenous ABA was purified and measured as previously described<sup>61, 62</sup> with the following modifications in detection conditions. LC-MS/MS analysis was performed on a UPLC system (Waters) coupled to the 5500 Qtrap system (AB SCIEX). LC separation used a BEH C18 column (1.7 $\mu\text{m}$ , 100  $\times$  2.1 mm; Waters) with mobile phase A, 0.03% (v/v) formic acid in water, and B, acetonitrile. The gradient was as follows: 0–6 min, 10% B to 90% B, 6–6.5 min, 90% B to 100% B; 6.5–8 min, 100% B; 8–9 min, 100% B to 10% B; 9–10 min, 10%B. ABA was detected in multiple reaction monitoring (MRM) mode with transitions. The transitions for ABA and [ $^2\text{H}_6$ ]-ABA are 263.0 > 153.1 and 269.2 > 159.2. Three biological replicates were analyzed for each sample.

## ABA Sensitivity Assays

For the seed germination assay, mature seeds of different rice varieties were harvested from the same batch and dried in the incubator (37°C) for 7 days. The dried seeds were then soaked in  $\text{dH}_2\text{O}$  with or without 10  $\mu\text{M}$  ABA, and grown in the incubator (28°C, dark) for two to three days before the statistics of grain germination. Relative seed germination of ABA was indicated by the ratio of ABA-treated germination rate to the control one.

For the seedling growth inhibition assay, mature seeds from homozygous *pyl1/4/6* mutants and GWJ21 plants, harvested from the same batch, were dried and dehulled. The dehulled-seeds were then soaked in 75% ethanol for 30s, followed by three washes with sterile water, and the seeds were then incubated in a 2% sodium hypochlorite solution for 20 min, shaking at 100 rpm. After six times washing by sterile water, the surface-sterilized seeds were sown on solid MS medium with different concentrations of ABA (0 $\mu\text{M}$ , 2 $\mu\text{M}$ , 5 $\mu\text{M}$ , 10 $\mu\text{M}$ ). The seedlings were cultivated in a light-controlled growth chamber with a 12-hour light and 12-hour dark cycle for 7 days, before the measurement of shoot and root.

## Heat Stress Assays

For the outdoor heat wave assay, rice seedlings were sown in the trays with potting soil and cultivated on the outdoor dry land at Sanya in June for 3 weeks, when heat waves occur frequently, and the highest daily temperatures were recorded by a temperature logger (GPS-8, Elitech).

For the controlled-heat stress assay, rice seedlings were grown in Yoshida medium in a chamber with a 12 h light (28°C)/12 h dark (25°C) photoperiod, 70% humidity and about 75  $\mu\text{mol m}^{-2} \text{s}^{-1}$  photon density.

After 7 days of cultivation, rice seedlings grown in Yoshida medium with or without 5  $\mu$ M ABA were treated with heat stress under a period of 12 h light (45°C)/12 h dark (35°C) for 7 days. Then, shoot lengths of seedlings were collected, and chlorophyll content was measured via spectrophotometry (647 and 664 nm) after acetone-mediated chlorophyll extraction <sup>63</sup>.

For the heat stress assay at the reproductive stage, GWJ21 and its *pyl1/4/6* mutant plants were cultivated in pots on the outdoor dry land of Sanya during the Off-season (December to March of the next year). After the first heading, plants were then moved into a chamber with a 12 h light (37°C)/12 h dark (37°C) photoperiod for a 7-day heat stress treatment, then plants were grown outdoors for recovery, and the phenotypes of panicles were photographed, and grain setting rates were collected.

## Statistical analysis of data

Data were statistically analyzed by Student's *t*-test (one factor) or two-way ANOVA followed by Tukey's multiple comparisons test (two factors) using GraphPad Prism version 9 ([www.graphpad.com](http://www.graphpad.com)). P-values of \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001 or letters were considered to indicate statistical significance.

## Declarations

## Data availability

All data supporting the findings of this study are available within the article and its supplementary information files. Any additional raw or processed datasets that are not included in the main text or supplementary materials are available from the corresponding author upon reasonable request.

## Competing interests

The authors declare no conflict of interest.

## Author Contributions

H.Z., J.-K.Z., C.J., A.G. and F.L. designed research and supervised the project; H.S., F.W., H.H., and Y.Z. performed experiments, analyzed the data and drafted the manuscript. X.W., Y.W., X.D., S.H., L.L., C.W., H.Q., J.K., Q.X., H.L., L.Z., S.H., W.L., S.Z., R.Y. J.Z., P.X., J.C. and J.Z. conducted mutant construction, analyzed endogenous ABA, or provided necessary experimental assistances; H.S., H.Z., J.-K.Z., C.J. revised the manuscript. All authors have read and approved the final manuscript.

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## Figures

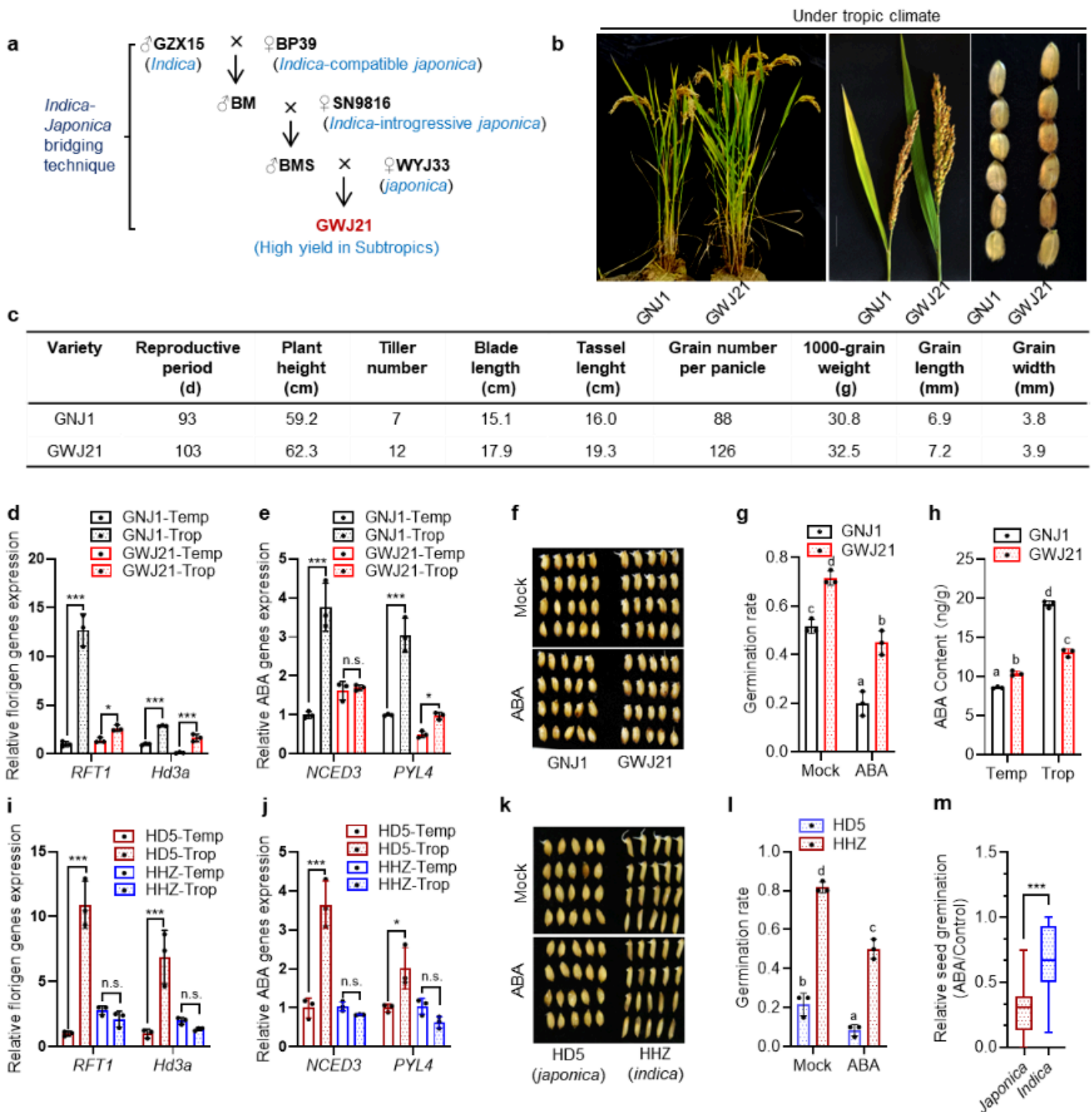


**Figure 1**

**The maladaptation of *japonica* under tropical conditions is associated with an enhanced ABA pathway.**

**a**) A technology roadmap for breeding subtropical-adapted *japonica* variety *Ganwan Jing* (GWJ21); **b**) Comparison of phenotype between GWJ21 and similar variety *Ganning Jing* (GNJ1) (subtropical-adapted) plants grown in the field of Sanya (tropical region) for 90 days. **c**) Reproductive traits of GWJ21 and GNJ1 collected from a typical plant grown in the field of Sanya for 90 days; The relative expression of florigen genes (*Hd3a*, *RFT1*) (**d**) and ABA pathway genes (*NCED3*, ABA biosynthesis; *OsPYL4*, ABA perception) (**e**) in 14-day old seedlings of GWJ21 and GNJ1 grown under temperate and tropical

conditions, n=3; **f**) Germinating seeds of GWJ21 and GNJ1 treated with or without 10  $\mu$ M ABA for 48 h; **g**) Quantitative analysis of seed germination rate, n=3 and 20 seeds were used for each replication; **h**) Quantitative analysis of endogenous ABA content in 14-day old seedlings of GWJ21 and GNJ1 grown under temperate and tropical conditions, n=3; Relative expression of florigen genes (**i**), ABA pathway genes (**j**) in 14-day old seedlings of *Huaidao 5* (HD5, temperate *japonica*) and *Huanghua Zhan* (HHZ, tropical/subtropical *indica*) grown under temperate and tropical conditions, n=3; **k**) Germinating seeds of HD5 and HHZ treated with or without 10  $\mu$ M ABA for 48 h; **l**) Quantitative analysis of seed germination rate, n=3 and 20 seeds were used for each replication; **m**) Relative seed germination ratio (ABA/control) of temperate *japonica* and tropical/subtropical adapted indica rice, 23 varieties for each subtype were used. Data present the mean $\pm$ SD, and letters/asterisks indicate statistical differences (\*\*\*,  $P < 0.001$ ; \*,  $P < 0.05$ ; n.s., not significant); biological applications were indicated by black points in columns.

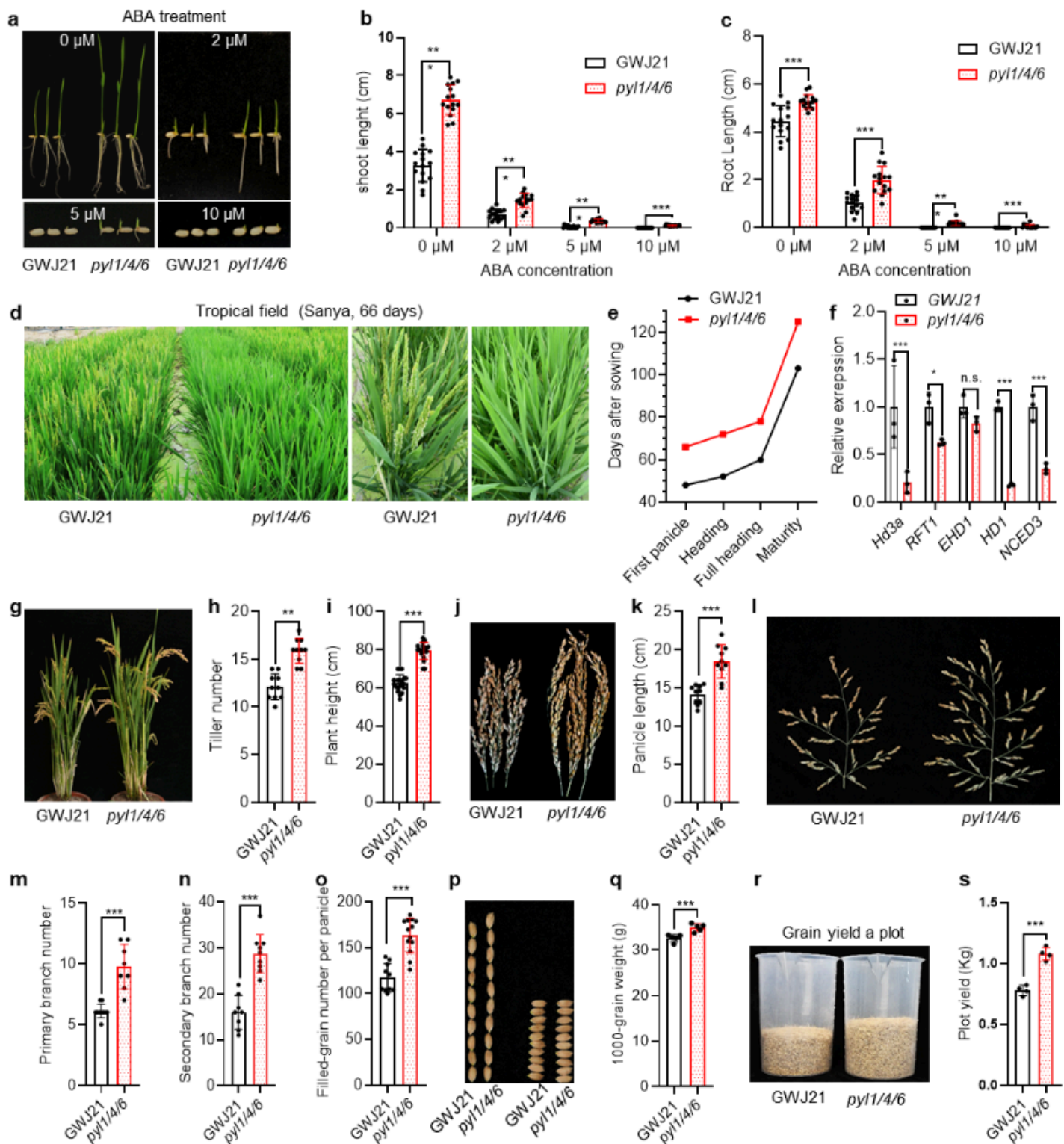


**Figure 2**

**Reducing ABA sensitivity via *PYL1/4/6* mutations enhances the adaptability of GWJ21 to tropics.** **a)** Seedlings of GWJ21 and *py1/4/6* grown on MS solid medium with 0  $\mu$ M, 2  $\mu$ M, 5  $\mu$ M and 10  $\mu$ M ABA for 5 days; Quantitative analysis of shoot length **b)** and root length **c)** from seedlings treated with different concentration of ABA, n=15; **d)** Overview of GWJ21 and *py1/4/6* plants grown in the field of Sanya for 66 days; **e)** Comparison of different reproductive date between GJW21 and *py1/4/6* plants in the field; **f)**

Relative expression of flowering regulatory genes and *NCED3* in 30-day old plants of GWJ21 and *pyl1/4/6*; **g**) Representative plants grown in the field for 90 days, and quantitative analysis of tiller number (**h**) and plant height (**i**),  $n=10$  and  $20$ , respectively; Overview of panicles (**j**) and quantitative analysis of panicle length (**k**),  $n=10$ ; Branch phenotype of panicles (**l**), and the statistical analysis of primary branches (**m**), secondary branches (**n**), and filled-grain number per panicle (**o**),  $n=10$ ; Grain size (**p**) and 1000-grain weight analysis (**q**),  $n=5$ . (**r**) Total grains per plot ( $1\text{ m}^2$ ). (**s**) Grain yield per plot,  $n=4$ . Values are means  $\pm$  SD, and asterisks represent significance ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ; n.s. represents no significant difference); biological applications were indicated by black points in columns.

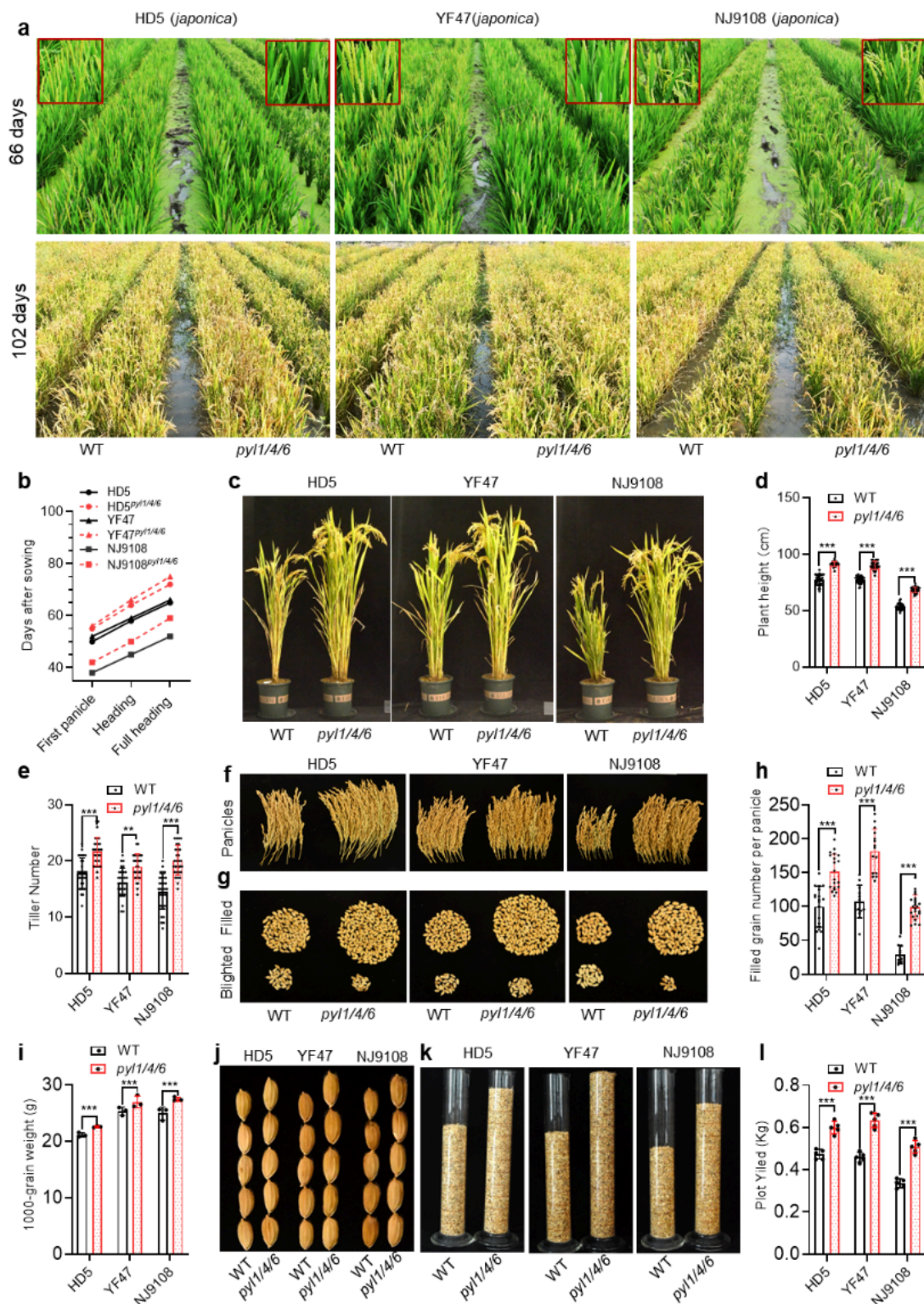


**Figure 3**

**The *PYL1/4/6* mutations comprehensively improve tropical adaptation of *japonica* varieties.** **a)** Overview of temperate *japonica* varieties (WT) and their *pyl1/4/6*-mutant plants grown under tropical field conditions for 66 days and 102 days, and the red boxes indicate the heading phenotype of different lines, HD5 (*Huaidao* 5), YF47 (*Yanfeng* 47), NJ9108 (*Nan Jing* 9108); **b)** Comparison of different reproductive date between *japonica* WTs and *pyl1/4/6* mutants in the field; **c)** Plant architecture of the mature *japonica*

WTs and their *pyl1/4/6* mutants; Quantitative analysis of the plant height (**d**) and tiller number (**e**), n=30; Total panicles from a typical plant (**f**) and total filled/blighted grains from a typical panicle (**g**); Statistical analysis of filled-grain number per plant (**h**) and 1000-grain weight (**i**), n=11 and 3, respectively; Comparison of grain size (**j**) and total grains per plot (1 m<sup>2</sup>) (**k**) between *japonica* WTs and their *pyl1/4/6* mutants, and their Quantitative comparison of plot yield (1 m<sup>2</sup>) (**l**), n=5. Values are means ± SD, and asterisks represent significance (\*\*\*)  $P < 0.001$ ; biological applications were indicated by black points in columns.

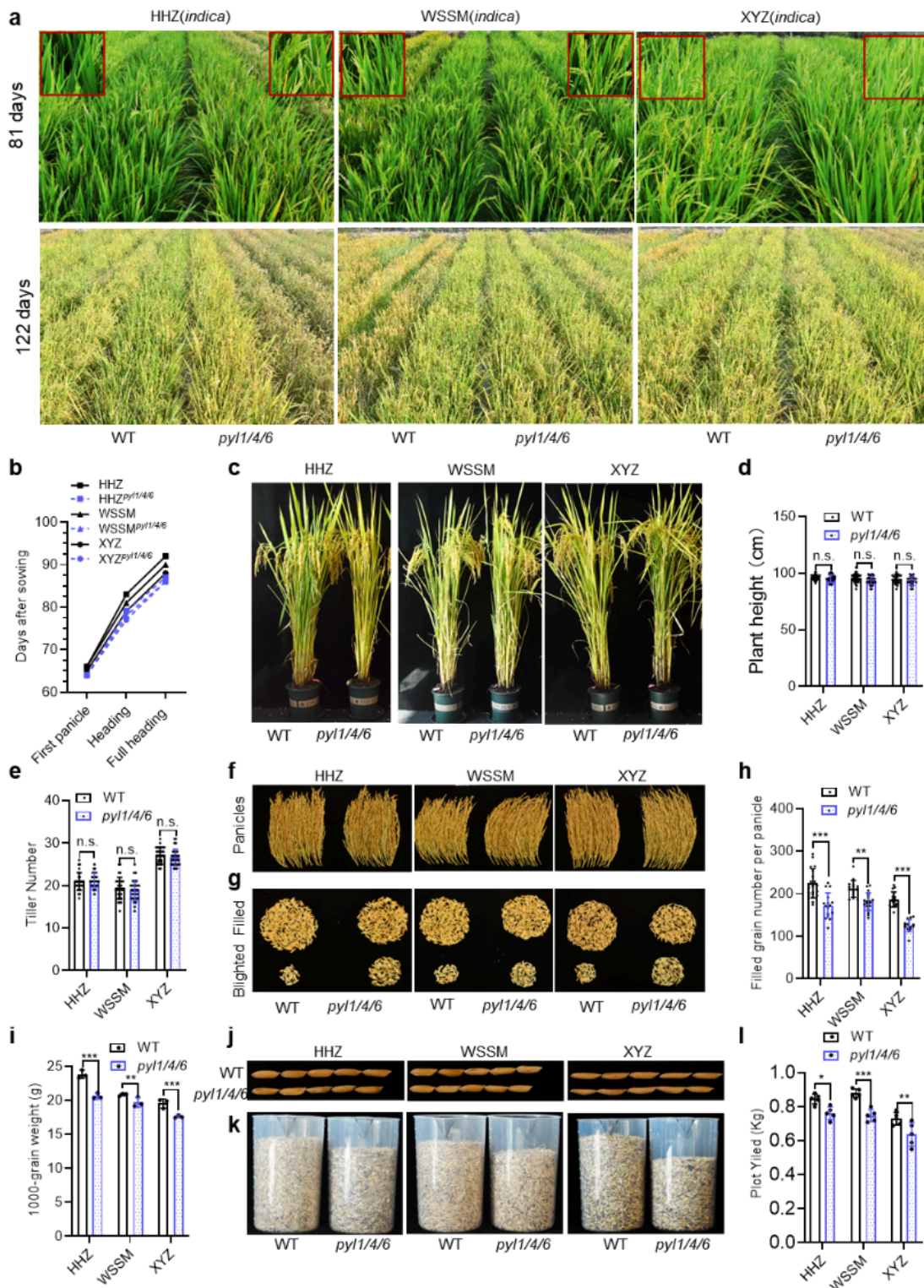
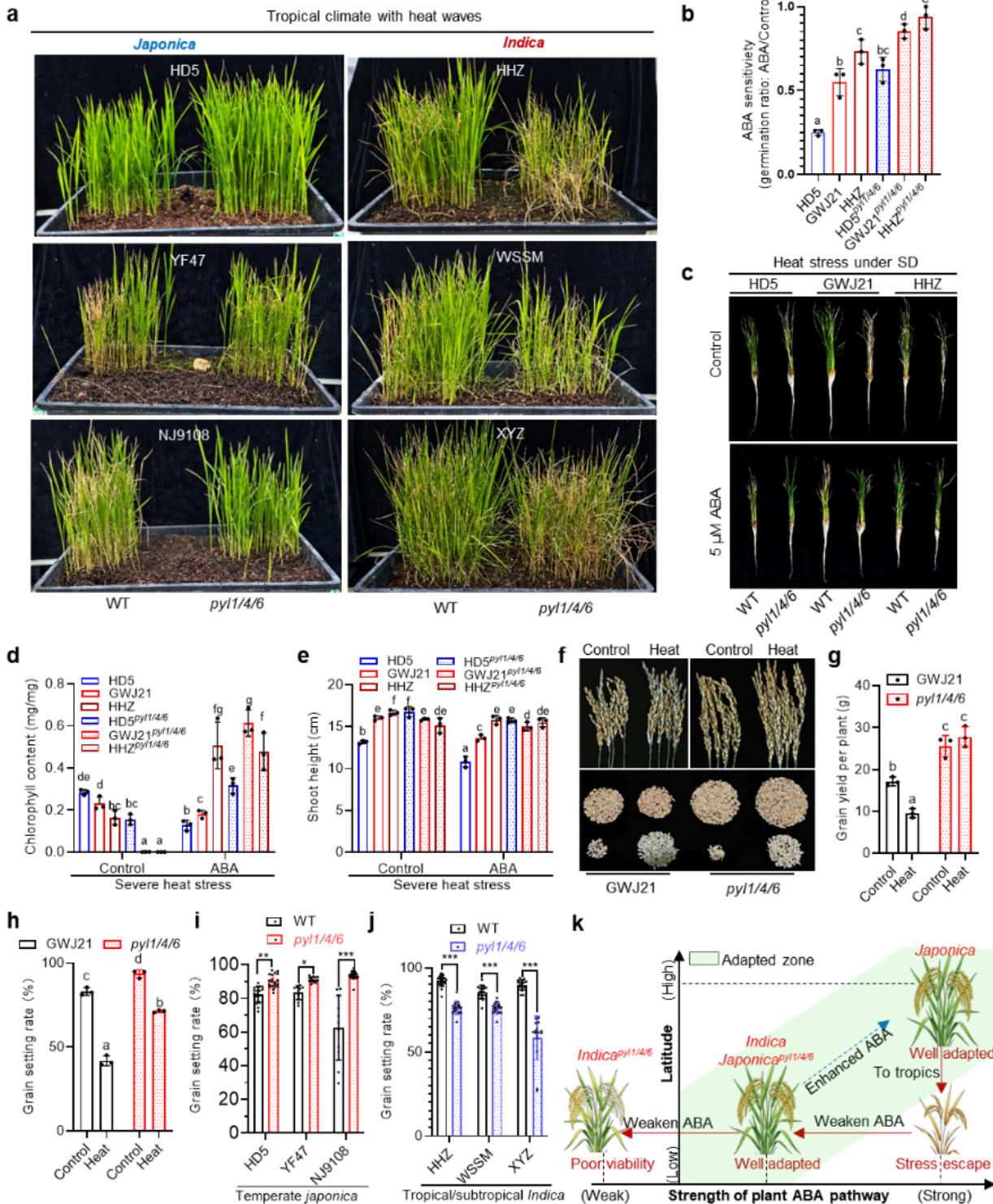


**Figure 4**

**The *PYL1/4/6* mutations impair the adaptability of *indica* cultivars to tropics.** **a)** Overview of three tropical/subtropical *indica* cultivars (WT) and their *pyl1/4/6*-mutant plants grown under tropical field conditions for 81 days and 122 days, and the red boxes indicate the heading phenotype of different lines, HHZ (*Huanghua Zhan*), WSSM (*Wushan Simiao*), XYZ (*Xiangya Zhan*); **b)** Analysis of reproductive date; **c)** Architecture of 120-day old plants; Statistical analysis of plant height (**d**) and tiller number (**e**),  $n=30$ ; total

panicles from a typical plant (f) and total filled/blighted grains from a typical panicle (g); Statistical analysis of filled-grain number per plant (h) and 1000-grain weight (i),  $n=11$  and 3, respectively; Comparison of grain size (j) and total grains per plot ( $1\text{ m}^2$ ) (k) between *indica* WT and their *pyl1/4/6* mutants, and the quantitative analysis of plot yield ( $1\text{ m}^2$ ) (l),  $n=5$ . Values are means  $\pm$  SD, and asterisks indicate significance ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ; n.s. represents no significant difference); biological applications were indicated by black points in columns.



## Figure 5

**The intensity of ABA signaling shapes rice adaptation to tropical heat stresses by balancing growth and viability.** **a)** 3-week old seedlings of *japonica/indica* WT plants and their *pyl1/4/6* mutants grown under tropical heat waves; **b)** ABA sensitivity of different rice materials are indicated by relative seed germination ratio (ABA/control) between treatment of 10  $\mu$ M ABA and mock control for 36 h, n=3; **c)** 14-day old seedlings grown in Yoshida medium with/without 5  $\mu$ M ABA under short-day heat conditions; Quantitative analysis of chlorophyll content (**d**) and shoot height (**e**) of seedlings after a short-day heat treatment, 3 biological replications and 10 seedlings for each replication; Comparison of grain setting (**f**), grain setting rate (**g**), and grain yield per plant (**h**) between GWJ21 and its *pyl1/4/6* mutant plants treated with heat stresses (37°C, 7 days) or control conditions (30°C, 7 days) at heading date; **i,j**) Statistical analysis of grain setting rates of *japonica* and *indica* WT plants and their *pyl1/4/6* mutants grown in the tropical field of Sanya during summer season (March to July), when heat waves occur frequently. **k)** a proposed model for the intensity of ABA signaling shapes rice latitudinal adaptation: A suppressed ABA signaling is observed in *indica* rice adapted to low-latitude tropical/subtropical regions, while an enhanced ABA pathway in temperate *japonica* rice benefits its adaptation to high-latitude temperate regions. Due to the activation of the ABA pathway in the tropics, the temperate *japonica* rice displays ABA-dependent stress escape responses, causing early heading, yield penalties, and heat sensitivity. The suppression of ABA signaling via *PYL1/4/6* mutations improves its adaptation to the tropics. Meanwhile, the further attenuation of ABA signaling in *indica* by *PYL1/4/6* mutations impairs its adaptability to the tropics, leading to poor viability, low grain setting, and yield penalties. Values are means  $\pm$  SD, and asterisks/letters indicate the significance (\* $P$ <0.05, \*\* $P$ <0.01, \*\*\* $P$ <0.001); biological applications were indicated by black points.

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