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Gradual daylength sensing coupled with optimum cropping modes enhances multi-latitude adaptation of rice and maize

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ABSTRACT

To expand crop planting areas, reestablishment of crop latitude adaptation based on genetic variation in photoperiodic genes can be performed, but it is quite time consuming. By contrast, a crop variety that already exhibits multi-latitude adaptation has the potential to increase its planting areas to be more widely and quickly available. However, the importance and potential of multi-latitude adaptation of crop varieties have not been systematically described. Here, combining daylength-sensing data with the cropping system of elite rice and maize varieties, we found that varieties with gradual daylength sensing coupled with optimum cropping modes have an enhanced capacity for multi-latitude adaptation in China. Furthermore, this multi-latitude adaptation expanded their planting areas and indirectly improved China's nationwide rice and maize unit yield. Thus, coupling the daylength-sensing process with optimum cropping modes to enhance latitude adaptability of excellent varieties represents an exciting approach for deploying crop varieties with the potential to expand their planting areas and quickly improve nationwide crop unit yield in developing countries.

Key words: multi-latitude adaptation, daylength sensing, cropping mode

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INTRODUCTION

Crop adaptation to new latitudes requires retuning flowering time to ensure yields (Eshed and Lippman, 2019); the known examples of crop latitude adaptation reestablishment involve genetic modification of photoperiodic genes. In potato (*Solanum tuberosum*), for instance, the natural allelic variants of *S. tuberosum* CYCLING DOF FACTOR 1, a DNA-binding with one finger transcription factor, are no longer post-translationally regulated by light, enabling cultivation outside the geographic center of potato origin (Kloosterman et al., 2013). In soybean (*Glycine max*), *J* (*Glycine max ELF3*) is the ortholog of *Arabidopsis thaliana EARLY FLOWERING 3*, and its loss-of-function variants extend the vegetative phase and improve soybean yield under short-day conditions, thereby enabling cultivation in tropical regions (Lu et al., 2017). In addition, accumulated impairments in the *pseudo-response-regulator* gene orthologs *Tof11* and *Tof12* function likely permitted earlier harvest and improved adaptation to the limited summer growth period at higher latitudes during soybean domestication (Lu et al., 2020). In maize (*Zea mays*), natural variations in the regulatory regions of *ZmCCT9*, *ZmCCT10*, and *ZCN8* (an ortholog of *A. thaliana FLOWERING*

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LOCUS T) were essential for its spread from tropical to temperate regions during early domestication (Hung et al., 2012; Yang et al., 2013; Guo et al., 2018). In rice (*Oryza sativa*), *Grain number, plant height and heading date 7* (*Ghd7*), *Heading date 1* (*Hd1*), *DAYS TO HEADING 8* (*DTH8*/*Ghd8*/ *LHD1*), and *Grain number, plant height and heading date 7.1* affect geographic distribution (Xue et al., 2008; Yan et al., 2011; Dai et al., 2012; Koo et al., 2013; Yan et al., 2013; Gao et al., 2014; Zhang et al., 2015). We recently found that genetic variations in *Hd1*, *DTH8*, *Ghd7*, and *DTH7* enhance rice latitude adaptation by altering the original critical daylength-sensing threshold (Qiu et al., 2021). Rice varieties with *ghd7* alleles are able to adapt to higher latitudes (Xue et al., 2008). In high latitudes, rice varieties mainly carry the haplotype *hd1 DTH8 ghd7 dth7*, whereas in low latitudes, rice varieties mainly carry the haplotype *Hd1 DTH8 Ghd7 DTH7* (Zong et al., 2020; Qiu et al., 2021; Chen et al., 2022). These examples demonstrate how different genotypes adapt to multiple latitudes.

The growing human population and adverse effects of global climate change threaten global food security (Godfray et al., 2010; Wheeler and von Braun, 2013). In the past several decades, innovations in germplasm resources, such as the successful application of hybrid rice in China, have contributed to ensuring global food security (Xie and Zhang, 2018; Varshney et al., 2020). High yields, high quality, disease resistance, stress resistance, and adaptation to varied latitudes are important for hybrid rice success in China (Wang et al., 2005; Anacleto et al., 2015). Ideal varieties also need to be able to grow at different latitudes to realize food security goals globally rather than locally (Qiu et al., 2021). However, how to achieve multi-latitude adaptation of a suitable variety is still unknown. At present, adaptation to latitude can be modified by targeting photoperiodic genes for genetic improvement, but this process is very time consuming (Wang et al., 2021). Indeed, this strategy adds 5–10 years to the development of suitable varieties, which can decrease the genetic gain from other traits in target environments (Kusmec et al., 2021). Therefore, focusing only on the genetic improvement of latitude adaptability in crops may not fully ensure food security under current global climate conditions.

Multiple cropping, which is defined as harvesting more than once per year, is a widespread land management strategy in tropical and subtropical agriculture (Waha et al., 2020). Multiple cropping has been proposed to improve crop yields and offset cropland losses in the face of global climate change (Cohn et al., 2016; Waha et al., 2020; Xu et al., 2021). Therefore, increasing cropping frequency (the number of harvests per growing season) is an agricultural intensification strategy that may help to alleviate land burdens in pantropical countries with increasing global food demand (Xu et al., 2021). However, another advantage of multiple cropping has received little attention. Based on statistical analysis of historical data, we demonstrate that multiple cropping modes with different cropping frequencies resulted in an enhancement of latitude adaptation for rice and maize varieties in China. Multi-latitude adaptation of these varieties has expanded their cropping areas and indirectly improved China's crop production. Furthermore, we found that multi-latitude-adapted rice and maize varieties performed gradual daylength sensing and generated the perfect flowering time plasticity to match the optimum cropping modes with different cropping frequencies. Therefore, our data show how the daylength-sensing process of excellent crop varieties, coupled with optimum cropping modes, was used as a rapid method of enhancing latitude adaptation to cope with the typical lag associated with genetic improvement and increase global food production.

RESULTS

The paradox between photoperiod response and latitude adaptation of summer crops

For agricultural purposes, crop adaptation to a specific latitude should consider yield. Flowering too early will shorten the vegetative growth period, reduce biomass, and ultimately reduce production and yield (Xue et al., 2008; Wei et al., 2010; Yan et al., 2011; Dai et al., 2012; Koo et al., 2013; Yan et al., 2013; Gao et al., 2014). Conversely, flowering too late will limit crop production owing to sterility caused by exposure to low temperatures in the late growth period (Koo et al., 2013; Zhang et al., 2014). The timing of flowering is thus a crucial determinant of latitude adaptation. Accordingly, we defined crop latitude adaptation here as follows: assuming optimal flowering time, the full growth period of the crop precisely matches its cropping season length at a given latitude (Supplemental Figure 1).

Flowering time in summer crops gradually shortened from higher latitudes to lower latitudes (Figure 1A). Moreover, we observed this phenomenon universally across all genetic materials with different combinations of photoperiodic genes. Regardless of the photoperiod gene combinations, the flowering time was always longer at high latitudes than at low latitudes (Figure 1B). We also determined that increasing average temperatures at lower latitudes prolonged the length of the safe growing season for rice (Figure 1C). Therefore, the flowering time plasticity of any summer crop variety did not necessarily match the length change in the growing seasons at multiple latitudes (Figure 1D).

Different optimizations of cropping frequency to enhance rice and maize latitude adaptation

In traditional crops, some summer varieties are adapted to multiple latitudes. To understand why they are adapted to different latitudes, we analyzed planting types from approved varieties in all provinces of China between 2011 and 2020. We determined that only *indica* rice has been historically planted for two rounds at middle and low latitudes from 20°N to 35°N (Figure 2). Thus, these results indicated that *indica* rice varieties have adapted to low-latitude areas through increasing cropping frequency (Figure 2). Interestingly, at low latitudes (26.28°N), the safe rice growing season was precisely twice as long as the cropping season of NIL$^{Hd1\ dth8\ Ghd7}$ (Figure 1B). Therefore, these results indicated that the current mode of *indica* rice by double cropping *indica rice* at low latitudes can maximize yield.

Optimizing cropping modes with different cropping frequencies could be a sustainable method for improving crop yields and offsetting cropland losses (Cohn et al., 2016; Waha et al., 2020; Xu et al., 2021). We also hypothesized that optimizing cropping modes based on different cropping frequencies

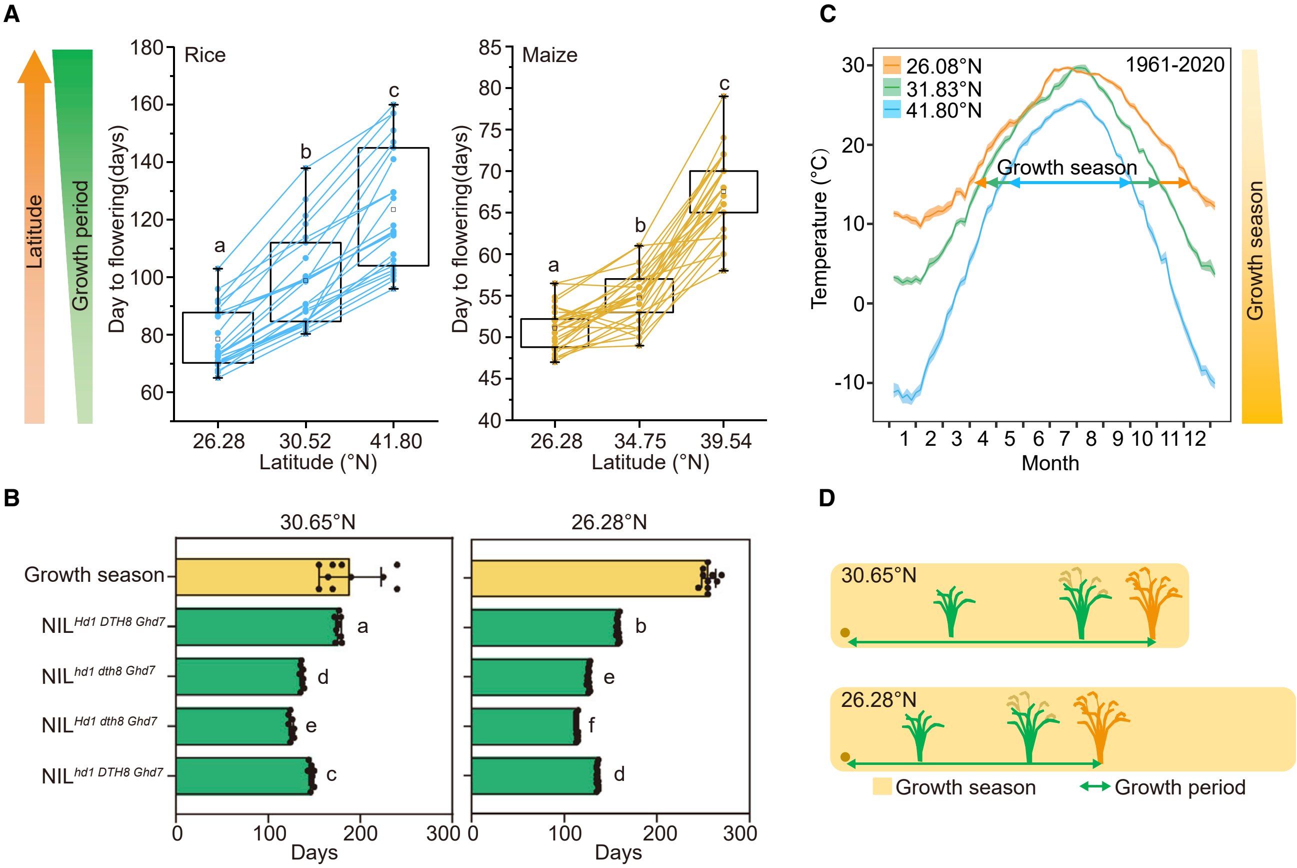

Figure 1. The growth period does not match the growth season length at low latitudes.

(A) Flowering time of rice and maize varieties in different latitudes. One line represents one variety.

(B) Growth period of the near-isogenic lines (green column) and the cropping season length (yellow column) at different latitudes. The growth period is defined as flowering time plus 30 days, and the growth season is defined as the number of days when the ambient temperature was over 15°C in 2011–2020.

(C) Annual temperature profiles at different latitudes and length of the growth season over the past 60 years. The horizontal line with the double arrow represents the growth season.

(D) Schematic diagram of the mismatch between the growth period and the growth season.

For **(A) and (B)**, lowercase letters indicate significant differences based on Duncan's multiple-range test ($p < 0.05$).

might enhance crop variety adaptation to multiple latitudes. To test this hypothesis, we analyzed the relationship between planting mode and latitude distribution of varieties. Accordingly, we divided rice varieties into three planting types: middle season, early season, and late season. Previous studies reported pairing middle-season varieties as one-round rice with winter wheat (*Triticum aestivum*) to achieve double-season cropping at middle latitudes (Wang et al., 2015; Zhang et al., 2017). Early-season and late-season varieties were used as two-round rice for a triple-season cropping mode at low latitudes (Figure 3A). Our results showed that varieties with multiple cropping modes were always distributed in broader latitude regions (Figure 3B). For example, the cropping area of one-round rice Shanyou63 also coincided with that of winter wheat, allowing for double-season cropping in middle latitudes (Figure 3C and Supplemental Figure 2D). Otherwise, Shanyou63 was planted as two-round rice at low latitudes (Figure 3D). Therefore, we conclude that the adaptation of rice varieties can be enhanced by optimizing cropping modes with different cropping frequencies to eliminate the paradox between photoperiod response and latitude adaptation.

Furthermore, we noticed that the one-round maize varieties Zhengdan958 and Xianyu335 can adapt to multiple latitudes from 25°N to 53°N (Supplemental Figures 2A and 2B). In contrast to two-round rice varieties, maize may therefore benefit from other cropping strategies to enhance multi-latitude adaptation. For example, the single-season maize varieties Zhengdan958 and Xianyu335 always exhibited delayed flowering and produced higher yields at high latitudes (31°N–53°N) than at lower latitudes (27°N–38°N) (Supplemental Figure 2C). Notably, we observed that the cropping area of Zhengdan958 and Xianyu335 partially coincided with that of winter wheat at middle latitudes (25°N–38°N) (Supplemental Figure 2D–2F). Based on previous reports (Xin and Tao, 2019), our results suggest that these areas use the winter wheat–maize double-season cropping mode to enhance latitude adaptation of Zhengdan958 and Xianyu335 (Supplemental Figure 2G). Overall, our results show that increasing the cropping frequency from high

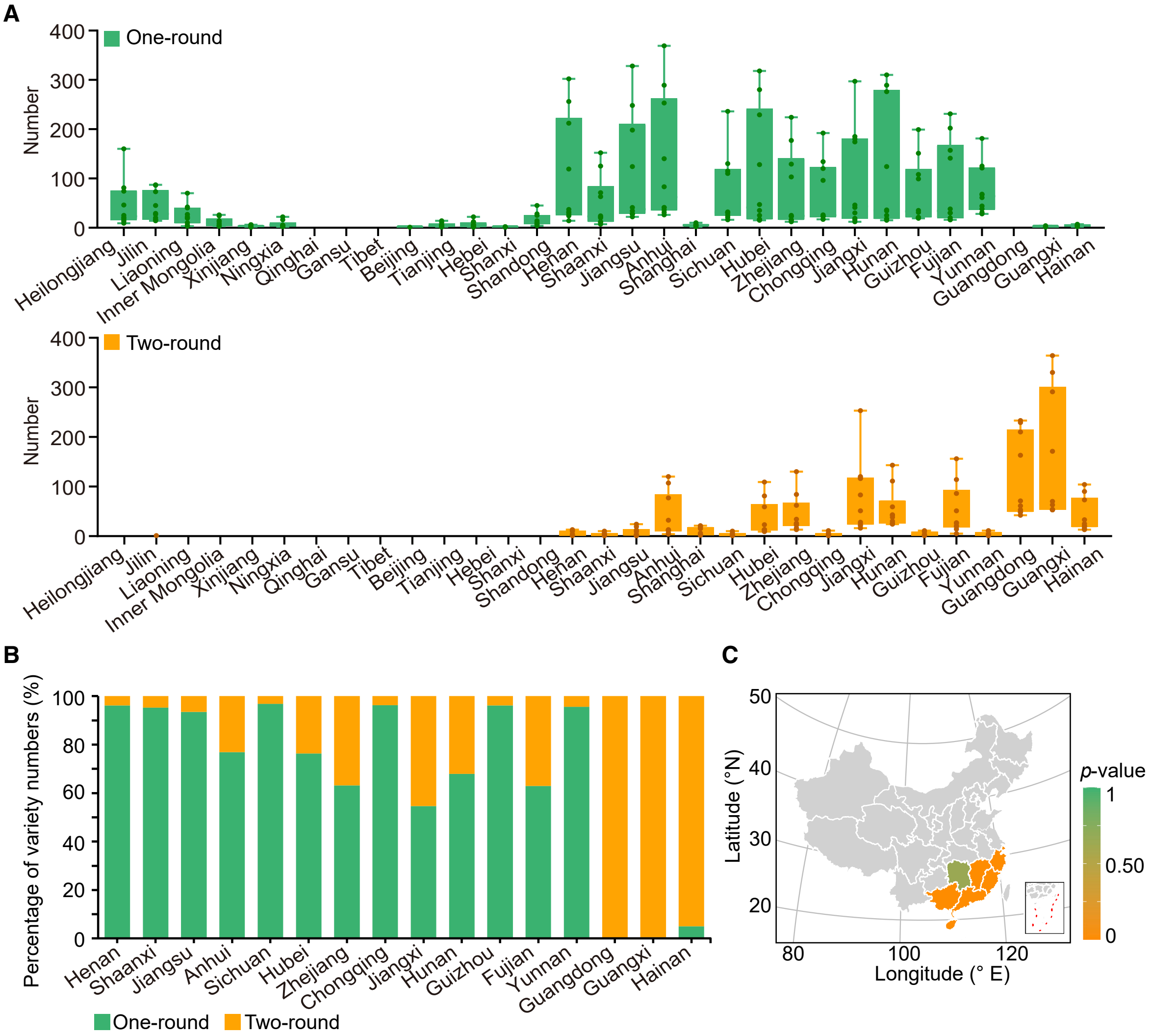

Figure 2. Cropping frequency and distribution of rice varieties in China from 2011 to 2020.

(A) Distribution of one- and two-round rice varieties in each province.

(B) The percentage of one- and two-round rice varieties in middle and low latitudes.

(C) Heatmap of two-round rice distribution in China. The *p* value represents the comparison between the number of two-round rice in a province and in all provinces by a hypergeometric test.

to low latitudes shortened the cropping season length to match the shortening growth period length of Chinese summer crops and achieve multi-latitude adaptation in these crops.

The daylength-sensing process is central to achieving multi-latitude adaptation

Shanyou63, a mega hybrid rice variety derived from the parents Zhenshan97A and Minghui63, was a milestone in China's hybrid rice development and production because of its high yield and wide adaptability. It was planted in 16 provinces and covered 17% of the national hybrid rice area annually from 1984 to 2012 (Xie and Zhang, 2018). Here, we analyzed the first approval times of hybrid *indica* varieties as both one- and two-round rice with a cumulative planting area of more than 30 million hectares in China and found that Shanyou63 was the first hybrid variety approved as both one- and two-round rice (Figure 4A). Moreover, in the 15 years after Shanyou63 was first approved (up to 1999), only six varieties were approved as both one- and two-round rice with a cumulative planting area of over 30 million hectares (Figure 4A). Notably, many hybrid varieties were approved and planted after 1999 as both one- and two-round rice with a cumulative planting area of more than 30 million hectares (Figure 4A). Among these hybrid *indica* varieties, 37% derived from the common genetic ancestors of the Shanyou63 parents Zhenshan97A and Minghui63 (Figure 4A). In addition, our previous study indicated that almost all three-line hybrid varieties use the Shanyou63 photoperiod module *Ghd7ghd7 Hd1hd1 dth8dth8 DTH7dth7* (Qiu et al., 2021). These results suggest that the photoperiod module of Shanyou63 can help these varieties achieve multi-latitude adaptation.

Our previous studies demonstrated that the rice photoperiod module regulating daylength sensing directly determines latitude adaptation (Qiu et al., 2021; Wang et al., 2021). We also

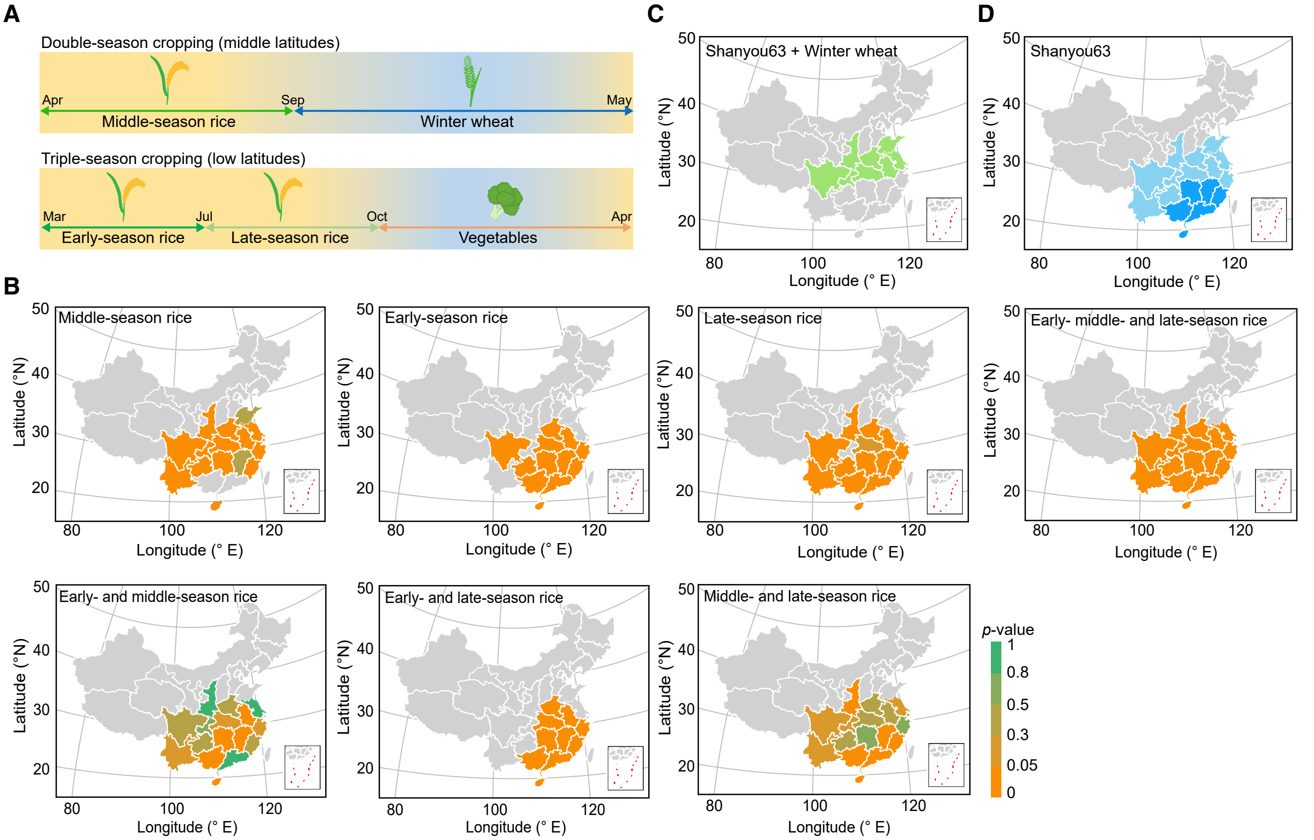

Figure 3. Optimum cropping modes enhance the adaptation of rice varieties to multiple latitudes.

(A) Cropping modes of *indica* rice at different latitudes. At middle latitudes, a double-season cropping mode (middle-season rice–winter wheat) is mainly used. In low latitudes, a triple-season cropping mode (early-season rice–late-season rice–vegetable) is mainly used.

(B) Distribution of middle-season rice, early-season rice, later-season rice, early- and middle-season rice, early- and later-season rice, middle- and later-season rice, and early-, middle-, and later-season rice at different latitudes. The *p* value represents the extent of enrichment for different planting types in a province calculated by Fisher's exact test.

(C) Overlapping planting areas of Shanyou63 and winter wheat.

(D) Cropping area of Shanyou63. The light blue color represents one-round rice, and the dark blue color represents two-round rice.

compared the daylength-sensing processes between *HGD* with the *Ghd7 Hd1 DTH8 DTH7* photoperiod module (Zong et al., 2020) and Shanyou63. We found that the florigen genes *Hd3a/RFT1* were repressed at daylengths of more than 12 h in *HGD* (Figure 4B). However, *Hd3a/RFT1* decreased slowly when daylength gradually increased in Shanyou63 (Figure 4C). Compared with *HGD*, which senses a 13-h critical daylength threshold, Shanyou63 displays gradual daylength sensing. Therefore, the photoperiod module of Shanyou63 produces a gradual daylength sensing that confers perfect flowering time plasticity to match rice cropping season length as one- or two-round rice at different latitudes (Figures 4D–4G). After 15 years of genetic improvement, the use of this photoperiod module has enabled subsequent varieties to gain the ability to adapt to multiple latitudes (Figure 4A).

We also detected the daylength-sensing processes of the maize cultivars Zhengdan958 and Xianyu335 and the soybean cultivar Zhonghuang13 (a high-yield soybean variety with the largest cropping area in China). We found that the expression of *ZCN8* in Zhengdan958 gradually decreased with increasing daylength, exhibiting gradual daylength sensing (Figure 5A and Supplemental Figure 3A). Gradual daylength sensing of Zhengdan958 directly caused a visible difference in *ZCN8* expression heatmaps between high and middle latitudes (Figure 5B). Compared with that in Zhengdan958, the expression of *ZCN8* in Xianyu335 decreased slightly as daylength increased and maintained a high expression level with different daylength treatments (Figure 5C). Therefore, the *ZCN8* expression heatmap of Xianyu335 exhibited a high expression level only at high and middle latitudes (Figure 5D). However, this evidence was insufficient to conclude that Xianyu335's slight daylength sensing led to its smaller planting area relative to Zhengdan958 at middle latitudes (Figures 5E and 5F and Supplemental Figures 2A and 2B).

Furthermore, we found that the expression levels of *GmFT2a* and *GmFT5a* (an ortholog of *FT*) in Zhonghuang13 did not change with increasing daylength and showed insensitivity to daylength, consistent with the lack of multi-latitude adaptation in this variety (Supplemental Figures 3B–3D). The daylength-sensing processes of Shanyou63 and Zhengdan958 indicated that varieties with gradual daylength sensing can be grown in a wider latitude range. Overall, these results support the conclusion that optimum

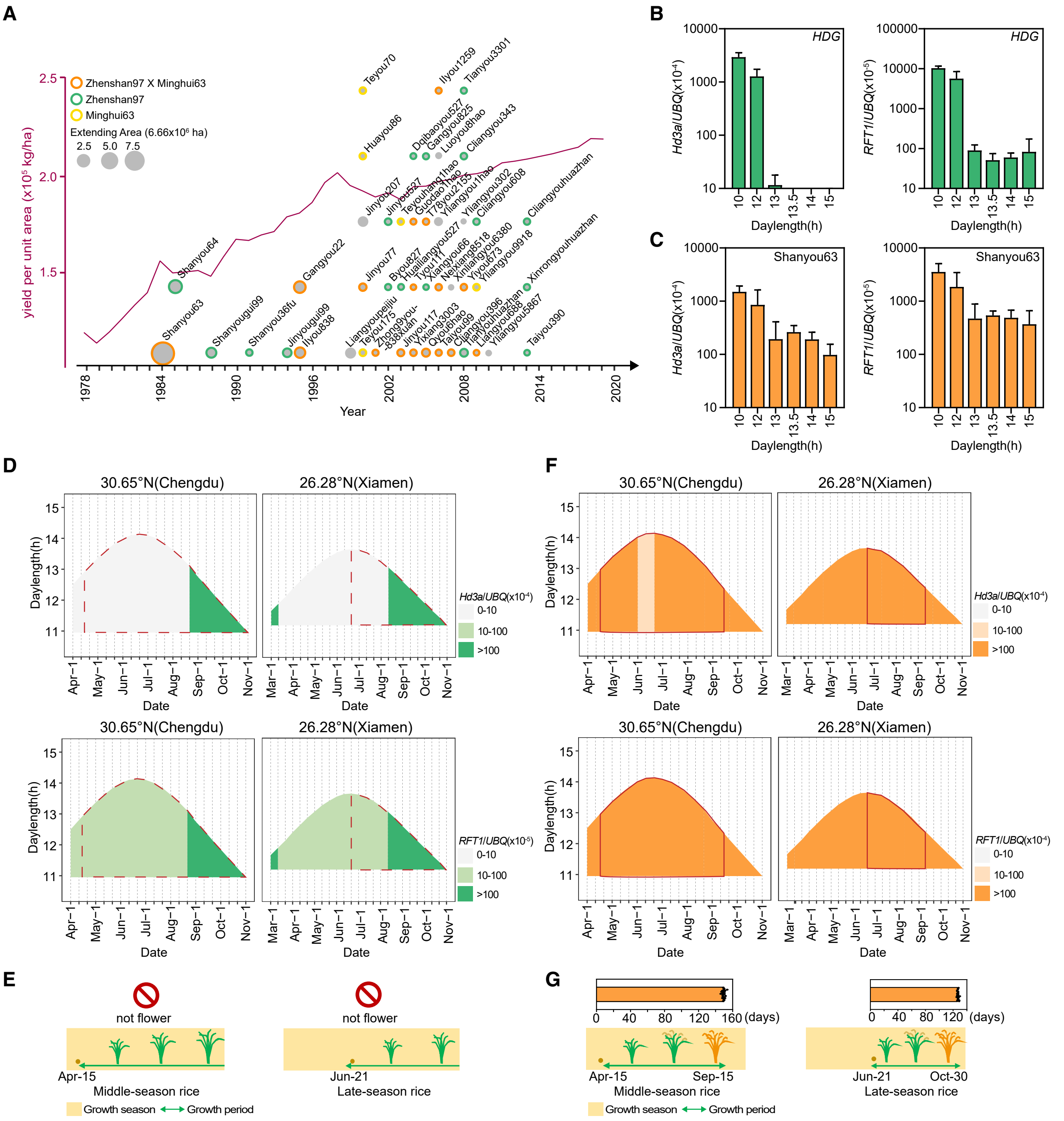

Figure 4. The daylength-sensing process of Shanyou63 enhanced its multi-latitude adaptation.

(A) Timeline of the introduction of hybrid *indica* rice varieties with multi-latitude adaptation. The dark red line represents the change in rice yield per unit area from 1978 to 2020. The size of the circle represents the total cropping area. Orange circles represent varieties derived from the common genetic ancestors of the Shanyou63 parents Zhenshan97A and Minghui63. Green circles represent varieties derived from Zhenshan97A, and yellow circles represent varieties derived from Minghui63.

(B and C) The expression of *Hd3a* and *RFT1* under different daylength conditions in *HDG* **(B)** and Shanyou63 **(C)**. Error bars represent the standard deviation of four biological replicates.

(D and F) Florigen gene-expression heatmap of *HGD* **(D)** and Shanyou63 **(F)** at different latitudes. The solid red lines represent the range of the growth period, and the dotted red lines represent the range of the assumed growth period.

(E and G) Schematic diagrams of the growth period and growth seasons of *HGD* **(E)** and Shanyou63 **(G)** at different latitudes.

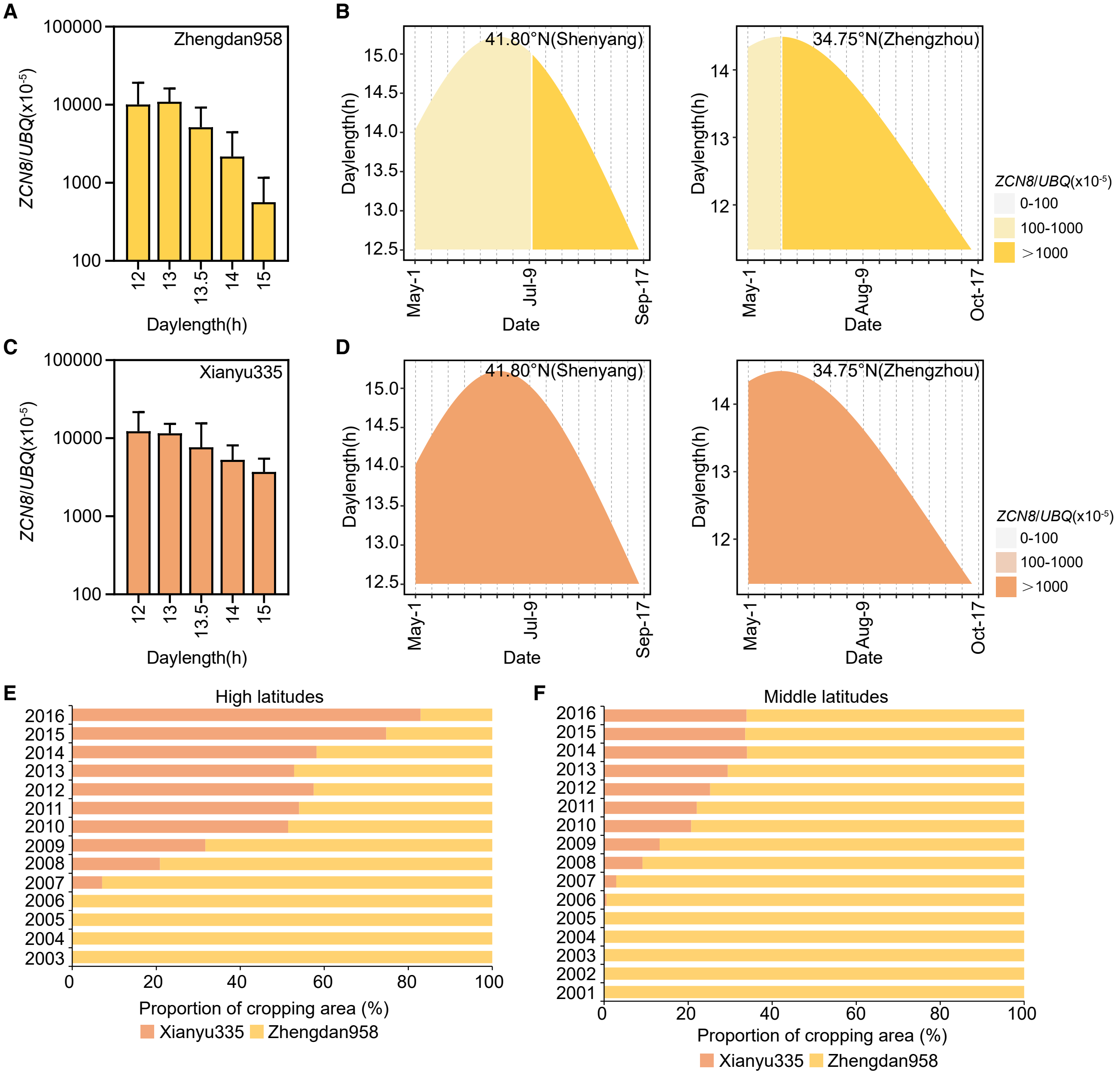

Figure 5. The daylength-sensing process of Zhengdan958 and Xianyu335.

(A and C) The expression of *ZCN8* under different daylength conditions in Zhengdan958 **(A)** and Xianyu335 **(C)**. Error bars represent the standard deviation of four biological replicates.

(B and D) Florigen gene-expression heatmap of Zhengdan958 **(B)** and Xianyu335 **(D)** at different latitudes.

(E and F) The proportion of cropping area of Zhengdan958 and Xianyu335 in high latitudes **(E)** and middle latitudes **(F)**. High latitude range: 40°N–53°N; middle latitude range: 28°N–40°N.

cropping modes must be coupled with a suitable daylength-sensing type to confer multi-latitude adaptation in a given variety.

Adaptation of super-high-yield varieties to multiple latitudes indirectly improved nationwide unit yield

Does crop multi-latitude adaptation affect yield? We observed that the rice variety Shanyou63 is suitable for cultivation as both one- and two-round rice (Figures 3C and 3D). Our results showed that the increase in rice yield per unit area in China occurred mainly in the 15 years following the initial promotion of Shanyou63 rather than following the release of varieties adapted to multiple latitudes after 1999 (Figure 4A and Supplemental Figure 4). This observation prompted us to ask whether Shanyou63 promoted this increase in rice yield during the Shanyou63 cropping period. To this end, we compared varieties adapted to multiple latitudes (Shanyou63 and Shanyou64) or local latitudes (Eyi105, Zhefu802, Zunxian3hao, and 79106) (Supplemental Figure 5). We observed a strong positive correlation between the increase in cropping area of

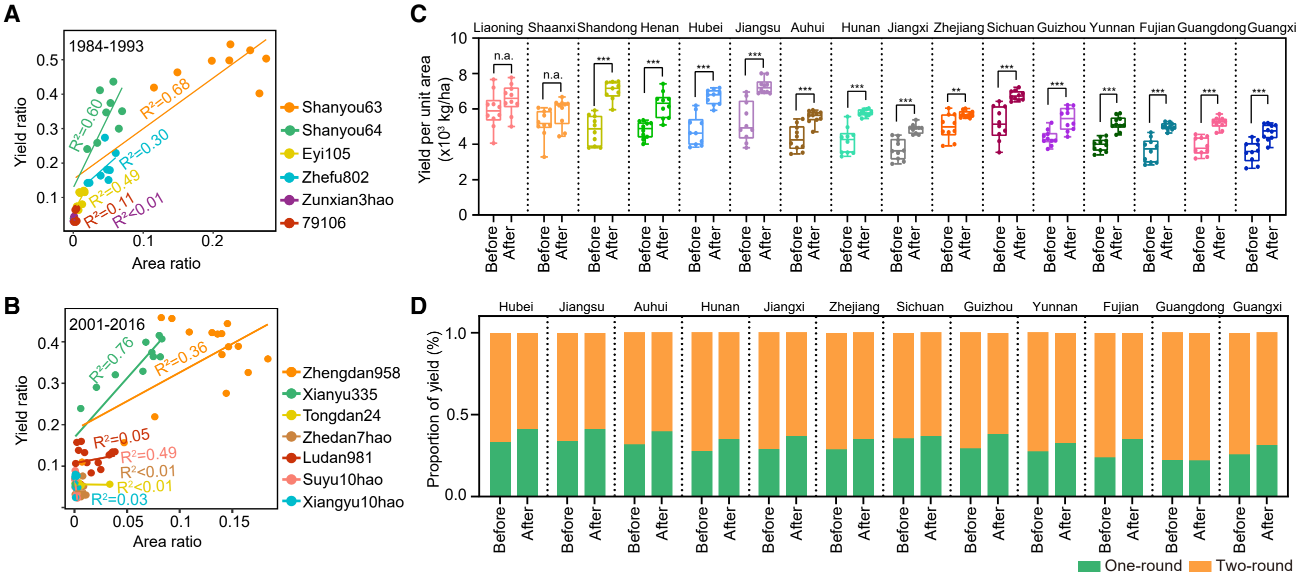

Figure 6. Multi-latitude-adapted varieties improved nationwide unit yield during the cropping period.

(A and B) Linear correlation analysis between the area ratio and the yield ratio for rice **(A)** and maize **(B)**. The coefficient of determination R^2 was calculated using R software as an indication of the goodness of fit.

(C) Changes in yield per unit area before and after the promotion of Shanyou63 in the provinces where Shanyou63 is planted. Liaoning province did not plant Shanyou63 and served as a control province. Asterisks indicate a significant difference by Student's *t*-test (***p < 0.001).

(D) Proportion of yield for one- and two-round rice before and after the promotion of Shanyou63.

Shanyou63 and Shanyou64, which are adapted to multiple latitudes, and China's per unit increase in rice yield (Figure 6A). Moreover, Shanyou63 occupied a greater cropping area than Shanyou64, resulting in a larger contribution to yield improvement, as it could be planted in different provinces in China (Figures 6A and 6C and Supplemental Figures 5A and 5B). Interestingly, we noticed that the per unit yield ratio of one-round rice increased in middle-latitude provinces, including Hubei, Jiangsu, Zhejiang, and Anhui (Figure 6D). This result provided support for the improvement of rice production in these provinces by optimizing the cropping frequency of Shanyou63 from two-round rice to one-round rice. Based on previous reports (Yang et al., 2015; Zhao et al., 2016; Gao et al., 2019), we hypothesize that the massive transition of cropping mode in middle-latitude provinces around 1984 was a consequence of the expansion of Shanyou63 planting area. Indeed, our results support the notion that the optimization of planting frequency at various latitudes, combined with the photoperiodic response of Shanyou63, enabled its multi-latitude adaptation and improved the unit yield of rice in China.

Similar to that of Shanyou63, the cropping areas of maize varieties Zhengdan958 and Xianyu335, which are adapted to multiple latitudes, also showed a more positive correlation with the unit yield of maize compared with local-latitude varieties (Tongdan24, Zhedan7hao, Ludan981, Suyu10hao, and Xiangyu10hao) (Figure 6B and Supplemental Figures 2A, 2B, and 6). However, the contribution of the multi-latitude-adapted varieties Shanyou63 (rice), Zhengdan958 (maize), and Xianyu335 (maize) to the unit yield increase did not last for more than 15 years (Figures 6A and 6B). These results illustrate that when a super-high-yield crop variety appears, its multi-latitude adaptation must be established quickly to achieve comprehensive improvements in grain yield.

Global climate change affects crop adaptation to multiple latitudes

Once cropping strategies based on adaptation to multiple latitudes in rice and maize have been established, is there any need to maintain selection pressure in the future? To address this question, we collected annual temperature data at different latitudes from 1953 to 1962 and 2011 to 2020. Mean annual and daily temperatures were higher between 2011 and 2020 compared with 50 years ago (Supplemental Figures 7A–7D). A direct consequence of global warming was the extension of growing season length at all latitudes (Supplemental Figures 7E and 7F). Thus, the length of the growth period of historically adapted (pre-2000) varieties no longer matched the length of the current growing season (Supplemental Figure 7G). For example, the growing season in Jiangxi (28.68° N) has extended by 40 days (for *indica*) owing to the increase in summer temperatures over the past 50 years (Supplemental Figures 7E and 7F). Furthermore, this extension of the growing season caused an increase in the cropping area of two-round rice in Jiangxi (Supplemental Figure 7H). These results indicate that increasing cropping frequency and selecting corresponding crops can enable a rapid response to the lengthening growing season at different latitudes under a warming climate.

DISCUSSION

Optimum cropping modes that enhance super-high-yield variety adaptation to multiple latitudes are a fast and sustainable approach to improving nationwide unit yield

In 1973, the three-line hybrid rice technique was introduced, leading to a great improvement in rice yield per unit area in China

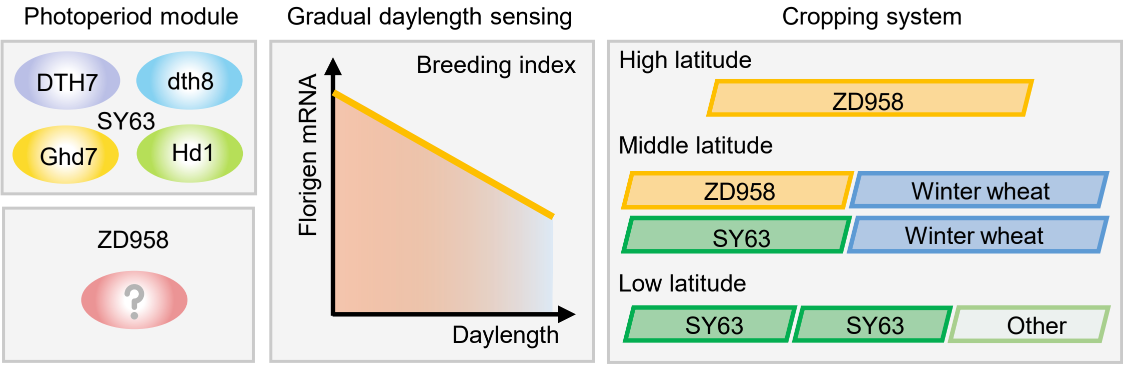

Figure 7. Gradual daylength sensing coupled with optimum cropping modes enhanced the multi-latitude adaptation of rice and maize.
The photoperiod module of Shanyou63 (SY63) is *Ghd7 DTH7 dth8 Hd1*, and the photoperiod module of Zhengdan958 (ZD958) is unknown at present. Their photoperiod gene modules determine the gradual daylength sensing. Coupled with various cropping systems at different latitudes, these varieties with gradual daylength sensing can achieve multi-latitude adaptation.

based on increasing the cropping area of Shanyou63 hybrid rice (Figures 4A, 6A, and 6C and Supplemental Figure 4). Thus, hybrid rice experienced a massive success in China. This study showed that the rapid increase in rice yield per unit area in China was achieved simply by coupling optimum cropping modes with the daylength sensing of Shanyou63 to enhance its latitude adaptation from 1984 to 1993 (Figures 4A, 6A, and 6C and Supplemental Figure 4). As a result, rice yield per unit area increased by 40.65% in just 15 years from 1984 to 1998 (Supplemental Figure 4). Similarly, the maize variety Zhengdan958, which also has gradual daylength sensing, demonstrated enhanced multi-latitude adaptation based on different cropping modes at middle and high latitudes (Figures 5A and 5B and Supplemental Figure 2). Therefore, the examples of Shanyou63 and Zhengdan958 suggest that the use of optimum cropping modes with different cropping frequencies to improve the latitude adaptation of super varieties is a rapid and effective method for increasing nationwide unit yield. Based on breeding and upgrading the Shanyou63 parents, many hybrid rice varieties exhibited multi-latitude adaptation traits after 1999. However, rice yield per unit area increased by only 4.25% in the subsequent 15 years from 1999 to 2013 (Supplemental Figure 4). Therefore, a greater number of multi-latitude-adapted varieties was not a main cause of increased rice yield per unit area. Nevertheless, our results demonstrated that enhancing the adaptation of a super-high-yield variety to multiple latitudes is a fast and sustainable approach for widely increasing the crop per unit area.

Gradual daylength sensing can be an efficient marker for selecting multi-latitude adaptation varieties

Currently, a plethora of methods are available to accelerate breeding, including speed breeding (Watson et al., 2018; Hickey et al., 2019), genome selection (Desta and Ortiz, 2014), gene editing (Chen et al., 2019; Gao, 2021), and other tools (Chang et al., 2016; Wu et al., 2021; Zhu and Zhu, 2021). These approaches can quickly increase latitude adaptation in varieties whose core photoperiodic modules are known. However, unlike rice, the photoperiodic networks of many crops are not fully established or are uncertain with respect to multi-latitude adaptation. Therefore, the rice variety Shanyou63 offers a successful example of how to enhance latitude adaptation without modifying photoperiodic genes. When Shanyou63 was first approved for cropping in 1984, none of the rice photoperiodic genes had been cloned. Instead, Shanyou63 latitude adaptation was directly enhanced by selection for optimal daylength sensing, combined with the use of cropping modes with different cropping frequencies (Figures 3C, 3D, 4C, 4F, and 4G). Similarly, the multi-latitude adaptation of the maize variety Zhengdan958 was also established without information on photoperiodic genes (Figure 5A and Supplemental Figures 2A, 2E, and 2G). Furthermore, our study shows that we can improve the latitude adaptation of varieties with gradual daylength sensing by combining cropping modes with different cropping frequencies (Figures 4B–4G, 5, and 7). Although we still do not know the core photoperiod module of Zhengdan958, it is clear that the respective photoperiod modules determine the gradual daylength sensing of Shanyou63 and Zhengdan958 (Figure 7). Although early breeders selected Shanyou63 and Zhengdan958 with gradual daylength sensing, they did not directly detect daylength sensing of these varieties but instead selected gradual daylength sensing indirectly based on selection for weak photosensitivity through multi-point field experiments. Based on current cropping modes, gradual daylength sensing can be used as a breeding index for the selection of a potential multi-latitude-adapted variety in future breeding.

Optimal cropping mode is a potential method for quickly enhancing latitude adaptation of soybean

Data from the National Bureau of Statistics (https://data.stats.gov.cn/) show that soybean became China's largest imported agricultural product in 2020, with over 1×10^{12} kg. Although the tonnage of imported soybeans continues to rise, domestic soybean production has been hovering below 2×10^{11} kg, which represents only 20% of Chinese soybean needs. To address this issue, the Chinese government proposed the soybean revitalization plan in 2019. However, it is impossible to quickly improve the unit yield of Chinese soybean varieties through breeding. Our results show that the soybean variety Zhonghuang13 has a remarkable ability to increase yield per unit area (Supplemental Figure 8). However, Zhonghuang13 is only suitable for cultivation in the Huang-Huai region (25°N–43°N) (Supplemental Figure 8A). In contrast to the gradual daylength sensing of Shanyou63 (rice) and Zhengdan958 (maize), Zhonghuang13 (soybean) showed daylength insensitivity with high-level expression of florigen genes (Supplemental Figures 3C and 3D). Therefore, the flowering time plasticity of Zhonghuang13 did not match the current cropping system (Supplemental Figure 3E). Zhonghuang13 varieties have not achieved multi-latitude adaptation through multiple cropping modes (Supplemental Figures 3C–3E and 8). In order to match the current cropping system, we can modify Zhonghuang13 photoperiodic genes to prolong the growth period and integrate the variety into the southern double-cropping rice tillage system to replace early-season rice. However, the process of genetic improvement always takes time.

If a new cropping system can be established quickly, Zhonghuang13 may directly adapt to low latitudes without genetic improvement. As a novel sustainable cropping method, ratoon rice can provide high productivity with relatively low cost and labor requirements (Yuan et al., 2019; Shen et al., 2021). Another study showed that double-cropping rice could be replaced by ratoon rice, thereby reducing the carbon footprint and enhancing net ecosystem economic benefit (Xu et al., 2022). However, the growth period length (first growth period length + ratoon growth period length) of ratoon rice varieties does not match the existing cropping system, dramatically limiting the latitude adaptation of ratoon rice varieties. We therefore propose that a rotation cropping system between Zhonghuang13 and ratoon rice varieties at low latitudes could potentially enhance the multi-latitude adaptation of Zhonghuang13 and ratoon rice varieties in China.

We thus posit that as long as the growth period of various crops can be rapidly predicted under different multiple-cropping strategies, their adaptation to multiple latitudes can be rapidly established via multiple-cropping design. We and others have previously reported rapid methods for predicting latitude adaptation and flowering time as a means of predicting the growth periods of various crop varieties (Guo et al., 2020; Qiu et al., 2021). With global warming, the growing season length of summer crops is increasing, and planting strategies are changing in some regions (Supplemental Figure 7). In the future, improvement in rapid prediction of growth periods may empower the selection of latitude adaptation for superior varieties quickly and efficiently through cropping mode optimization.

MATERIALS AND METHODS

Plant materials and growth conditions

The $\text{NIL}^{Hd1\ DTH8\ Ghd7}$, $\text{NIL}^{hd1\ DTH8\ Ghd7}$, $\text{NIL}^{Hd1\ dth8\ Ghd7}$, and $\text{NIL}^{hd1\ dth8\ Ghd7}$ genotypes correspond to the previously reported lines *DDHH*, *DDhh*, *ddHH*, and *ddhh*, respectively (Du et al., 2017). *HGD* plants (with *Hd1*, *Ghd7*, and *DTH8*) were selected from an F5 family from a cross between an *indica* landrace (accession no. I7) and the *indica* cultivar Qinghuazhan (Zong et al., 2020). $\text{NIL}^{Hd1\ DTH8\ Ghd7}$, $\text{NIL}^{hd1\ DTH8\ Ghd7}$, $\text{NIL}^{Hd1\ dth8\ Ghd7}$, and $\text{NIL}^{hd1\ dth8\ Ghd7}$ were grown in Chengdu, China (May to September) and Xiamen, China (May to August). Heading dates were measured on 16 plants per line, and the growth period was calculated as the heading date plus 30 days. For days to flowering under different latitudes, seedlings for 23 rice cultivars were grown in a growth chamber with 70% relative humidity under 14 h/10 h light/dark and 30°C/25°C day/night conditions for 30 days and then transplanted to fields in Xiamen (26.28°N, May 1, 2021), Anqing (30.52°N, April 7, 2021), and Shenyang, China (41.80°N, April 20, 2021). Similarly, seeds from 29 maize cultivars were planted in Xiamen (26.28°N, April 21, 2021), Zhengzhou (34.75°N, June 20, 2021), and Beijing (39.54°N, May 10, 2021). To determine the flowering time of Zhonghuang13, seeds were planted in Xiamen (April 7, 2022), and the days from sowing to flowering were counted.

Daylength-sensing assay

Daylength-sensing processes were characterized using a daylength-sensing-based environment adaptation simulator (Qiu et al., 2021). In brief, seedlings were grown in different growth chambers at 28°C for different periods (32 days for rice, 7–8 leaves for maize, 14 days for soybean), and the growth chambers provided a gradient of daylengths (15, 14.5, 14, 13.5, 13, 12, and 10 h). On the next day, the leaves of all seedlings were harvested at different times after dawn (3 h after dawn for rice, 1 h after dawn for maize, 4 h after dawn for soybean). Transcriptional data for florigen genes were then collected by quantitative real-time PCR. When florigen gene expression changed gradually with the change in daylength and the expression difference between adjacent daylengths was less than 10-fold, we categorized this expression pattern as gradual daylength sensing. When the expression of florigen genes differed more than 10-fold between adjacent daylengths, we defined this expression pattern as critical daylength sensing. When the expression of florigen genes was almost constant between adjacent daylengths, we defined this expression pattern as daylength insensitivity.

Analysis of gene expression

Total RNA was extracted from seedlings using the Eastep Super Total RNA Extraction Kit (Promega) following the manufacturer's instructions. Complementary DNA was synthesized from 1 μg total RNA using GoScript Reverse Transcription Mix using oligo(dT) (Promega). Quantitative real-time PCR was performed by the SYBR Green PCR method on a CFX384 Real-Time PCR System (Bio-Rad) according to the manufacturer's instructions. The primers used for PCR are listed in Supplemental Table 1.

Florigen gene-expression heatmap

First, we divided the expression of florigen genes into three levels in the inferred *Hd3a*, *RFT1*, and *ZCN8* expression profiles. When *Hd3a* or *RFT1* expression was <10 or *ZCN8* expression was <100, we defined the genes as being inactivated. When 10 < *Hd3a* or *RFT1* expression < 100 or 100 < *ZCN8* expression < 1000, we defined them as being weakly activated. When *Hd3a* or *RFT1* expression was >100 or *ZCN8* expression was >1000, we defined them as being highly activated. Second, we divided the daylength data within the cropping season at a specific latitude into six intervals of increasing daylength (10–12, 12–13, 13–13.5, 13.5–14, 14–15, >15 h) and six intervals of decreasing daylength (15–14, 14–13.5, 13.5–13, 13–12, 12–10, <10 h). Third, we determined the expression levels of *Hd3a*, *RFT1*, and *ZCN8* at each daylength interval; the level at each interval was determined based on the expression level of *Hd3a*, *RFT1*, or *ZCN8* corresponding to the daylength at the end of the interval. By following these steps, all the intervals were filled in sequence, and the florigen gene expression heatmap for the cropping season at a specific latitude was obtained.

Data sources

Temperature data were collected from the China Meteorological Data Service Centre (http://data.cma.cn/). Data on rice, maize, and soybean varieties were obtained from the China Rice Data Center (https://www.ricedata.cn/) and from http://www.a-seed.cn/. The yield data were collected from the National Bureau of Statistics (https://data.stats.gov.cn/). The cropping area data were collected from http://202.127.42.47:6006/Home/BigDataIndex. Data cleaning, analysis, and visualization were performed using Python and R software. The maps were drawn in R.

Temperature data analysis

For temperature data, the year was divided into 73 intervals based on 5 days, and the average temperature for each interval was calculated. The temperature of each interval in the year range was the average temperature in the corresponding interval for all years, with a 95% confidence interval.

Analysis of rice planting types in different regions

Rice varieties were classified based on their planting types: one-round rice and two-round rice. The numbers of one-round rice and two-round rice varieties in 31 regions of China from 2011 to 2020 were counted. To determine whether two-round rice was enriched in low latitudes, a hypergeometric distribution was used to calculate the enrichment of double-season rice in the varieties, with a threshold p value of <0.05. The map distribution was drawn in R.

To explore the relationship between the planting type and latitude distribution of varieties, *indica* rice was divided into seven planting types: early-season rice; middle-season rice; late-season rice; early- and late-season rice; early- and middle-season rice; middle- and late-season rice; and early-, middle-, and late-season rice. We counted the numbers and planting types of varieties in each region. For each province, $n_{province\_all}$ represents the total number of varieties in the province, and $n_{province\_i}$ represents the number of varieties with different planting types in the region. For the country, $n_{country\_all}$ represents the total number of varieties, and $n_{country\_i}$ represents the number of varieties of different planting types. Then, the percentages $m_{\mathrm{province}} = \frac{n_{\mathrm{province\_i}}}{n_{\mathrm{province\_all}}}\%$ and $m_{\mathrm{country}} = \frac{n_{\mathrm{country\_i}}}{n_{\mathrm{country\_all}}}\%$ were calculated. Fisher's exact test was used to calculate the distribution of *indica* rice varieties of seven planting types in various regions, and p values were used to indicate the degree of enrichment. Fisher's exact test was used to calculate the distribution of planting mode in each province under the null hypothesis that the cropping type was not enriched in the province, i.e., $m_{province}$ and $m_{country}$ were the same. If the p value was <0.05, the null hypothesis was rejected, indicating a significant difference in the province. The p value was calculated using the Fisher's test function in R. To calculate the proportion of the cropping area dedicated to one-round and two-round rice in the provinces, cropping area data were obtained for each province from 1984 to 2016 and divided into six five-year intervals. The number of varieties and the cropping areas of one- and two-round rice were counted in each interval, and the proportions of the variety numbers and cropping areas of one- and two-round rice in each interval were calculated :

$$Area\_proportion_{\mathrm{one-round}} = \frac{\mathrm{Area}_{\mathrm{one-round}}}{\mathrm{Area}_{\mathrm{one-roun}} + \mathrm{Area}_{\mathrm{two-round}}}$$

$$Area\_proportion_{\mathrm{two-round}} = \frac{\mathrm{Area}_{\mathrm{two-round}}}{\mathrm{Area}_{\mathrm{one-roun}} + \mathrm{Area}_{\mathrm{two-round}}}$$

$$Variety\_proportion_{\mathrm{one-round}} = \frac{\mathrm{Number}_{\mathrm{one-round}}}{\mathrm{Number}_{\mathrm{one-roun}} + \mathrm{Number}_{\mathrm{two-round}}}$$

$$Variety\_proportion_{\mathrm{two-round}} = \frac{\mathrm{Number}_{\mathrm{two-round}}}{\mathrm{Number}_{\mathrm{one-roun}} + \mathrm{Number}_{\mathrm{two-round}}}.$$

Screening for rice varieties with multi-latitude adaptation

First, we selected hybrid *indica* rice varieties that can be used as early-season, middle-season, and late-season rice. We counted the provinces and the cumulative planted area of these varieties. The varieties planted in at least three provinces and with cumulative planting areas of more than 30 million hectares were selected as multi-latitude-adapted varieties. A timeline was drawn in R software according to the first approval time of these varieties and the cumulative planting area. The parental information for the varieties was obtained from the China Rice Data Center (https://www.ricedata.cn/variety/).

Correlation analysis between planting area and yield per unit area

The varieties with the largest planting areas and the widest distribution areas were selected as multi-latitude-adapted varieties. Using the planting period of multi-latitude-adapted varieties as a screening window, rice varieties in four ecological classes, maize varieties in five different growing regions, and soybean varieties in four different latitudes were screened. Crop varieties with a larger cropping area and a smaller cropping range were selected for subsequent analysis. Then, the annual cropping area ($Area_{\mathrm{i}}$) of the selected variety was calculated, as well as the annual cropping area ($Total\ area_{\mathrm{i}}$) of all varieties. The ratio of the variety cropping area was defined as $Area\ ratio = \frac{Area_{\mathrm{i}}}{Total\ area_{\mathrm{i}}}$. The yield per unit area of the selected varieties in the province ($Yield_{province\_i}$) was approximated as the yield per unit area of the province. The $\Sigma \mathrm{Yield}_{\mathrm{province\_i}}$ was expressed as the sum of the yield per unit of the province in which the variety was planted, and the total yield per unit area of the country per year ($Total\ yield_{\mathrm{i}}$) was expressed as the sum of the yield per unit of the 31 provinces. The yield contribution of the variety was defined as $Yield\ ratio = \frac{\sum Yield_{\mathrm{province\_i}}}{Total\ yield_{\mathrm{i}}}$. The area ratios and yield ratios were used for correlation analysis. The R^2 values and regression equations were calculated in R.

SUPPLEMENTAL INFORMATION

Supplemental information is available at *Plant Communications Online*.

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AUTHOR CONTRIBUTIONS

X.O. designed the research; X.W., J.H., R.L., L.Q., C.Z., M.L., R.H., X.W., J.Z., H.X., S.L., X.H., and X.O. performed the research; X.W. and X.O. analyzed the data; X.W. and X.O. wrote the paper.

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