

Evolution of flowering time genes in rice: From the paleolithic to the anthropocene

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Abstract

The evolutionary paths of humans and plants have crossed more than once throughout millennia. While agriculture contributed to the evolution of societies in prehistory, human selection of desirable traits contributed to the evolution of crops during centuries of cultivation. Among cereal crops, rice is currently grown around the globe and represents staple food for almost half of the world population. Over time, rice cultivation has expanded from subtropical to temperate regions thanks to artificial selection of mutants with impaired response to photoperiod. Additional regulatory mechanisms control flowering in response to diverse environmental cues, anticipating or delaying the floral transition to produce seeds in more favourable conditions. Nevertheless, the changing climate is threatening grain production because modern cultivars are sensitive to external fluctuations that go beyond their physiological range. One possibility to guarantee food production could be the exploitation of novel varieties obtained by crossing highly productive Asian rice with stress tolerant African rice. This review explores the genetic basis of the key traits that marked the long journey of rice cultivation from the end of the paleolithic to the anthropocene, with a focus on heading date. By 2050, will rice plants of the future flower in the outer space?

KEYWORDS

African rice, Asian rice, crop evolution, flowering time control, rice genetic improvement

1 | BACKGROUND

The complex relationship between human beings and plants started in prehistoric times when hominids explored their environment to procure food from wild species growing spontaneously. At the end of the old stone age, men and women transitioned from hunting to animal husbandry and from gathering wild grass seeds to plant cultivation. The birth of agriculture represented a turning point for human civilization that shifted from a nomadic to a sedentary

lifestyle. In particular, the cultivation of cereals is considered a landmark of the transition from the paleolithic to the neolithic era as food surplus sustained a remarkable growth of the human population and promoted the development of new organizational models for human societies (Schaal, 2019).

Almost 10 000 years ago, humans started to produce their own food by sowing seeds they had previously harvested from the best plants. Over time and over generations, primitive farmers had consciously and unconsciously selected variants of cereal species

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with novel morphological characteristics that facilitated their cultivation and improved grain production at harvesting (Harlan et al., 1973). Among favourable traits, ancient farmers first singled out modifications of plant architecture (e.g., compact growth habit, fewer but larger inflorescences) and seed characteristics (e.g., seed retention, grain size and weight, reduced seed dormancy), and then prioritized synchronized maturity for simultaneous harvesting and adaptation to new environments (Meyer & Purugganan, 2013). In this way, primitive cultivars gave rise to several landraces that better adjusted their growth to agricultural ecosystems different from the geographic region of their origin.

In the anthropocene epoch, the cultivation of cereal crops is facing multiple challenges, mostly related to increasing human population and decreasing natural resources to be exploited, and threads related to climate change, from global warming to reduced availability of fresh water.

While agriculture of the 20th century yearned for varieties with higher yield potential, agriculture of the 21st century yearns for varieties with greater yield stability over time. This means that novel cultivars should be able to maintain similar performance (with regard to grain production) from 1 year to another in each geographic location even in fluctuating environmental conditions.

In the last two decades, molecular genetic studies and improvements in OMICS technologies deciphered the origin and evolution of major cereal crops (Meyer & Purugganan, 2013). Recent advances in the analysis of plant genes and genomes have greatly increased our understanding of the regulatory mechanisms underlying the transformation of wild species into crops (i.e., domestication) and adaptation of cultivated species to different environments worldwide (i.e., diversification). In addition to the identification of genomic regions underpinning important agronomic traits, the use of biotechnological techniques also allowed to functionally characterize key plant growth regulators involved in crop evolution and to study genetic variation that led to important modifications of morphological, developmental and physiological characteristics of cultivated cereals.

This review examines the genetic basis of domestication and diversification of selected species belonging to the *Oryza* genus, with a particular focus on gene regulatory networks underlying the vegetative to reproductive phase change. In rice, the regulation of the floral transition [also known as *heading date* (*Hd*)] is a critical agronomic trait that determines the reproductive success and ultimately seed production. In addition, the modulation of days to heading in response to variation in daylength contributed to plant adaptation to different latitudes, thus allowing rice cultivation in a wider geographic range.

Regulatory genes involved in the control of flowering time are emerging as interesting candidates for genetic improvement of crop species as they fine-tune plant production by integrating internal developmental strategies and variations in external conditions. In a climate change scenario, farmers will be needing new genetic material able to perform well even in response to fluctuating environments.

2 | COMMON FEATURES OF CEREAL CROP EVOLUTION: A BRIEF INTRODUCTION

Over millennia of plant cultivation, similar evolutionary pathways guided the long journey from the original wild grasses to modern cereal crops cultivated worldwide [nicely reviewed by (Doebley et al., 2006); (Meyer & Purugganan, 2013)].

The initial domestication of feral plants represents the first step of crop evolution and involves complex processes that transformed a wild species into a cultivated species. The domestication syndrome encompasses a dozen traits underpinning changes in plant architecture that characterized the onset of evolutionary divergence from wild ancestors towards crop species.

Ancestral farmers selected seeds of wild grasses showing favourable traits—such as compact shoot and inflorescence architecture—and cultivated their progenies. This selection was based on phenotypic alterations associated with ease of harvesting and increased grain production, but also resulted in the selection of genotypic modifications since valuable alleles were fixed in the genome of cultivated plants. Altogether, these evolutionary changes associated with a reduction in phenotypic and genetic diversity but a boost in plant productivity under human exploitation. Nevertheless, domesticated species became completely dependent on humans for their growth in cultivated field and unfitted for survival in wild habitat (Harlan et al., 1973).

The subsequent diversification of landraces represents the second step of crop evolution and relies on the selection of novel variants in domesticated populations. Ancient farmers exploited natural allelic variation to select new varieties with improved yield or seed quality as well as to obtain new ecotypes with increased adaptability to different environments. These structural and functional changes increased the survival and fitness of landraces to local environments and correlated with a spread of phenotypic and genetic diversity (Meyer & Purugganan, 2013)

In the recent past, deliberate breeding represents the third step of crop evolution and includes genetic improvement programmes aimed at maximizing crop yield, optimizing seed quality and promoting ease of farming. A clear example is the green revolution that transformed cereal cultivation in the 1960s by employing semidwarf high-yield varieties of wheat and rice [(Hedden, 2003); (Sakamoto & Matsuoka, 2004)]. Furthermore, pyramiding QTLs controlling plant height and grain yield can greatly enhance yield potential of rice cultivars (Ashikari et al., 2005).

Currently, abiotic stresses caused by climate change are seriously threatening grain production as fluctuations in external conditions result in yield instability of cereal crops. This is particularly relevant for rice, which developmental stages are sensitive to environmental limitations and which cultivation requires abundant inputs (e.g., water) to achieve high grain yield. To fight against food insecurity, crop improvement should be aimed at developing novel varieties able to withstand those abiotic stresses that affect productivity of conventional varieties (Wing et al., 2018).

3 | HD: DOMESTICATION OR DIVERSIFICATION TRAIT?

Asian rice (*Oryza sativa*) was domesticated from the wild relative *Oryza rufipogon* 8000–9000 years ago in China. Although the precise geographic origin has long been discussed [Yangtze River valley as suggested by (Doebley et al., 2006) and (Molina et al., 2011); Pearl River basin as suggested by (Huang et al., 2012) and (Wei et al., 2012)], archaeobotanical evidence strongly supported the region watered by the Yangtze River as the centre of rice domestication [(Fuller et al., 2009); (Gross & Zhao, 2014)].

Surprisingly, the tremendous phenotypic differences between the cultivated species and their wild ancestors can be explained by small genetic changes in key plant growth regulators that produced alterations of morphological characteristics that facilitated farming and increased grain production, such as a more compact structure of vegetative organs and improved seed retention (Doebley et al., 2006). Among almost 40 000 genes in the rice genome [(Kawahara et al., 2013); (Z. Li et al., 2014)], it was estimated that the causal variants of the domestication traits are rare alleles associated with only 76 QTL (Thomson et al., 2003).

At the phenotypic level, wild rice plants have a prostrate growth habit during the vegetative phase and a shattering phenotype during the reproductive phase. By contrast, cultivated rice plants have an erect growth habit and have lost their capacity of seed dispersal at maturity (Meyer & Purugganan, 2013). These key alterations in shoot and inflorescence architecture (Figure 1a) are associated with spontaneous mutations in few developmental genes.

The modification of plant architecture was produced by a point mutation in the coding sequence of *PROSTRATE GROWTH (PROG1)*, a gene expressed at the base of the stem that encodes a C2H2-type transcription factor involved in the control of the angle of tiller formation [(Tan et al., 2008); (Jin et al., 2008)]. This loss of function mutation also associated with higher grain yield (Tan et al., 2008), likely due to increased photosynthetic efficiency in domesticated species.

The loss of seed dispersal capacity is caused by a point mutation in the regulatory sequence of *OsSHATTERING1 (OsSh1)*, a gene expressed at the base of the flower that encodes a homeo-domain transcription factor involved in the formation of the abscission layer (Konishi et al., 2006). This mutation reduced *OsSh1* gene expression, leading to lower detachment of the grain from the mother plant. Other loci controlling seed shattering have been identified, being *shattering4 (sh4)* a major QTL associated with increased seed retention (C. Li et al., 2006).

Beside plant architecture, additional mutations related to the domestication syndrome affected important characteristics of the grain including its size/weight, pericarp colour and seed dormancy (Meyer & Purugganan, 2013).

Natural genetic variation in plant response to photoperiod (i.e., period of daily illumination) contributed to the expansion of domesticated rice cultivation to a wider geographical range.

In rice varieties belonging to the *tropical japonica subspecies* cultivated at low latitudes (30°N), flowering is promoted under short

days (SD, when the length of the day is approximately 12–13 h) but inhibited under long days (LD, when the length of the day is higher than 13 h). Thought, mutations in genes involved in photoperiodic response have shaped the adaptability of rice species and subspecies to regions characterized by different daylengths. Indeed, rice varieties belonging to the *temperate japonica subspecies* cultivated at higher latitudes (45°N) flower under LD (Figure 1b).

Intriguingly, flowering time variation is considered as a domestication trait by some authors [Lee et al., 2022; (Paterson et al., 1995); (Thomson et al., 2003)] but as diversification trait by others (Meyer & Purugganan, 2013). Supporting the latter hypothesis, several studies reported that humans have selected plant varieties with altered photoperiodic sensitivity at the flowering stage to adapt domesticated crops to new agroecosystems [reviewed by (Doebley et al., 2006)].

In recent times, key mutations that have revolutionized rice cultivation affected the function of genes involved in the metabolism of the phytohormone Gibberellins that control cell/tissue elongation (Sasaki et al., 2002); (K. Zhao et al., 2011). Precisely, *semidwarf 1(sd1)* loss of function mutants have shortened internodes that confer increased lodging resistance (Figure 1c). In addition to reduced plant height, *sd1* mutants are more efficient in the use of nutrients and energies allocated to the growth of reproductive rather than vegetative organs. Intriguingly, stem elongation takes place at the vegetative to reproductive phase change but the connection between this process and the floral transition is still unresolved, despite the wealth of information on hormonal pathway controlling overall plant growth (Ferrero-Serrano et al., 2019).

4 | GENETIC BASIS OF HD IN O. SATIVA

In flowering plants, the onset of the reproductive phase is determined by the integration of critical environmental signals, such as photoperiod and ambient temperature, and developmental programmes. In particular, the accurate detection of changes in daylength provides information about the favourable conditions that maximize the production of seeds. Although some plants flower independently of daylength (day neutral plants), many others promote the floral transition when days are longer—as in the case of LD plants growing in temperate regions—or when nights are longer—as in the case of SD plants growing in tropical or subtropical regions.

Physiological analyses of different plant species clarified that daylength (relative duration of day and night in a 24 h cycle) is measured in the leaf during the vegetative phase. It was originally hypothesized that a 'mysterious' molecule, called the florigen, accumulates in the leaf vasculature in response to inductive photoperiods and then moves to the shoot apex to promote the development of reproductive structures (Chailakhyan, 1936). This hypothesis was later confirmed by two groups that independently discovered that the long-distance signalling molecule was a small protein belonging to the phosphatidylethanolamine binding protein (PEBP) family that is conserved in *Arabidopsis thaliana* (the model

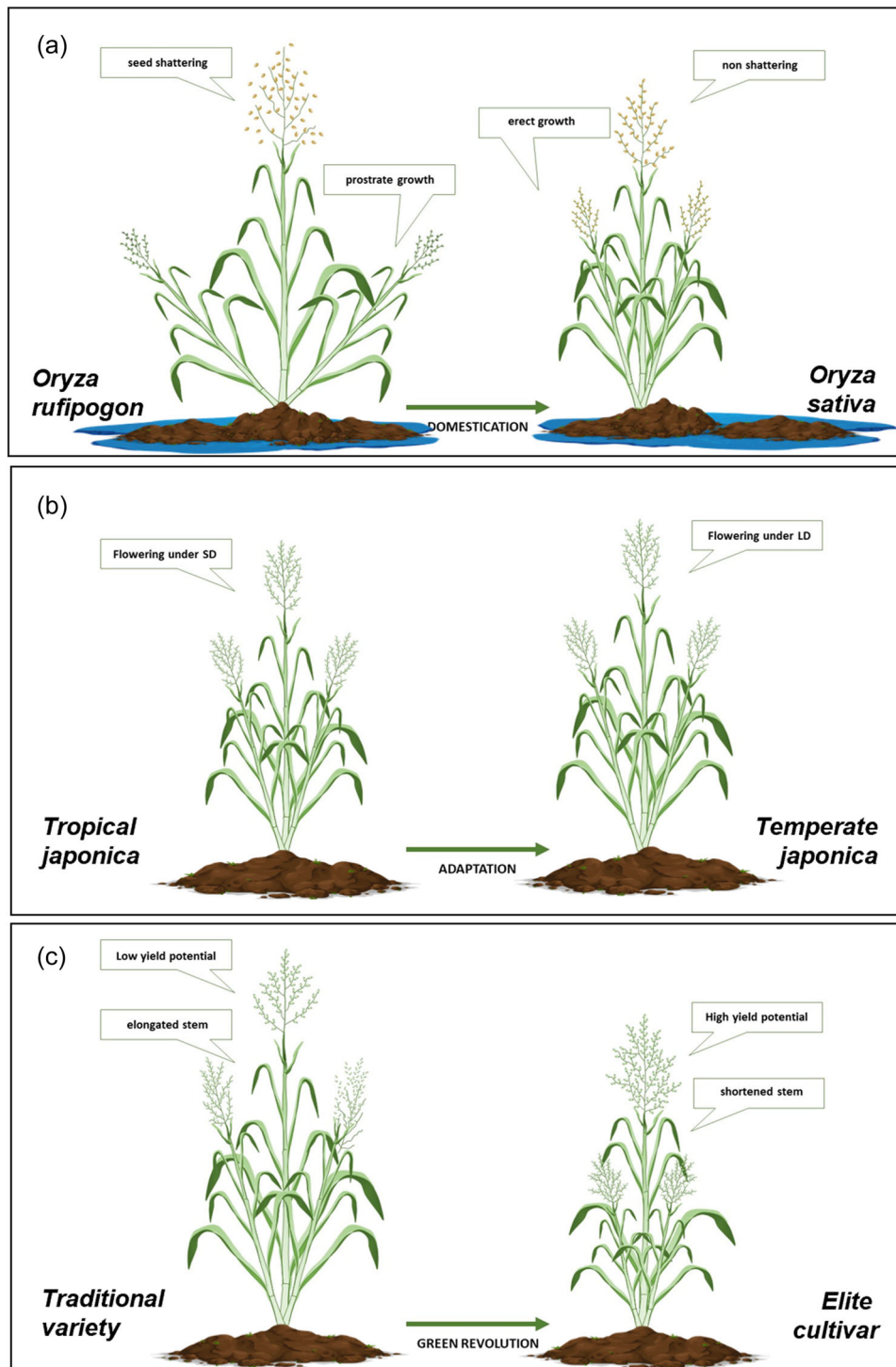


FIGURE 1 Rice evolution: from grain to green revolution. Example of domestication traits in rice (a), from prostrate and shattering phenotype of wild *Oryza rufipogon* to erect and non-shattering phenotype of cultivated *Oryza sativa*. Example of adaptive trait in rice (b), from SD flowering tropical japonica to LD flowering temperate japonica. Green revolution in rice (c), from tall traditional varieties to semidwarf high-yield elite varieties. LD, long days; SD, short days

species for dicot plants) and *O. sativa* (the model species for monocot plants). The *Arabidopsis* florigen is encoded by the *FLOWERING LOCUS T (FT)* gene and accumulates under LD (Corbesier et al., 2007), whereas the rice florigen is encoded by the *Heading date 3a (Hd3a)* gene and accumulates under SD (Tamaki et al., 2007). In the last 15

years, FT-like proteins with conserved function have been identified in several plant species and crops, supporting the existence of a universal florigen that triggers the transition from vegetative to reproductive growth in angiosperms [reviewed in (Wickland & Hanzawa, 2015)].

The *PEBP* family is composed of 6 genes in *Arabidopsis* and 20 genes in rice, including pairs of paralogs on duplicated segments of the genome [(Chardon & Damerval, 2005); (Danilevskaya et al., 2008); C. Zhao et al., 2022]. The encoded PEBP proteins are very similar in sequence but some of them have acquired a novel function as floral repressors during evolution of flowering plants, while some others have retained the florigenic activity.

In *Arabidopsis*, FT and its homolog TWIN SISTER OF FT (TSF) promote the floral transition in LD, whereas TERMINAL FLOWER1 (TFL1) and BROTHER OF FT (BFT) delays flowering in controlled and stress conditions; strikingly, the protein sequences of the florigen FT and the antiflorigen TFL1 show only small differences in few amino acids (Wickland & Hanzawa, 2015).

Rice contains 4 *TFL1*-like genes named *RICE CENTRORADIALIS* (*RCN1* to 4), and 14 *FT*-like genes (*OsFT-like1* to 14). Among the latter group, only *OsFTL2* (corresponding to *Hd3a*) and *OsFTL3* (also known as *RICE FT1*, *RFT1*) have been extensively characterized: *Hd3a* promotes heading under inductive SD (Tamaki et al., 2007) while *RFT1* induces heading under non-inductive LD (Komiya et al., 2008, 2009). Although phylogenetic analysis indicated that a third gene (*OsFTL1*) clusters together with *Hd3a* and *RFT1* (C. Zhao et al., 2022), functional studies suggested that *OsFTL1* plays multiple roles in the regulation of plant height, leaf size and inflorescence architecture (F. Wang, Yano et al., 2020). Therefore, a two florigen system operates in rice: *Hd3a* and *RFT1* modulate the timing of the reproductive phase depending on daylength.

Upon induction of the florigen in the leaf and translocation in the shoot apical meristem, *Hd3a* interacts with *OsFD1* and 14-3-3 proteins to form the so-called florigen activation complex that switches on the expression of the inflorescence meristem identity genes *OsMASD14* and *OsMASD15* (Taoka et al., 2011). Similar mechanisms have been identified in *Arabidopsis*, leading to the activation of *APETALA1* (*AP1*) and *FRUITFULL* (*FUL*) *MADS-box* genes that promote flower development [reviewed by (Kinoshita et al., 2020)].

5 | DETERMINATION OF CRITICAL DAYLENGTH IN *O. SATIVA*

In rice, flowering time is a complex trait, regulated by several genetic determinants. QTL mapping of *Hd* loci was initially carried out in populations obtained by crossing Nipponbare (subsp. *japonica*) with Kasalath (subsp. *indica*), two varieties characterized by different photoperiod sensitivity (Yano et al., 2001). Among the identified loci acting upstream of the florigen, *Hd1* shows opposite activity depending on daylength: *Hd1* activates *Hd3a* under SD, thus promoting flowering; *Hd1* represses *Hd3a* under LD, thus delaying flowering (Nemoto et al., 2016; Yano et al., 2000). Interestingly, the analysis of a progeny generated by crossing two landraces of subsp. *indica* having very strong and very weak photoperiod sensitivity, respectively, led to the identification of the *Hd1-17* allele that confers non-heading phenotype when the length of the day is higher than 14 h (Zong et al., 2021). This functional allele from *indica* rice encodes

a strong LD-specific floral repressor, whereas the *Hd1* from *japonica* rice (the reference cv. Nipponbare) represent a weak allele (Zong et al., 2021). *Hd1* is the ortholog of the *Arabidopsis* *CONSTANS* (*CO*), a floral promoter that directly activates the florigen *FT* under inductive conditions. Strikingly, both *Hd1* and *CO* are positively regulated by similar circadian-clock proteins named *GIGANTEA* (*GI*) and *OsGI* (Hayama et al., 2003).

Despite the functional conservation of FT-like proteins and gene networks acting upstream and downstream, the floral transition in rice is also modulated by species-specific regulators. Precisely, *Early heading date* (*Ehd*) loci play crucial roles in the control of photoperiodic flowering (Doi et al., 2004; Matsubara et al., 2008). Map-based cloning revealed that *Ehd1* encodes a B-type response regulator with no obvious homologs in *Arabidopsis* (Doi et al., 2004), whereas *Ehd2* encodes a Zinc-Finger type transcription factor showing similarities to the maize floral activator *INDETERMINATE1* (Matsubara et al., 2008).

Genetic studies of the *Ehd1* gene in rice varieties of the subspecies *japonica* demonstrated that the cultivar Nipponbare carries a functional allele (*Ehd1-Nip*) that confers early flowering especially under SD, whereas the cultivar Taichung 65 (*T65*) harbours a loss-of-function allele (*ehd1-T65*) that reduces the photoperiodic response, thus conferring adaptation to a wider geographic area (Doi et al., 2004). The causal mutation of *ehd1-T65* is an amino acid change (Gly to Arg) in a conserved domain that affects the DNA binding activity of *Ehd1*, and consequently reduces the expression levels of the florigens *Hd3a* and *RFT1* (Doi et al., 2004).

A 4 bp deletion in the coding region of *Ehd2* (resulting in a premature stop codon) underlies the late heading phenotype of a variant identified in a population obtained by γ -ray mutagenesis of the cultivar Tohoku IL9 (subsp. *japonica*). Strikingly, the *ehd2* mutant flowers later than the wild type under SD but never flowers (in 1 year) under LD (Matsubara et al., 2008). At the molecular level, high expression of *Ehd2* in developing leaves (that later decreases as plants age) is followed by transcriptional activation of *Ehd1*, *Hd3a* and *RFT1* in wild-type plants. By contrast, the mRNA levels of the floral promoters are almost undetectable in the *ehd2* knock-out mutant, suggesting that *Ehd2* promotes flowering by acting upstream of *Ehd1*, *Hd3a* and *RFT1* (Matsubara et al., 2008).

The floral promoters *Ehd1* and *Hd3a* are induced when plants grow under SD but suppressed under LD by a regulatory protein containing a CCT (*CO*, *CO-LIKE* and *TIMING OF CAB1*)-type domain encoded by *Grain number, plant height and heading date 7* [*Ghd7*, (Xue et al., 2008)]. The *Ghd7* QTL was originally identified in an elite variety that shows not only late flowering but also increased plant height and inflorescence size (Xue et al., 2008).

The rice-specific regulators *Ehd1* and *Ghd7* are essential components of the molecular mechanism that sets the critical daylength for photoperiodic flowering (Itoh et al., 2010). Expression analysis of flowering time genes in rice plants grown in different photoperiods indicated that floral promoters *Ehd1* and *Hd3a* are transcriptionally activated at daylight <13.5 h whilst the floral repressor *Ghd7* at daylight >13.5 h (Itoh et al., 2010). Under SD,

the circadian-clock protein *OsGI* mediates *Ehd1* induction in response to blue light by establishing a sensitive phase in the morning, thus activating *Hd3a* in inductive conditions. On the other hand, phytochrome signalling modulates *Ghd7* induction in response to red light; though, the accumulation of *Ghd7* mRNA also relies on the length of the day, with a peak of expression at night under SD but at dawn under LD. Upon transcriptional activation, *Ghd7* requires a time interval to perform its repressive function: induction of *Ghd7* in LD morning suppresses *Ehd1* expression the next morning, thus repressing *Hd3a* under non inductive conditions (Itoh et al., 2010).

Similar to *Ghd7*, *Days to Heading 8 (DTH8)* also has pleiotropic effects on rice development as this locus controls important traits such as plant height, Hd and yield potential (Wei et al., 2010). *DTH8* encodes a putative HAP3 subunit (NF-YB/CBF-A) of the CCAAT-box-binding transcription factor and negatively regulates the floral transition by repressing *Ehd1* and *Hd3a* specifically under LD. *DTH8* plays pivotal role in plant response to photoperiod: cultivars harbouring nonfunctional *dth8* alleles are less sensitive to changes in daylength (Wei et al., 2010).

Although expression analyses indicated that the transcription of the *Hd1/Ghd7/DTH8* genes encoding LD floral repressors does not depend on each other (Wei et al., 2010), the three proteins are able to interact pairwise and to form a regulatory complex (Zong et al., 2021). Molecular genetics studies revealed a complex interaction among these floral regulators in LD: the activity of *Hd1* requires *Ghd7* in functional *DTH8* background (Nemoto et al., 2016) and *DTH8* in functional *Ghd7* background (Du et al., 2017). Moreover, the repressive activity of *DTH8* relies on *Ghd7* in functional *Hd1* background. The analysis of higher order mutants under different daylengths further corroborated the function of *Ghd7* as the major floral repressor in LD and of *Hd1* as floral promoter under SD (Zong et al., 2021). Nevertheless, functional *Hd1/Ghd7/DTH8* alleles confer strong photoperiod sensitivity by completely suppressing the floral inducers (*Ehd1-Hd3a/RFT1*) under LD but only moderately repressing them under SD (Zong et al., 2021).

Another important floral repressor is Pseudo Response Regulator 37 (*PRR37*), a protein characterized by a pseudo receiver domain at the N-terminal and a CCT domain at the C-terminal showing similarities to Arabidopsis *PRR* proteins involved in the regulation of circadian rhythms (Koo et al., 2013). *OsPRR37* has been identified as the gene responsible for *Heading date 2 (Hd2)*, a major QTL that controls photoperiod sensitivity. A missense mutation (Leu to Pro) in the conserved CCT domain of *OsPRR37* causes extreme early heading in the accession H143 (subsp. *japonica*) under different daylengths. Similarly, a T-DNA insertion in *OsPRR37* causes early flowering under LD in the loss of function mutant, likely because of *Hd3a* up-regulation (Koo et al., 2013).

A recent report demonstrated that the alterations in the expression levels of *OsPRR37* correlate with variation in flowering time (Liu et al., 2018). For example, plants overexpressing *OsPRR37* show late heading and mis-regulation of several genes related to circadian rhythms and flowering (Liu et al., 2018). Specifically, *OsPRR37* negatively regulates *Ehd1* and *RFT1* as well as *MADS-box*

genes acting downstream of the florigens (*OsMADS14*, *OsMADS15* and *OsMADS18*).

Although several studies demonstrated that *OsMADS14/15/18* act as inflorescence meristem identity factors during the reproductive phase, these *MADS-box* genes are also expressed in the leaf before the floral transition. Furthermore, simultaneous silencing of *OsMADS14/15/18* by RNA interference causes down-regulation of *Hd3a* and a modest delay in floral transition, suggesting that these *MADS-domain* regulators could also promote flowering upstream of the florigen, before they function in the specification of reproductive meristem (Kobayashi et al., 2012).

Under SD, another *MADS-domain* factor (*OsMADS51*) promotes the floral transition by acting downstream of *OsGI* and upstream of floral inducers. As supporting evidence, *OsGI* antisense plants exhibited reduced transcript levels of *OsMADS51*, and late flowering *osmads51* mutants show down-regulation of *OsMADS14*, *Ehd1* and *Hd3a* (Kim et al., 2007).

Recent coexpression analyses based on published transcriptomics data uncovered a negative correlation between *OsMADS14/15/18* and two *OsRAV* genes (Osnato et al., 2020), which encode putative orthologs of the floral repressors *TEMPRANILLO (TEM)* in Arabidopsis (Osnato et al., 2012). Molecular and functional characterization of *OsRAV9* silencing lines suggested that this novel transcription factor could repress photoperiodic flowering by acting upstream of the floral activators *OsMADS14* and *Hd3a* under SD (Osnato et al., 2020).

Last, photoperiodic flowering in rice is also regulated by phytochromes, red/far red light photoreceptors encoded by three rice genes (*PHYA*, *PHYB*, *PHYC*), which individual contributions have been elucidated by studying single, double and triple mutants grown in different conditions (Takano et al., 2001, 2005, 2009). Under natural daylength (>13 h), *phyB* and *phyC* single mutants and *phyB phyC* double mutant show moderate early heading; in the same conditions, *phyA* single mutant flowers similarly to wild-type plants but *phyA phyB/phyA phyC* double mutants show severe early flowering (Takano et al., 2005) and *phyA phyB phyC* triple mutants flower even earlier than all double mutant combinations (Takano et al., 2009). Surprisingly, double and triple mutants flower later than wild type plants under SD (Takano et al., 2005, 2009), suggesting that functional phytochromes mediate light signals that induce flowering in inductive conditions but repress the floral transition in non-inductive conditions.

At the molecular level, phytochromes activate the transcription of *Ghd7* in LD, likely by forming dimers. Indeed, the expression of *Ghd7* is detected in *phyA* but abolished in *phyA phyB* and *phyA phyC* (Osugi et al., 2011). In double mutants, the loss of *Ghd7* activity correlates with derepression of the floral inducers (*Ehd1*, *Hd3a* and *RFT1*) that leads to early flowering under LD. Additional experiments suggested that *PHYA* and *PHYB* predominantly function in non-inductive daylength by inhibiting *Ehd1* activity and promoting *Ghd7* activity, respectively (Osugi et al., 2011). Phytochromes also regulate *Ghd7* at the posttranscriptional level. Indeed, *PHYA* and *PHYB* physically associate with *Ghd7* and act antagonistically with *OsGI*,

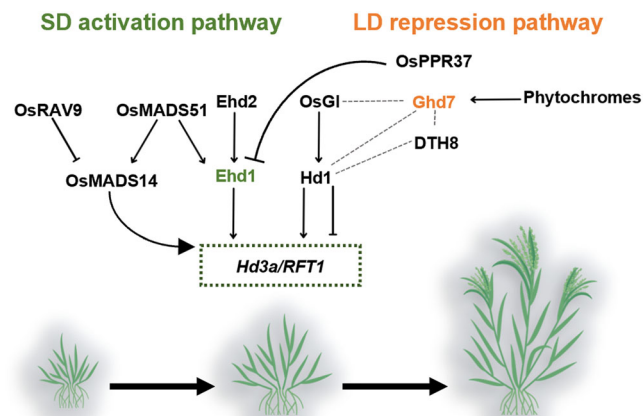


FIGURE 2 Regulatory mechanisms controlling photoperiodic flowering in rice. In rice, the florigens Hd3a and RFT1 trigger the floral transition under SD and LD, respectively. Ehd1/2, OsMADS51 and OsMADS14 positively regulate flowering while OsRAV9 negatively regulate flowering under SD. Ghd7, DTH8 and OsPRR37 suppress heading specifically under LD by repressing floral inducers. Hd1 acts downstream of OsGI and promotes flowering under SD but delays it under LD. Plain lines indicate transcriptional regulation, dashed lines indicate protein–protein interaction. LD, long days; SD, short days. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pce.14495)]

which promotes Ghd7 degradation through the 26S proteasome, to control Ghd7 protein stability by competing for interaction (Zheng et al., 2019).

To recap, Hd is controlled by at least three pathways: SD activation mediated by Hd3a, LD activation mediated by RFT1 and LD suppression mediated by major floral repressors (Figure 2). The complex interplay between floral regulators ultimately determines the activation of the florigen that triggers the formation of reproductive structure.

In the model species *Arabidopsis*, floral induction can be explained by the so-called external coincidence model: the coincidence between an external factor (light) and an internal factor (the circadian clock) induces plant response to photoperiod. In this LD plant, daylength measurement relies on transcriptional and posttranslational control of CO, a positive regulator of the florigen *FT*. The transcription of the florigen is not activated at a critical daylength but rather increases gradually in response to longer days. However, this model does not apply to all flowering plants: rice and some varieties of maize and soybean recognize critical daylength threshold to induce the reproductive phase (Itoh et al., 2010; Qiu et al., 2021).

Despite the substantial conservation of the molecular mechanisms underlying flowering in angiosperms, several factors involved in the perception and transduction of the signal (daylength) are species-specific and only the florigen is thought to be universal. Therefore, a new model was proposed to explain the mechanism that senses critical daylength based on the transcript levels of the florigen, the final output of the floral signalling network (X. Wang, He et al., 2021).

6 | REGULATION OF HEADING IN RESPONSE TO ENVIRONMENTAL FLUCTUATIONS

The molecular control of Hd in rice has been mainly deciphered by investigating natural variation in accessions showing different response to photoperiod (as discussed in the previous section). Interestingly, the selection of early flowering mutants defective in the LD suppression pathway underlies the expansion of rice cultivation outside the centre of domestication. Indeed, rice varieties cultivated in tropical and subtropical regions carry functional *Ghd7* and *OsPRR37* alleles that confer late heading under LD, whereas rice varieties cultivated at higher latitudes (north-eastern China, northernmost region of Japan) carry nonfunctional alleles of LD-floral repressors that reduce photoperiodic sensitivity at flowering (Koo et al., 2013; Xue et al., 2008). Likewise, loss of function mutations in these floral repressors have also been detected in LD-adapted varieties cultivated in Europe (Gómez-Ariza et al., 2015). Thus, genetic variation at loci encoding floral repressors has shaped adaptability of rice plants to geographic regions characterized by different latitude-dependent daylength: the adoption of varieties with reduced photoperiod sensitivity allowed the cultivation of rice in temperate regions and secured grain production even in a short growing season under natural LD.

Flowering time mutants in rice are valuable genetic resources not only for agriculture but also for basic research. Among the photoperiod insensitive varieties cultivated in Hokkaido (Japan, 42–45°N), the cultivar Kitaake (harbouring defective *Ghd7* and *OsPRR37* alleles) stands out for its extreme early flowering (Kim et al., 2013). In recent years, Kitaake has become a model cultivar for the model species rice thanks to its fast life cycle and short stature, and it is particularly suitable for functional genomics studies due to ease of transformation and propagation as well as the availability of the genome sequence (Jain et al., 2019).

Genetic variation at loci encoding floral activators also contributes to alterations in photoperiodic response. An emerging key player is *OsLHY/OsCCA1*, the only rice ortholog of the *Arabidopsis* MYB transcription factors LATE ELONGATED HYPOCOTYL (*LHY*) and CIRCADIAN CLOCK ASSOCIATED 1 (*CCA1*) that constitute the central oscillator of the circadian clock and negatively regulate flowering time by repressing *GI* [discussed in (Murakami et al., 2007)].

The first study (Sun et al., 2021) reported the functional characterization of loss of function mutant *oslhy*, that shows early flowering in 11 h light/13 h dark but late flowering in 12 h light/12 h dark. *OsLHY/CCA1* is proposed to act upstream of the *OsGI-Hd1* module by directly binding to the *OsGI* promoter and shifting its peak of expression. Downstream of *OsLHY*, Hd1 ultimately determines the critical day length to promote or suppress flowering (Sun et al., 2021).

Another study (Lee et al., 2022) demonstrated that *OsLHY/OsCCA1* positively regulate flowering by indirectly activating floral inducers. As supporting evidence, the *oscca1-1* knockout mutant (T-DNA insertion in the coding sequence) flowers later than the wild-type counterpart under natural LD in the field as well as under SD

and LD in controlled conditions. Delayed heading in the mutant correlates with down-regulation of crucial floral activators (*Ehd1*, *Hd3a* and *RFT1*) and up-regulation of few floral repressors including *OsPRR37*. Further experiments suggested that *OsCCA1* represses the transcription of *OsPRR37* by directly binding its promoter (Lee et al., 2022).

Moreover, the molecular and phenotypic analyses of more than 2000 *O. sativa* accessions grown under natural SD (in the Philippines) suggested that genetic variation at the *OsCCA1* locus also contributes to variation in Hd (Lee et al., 2022). Specifically, a polymorphism in the coding sequence (T418A) differentiates the functional allele of *japonica*-type accessions—that confers early flowering—from the defective allele of *indica*-type accessions—that confers late flowering. Considering the geographic distribution of the two alleles, the former is predominant at low latitudes whereas the latter at high latitudes (Lee et al., 2022).

Genes involved in plant response to photoperiod finely tune the floral transition depending on variation in daylength. However, Hd is also influenced by a large number of environmental cues, including ambient temperature and resource availability. While changes in photoperiod are predictable (depending on the geographic region and seasonal progressions), fluctuations in other external conditions (e.g., heat waves and pattern of precipitations) are hard to predict. Facing present and future climate change, research in the last few years has expanded our understanding of the function of floral regulators gained in controlled environments beyond optimal conditions.

Actually, heading in rice is accelerated under SD or at elevated ambient temperatures but delayed under LD or at low temperatures (Cho et al., 2017). Given that optimal temperature to grow rice is between 25°C and 35°C in the field and 27–28°C in controlled conditions, changes in ambient temperature (below or above the physiological range would affect the timing of flowering. Supporting this, rice plants growing at higher latitudes (characterized by longer days and cooler climates) often show delayed flowering (Song et al., 2012). Preliminary expression analysis of selected flowering time regulators in plants grown at low temperature (23°C) under different photoperiods suggested that the main floral activators (*Ehd1*, *Hd3a* and *RFT1*) are down-regulated at 23°C under both SD and LD, while the floral repressor *Ghd7* is up-regulated at 23°C compared to normal temperature (28°C) under LD (Song et al., 2012).

Recently, extended analyses of components of photoperiodic flowering in different conditions corroborated the relevance of *Ghd7* in the regulation of Hd in response to temperature changes (Nagalla et al., 2021). In cooler conditions, *Ghd7* mediates the inhibition of floral activators even under inductive daylength. In warmer conditions, down-regulation of *Ghd7* correlates with up-regulation of *RFT1*, suggesting that flowering of rice plants growing in temperate regions could be promoted by the lack of *Ghd7* repressive activity during the hot summer.

Flowering plants also modulates the floral transition in response to the changes in water availability, although adopting different strategies according to their habitat. Plants usually grown in dry environments use the so-called drought-escape response:

accelerated growth and shorter life cycle allow plants to reach maturity before the stress severely affects reproductive structures. As an example, *Arabidopsis* plants subjected to low watering anticipate flowering due to up-regulation of floral activators (*GI*, *CO*) and the florigen (*FT*), though only under LD (Riboni et al., 2013).

By contrast, plants typically grown in humid environments slow down their growth and delay flowering under water limitation. This is the case of rice, which cultivation often requires large volumes of fresh water (e.g., paddy fields). Rice plants are sensitive to water scarcity, and severe drought stress delays heading under both SD and LD through down-regulation of the major floral activators *Ehd1*, *Hd3a* and *RFT1* (Galbiati et al., 2016; Zhang et al., 2016).

Two functionally redundant basic leucine-zipper (bZIP) transcription factors, *O. sativa* ABA responsive element binding factor 1 (*OsABF1*) and *OsZIP40*, act upstream of *Ehd1* to negatively regulate flowering time in controlled and drought stress conditions (Zhang et al., 2016). At the molecular level, *OsABF1* and *Ehd1* show contrasting expression pattern in response to dehydration, being the former up-regulated and the latter down-regulated. At the physiological level, delayed heading induced by drought is more evident in wild type plants than in *RNAi* lines simultaneously silencing *OsABF1* and *OsZIP40*. Thus, these novel bZIP regulators might mediate the transcriptional repression of floral inducers (likely indirectly) in response to water scarcity independently of photoperiod (Zhang et al., 2016).

An additional mechanism controlling flowering time in response to water limitations involves *RCN1*, a member of the TFL1-subfamily of PEBP proteins with antiflorigenic activity (Kaneko-Suzuki et al., 2018). The negative effect of drought on heading is reduced in genome-edited plants carrying nonfunctional *rcn1* alleles as compared to wild-type (Y. Wang, Lu et al., 2020). *RCN1* is directly activated by two bZIP transcription factors, ABA-RESPONSIVE ELEMENT BINDING PROTEIN 1 (*OsAREB1*) and ABA RESPONSIVE ELEMENT (ABRE)-BINDING FACTOR (*OSBZ8*), upon accumulation of the stress hormone ABA. Increased *RCN1* activity can delay heading by out-competing *Hd3a* for binding with 14-3-3 proteins and *OsFD*, thus interfering with the formation of the FAC (Kaneko-Suzuki et al., 2018).

A third mechanism relies on the action of MADS-domain proteins belonging to the AP1-like subfamily, previously proposed to act in the leaf in a positive feedback regulatory loop with the florigen (Kobayashi et al., 2012). A large-scale molecular and phenotypic analyses of several rice accessions grown under wet and dry fields showed that higher expression of *OsMADS18* correlates with early flowering and higher fitness when water is scarce (Groen et al., 2020), although the precise mode of action remains to be clarified.

Elevated ambient temperatures and/or decreasing water availability often correlate with increasing soil salinity, which affects overall plant growth and can produce important yield losses even at low (up to 50 mM NaCl) concentrations (Lutts et al., 1995). In general, rice plants are moderately sensitive to salt stress, although some varieties show increased adaptability to saline environments. Accessions with different degree of salt sensitivity have been used in Genome Wide

Association Studies (GWAS) to identify polymorphisms in genetic determinants associated with tolerance to soil salinity at the seedling and flowering stages, which are the most affected by this abiotic stress (Lekklar et al., 2019; Liu et al., 2019). The first study employed almost 700 accessions (belonging to different *O. sativa* subspecies) and identified 15 promising candidates for salt tolerance at the seedling stage—such as some protein kinases, transcription factors of the MYB family and transporters involved in Na⁺ exclusion (Liu et al., 2019). The second study employed more than 100 accessions (subsp. *indica*) from Thailand and identified several genes associated with previously described QTLs related to salt tolerance or grain yield under salt stress at the reproductive phase (Lekklar et al., 2019). Although more than a 100 genes have been characterized as key components of cellular/physiological/metabolic pathways underlying the response to salt stress (Reddy et al., 2017), none of them seem to be directly involved in the regulation of Hd in rice plants growing in saline soils. Nevertheless, a recent article reported that a transcriptional module composed of the rice evening complex and the downstream target *OsGI* integrates circadian clock and salt tolerance. Indeed, genome-edited *osgi-101* mutants flower earlier under LD and better tolerate salt stress (X. Wang, He et al., 2021).

7 | AFRICAN RICE: FAST GROWTH AND TOLERANCE TO ABIOTIC STRESSES

The productivity of Asian rice varieties has enormously increased in the last century thanks to the generation of high-yield elite cultivars through genetic improvement as well as technological advances in farming techniques. Nevertheless, changing climatic conditions are threatening grain production as rice cultivars are susceptible to several abiotic stresses such as heat waves, rainfall deficit and soil salinity. These adverse conditions not only affect different developmental stages throughout the life of a plant but also reduce photosynthetic capacity, leading to tremendous decline in plant biomass and grain yield.

Conversely, another species of the *Oryza* genus—*O. glaberrima*, cultivated as subsistence crop in West Africa—show an extraordinary hardiness to environmental limitations (Linares, 2002). African rice (*O. glaberrima*) was domesticated from the wild relative *O. barthii* 2000–3000 years ago in the Niger River delta, a muddy coastal area with tropical climate (Purugganan, 2014). Several evidence supported the independent domestication of Asian and African rice in time (9000 vs. 3000 years ago) and space (Yangtze River vs. Niger River). Nonetheless, ancient Asian and African farmers unintentionally fixed in the population rare alleles of same or similar genetic determinants underlying domestication traits, indicating convergent evolution of the two *Oryza* species (Purugganan, 2014). Indeed, genetic variants that determine morphological changes in the plant architecture and seed shattering underwent strong selection during domestication also in African rice. For instance, the orthologs of *OsSh1* and *PROG1* genes (that control seed dispersal and growth habit in Asian rice) are deleted in cultivated African rice but present in most wild populations (Cubry et al., 2018; M. Wang et al., 2014; Wu et al., 2018).

In the last decade, advances in molecular genetics and functional genomics shed lights on the origin and evolution of African rice, including adaptation to tropical climate and harsh conditions. Detailed analysis of the *O. glaberrima* genome uncovered interesting features in flowering time genes (Table 1). On the one hand, genes encoding orthologs of major floral activators (*Ehd1*, *Ehd2*, *OsMADS51*) and the florigen *Hd3a* are conserved in African rice (M. Wang et al., 2014). Curiously, the floral integrator *Ehd1* was originally identified in a study that mapped a QTL controlling Hd by using a population obtained crossing an accession of *O. glaberrima* with the T65 variety of *O. sativa*: *Ehd1-gla* appeared to be dominant over *Ehd1-osa*, thus conferring anticipated flowering (Doi et al., 1998). On the other hand, African rice lacks key factors involved in plant response to variation in daylength, such as the orthologs of *RFT1*, *OsGI* and *Hd1* (M. Wang et al., 2014). Nevertheless, recent sequencing of *O. glaberrima* cultivars revealed that *Hd1* is present in some accessions (Monat et al., 2017) although absent in the CG14 reference genome (M. Wang et al., 2014). In addition, genes showing similarities with the LD floral repressor, including *Ghd7* and *PRR37*, are found in African rice genomes. Anyhow, further studies are required to understand their function in photoperiodic sensitivity in accessions cultivated near the equator.

African rice displays interesting developmental and physiological characteristics. Indeed, several cultivated *O. glaberrima* species are fast growing and early maturing, thus able to escape terminal drought at the end of the growing season. Still, African farmers cultivate both fast and slow maturing varieties to stagger grain harvesting (Linares, 2002). In addition, several accessions have acquired tolerance to a broad range of abiotic stresses (Wambugu et al., 2021). For example, whole genome resequencing of 93 landraces of African rice supported the selection of genomic regions containing QTLs for salt tolerance that have allowed adaptation to coastal regions of West Africa (Meyer et al., 2016). Another study identified a QTL in *O. glaberrima*, named *Thermo-tolerance 1 (TT1)*, that encodes a subunit of the 26S proteasome involved in the degradation of denatured proteins (X.M. Li et al., 2015). Genetic variants in *OgTT1*, which increase protection of plant cells by eliminating cytotoxic molecules during heat stress, have been selected during adaptation to regions with elevated ambient temperatures (X.M. Li et al., 2015).

Altogether, these features make African rice a good candidate as 'gene bank' for genetic improvement of climate resilience varieties. Indeed, these genetic resources can be exploited to transfer adaptive traits (controlled by gene pools for tolerance to diverse abiotic stresses) to elite varieties. However, African rice also shows undesirable characteristics such as small and brittle grains that are difficult to mill, and low yield (Linares, 2002).

In the 1990s, pioneering breeding programmes employed crosses between the two species (*glaberrima* and *sativa*) of the same genus (*Oryza*) to combine stress tolerance of African rice with the productivity of the Asian rice, and to generate novel varieties with enhanced adaptability to environmental fluctuations and increased grain yield. Yet, the feasibility of this approach was hampered by reproductive barriers between Asian and African rice species

TABLE 1 List of genes involved in heading date in Asian rice and putative orthologs in African rice

<i>Oryza sativa</i> gene name	<i>O. sativa</i> locus ID	<i>O. sativa</i> protein function	<i>Oryza glaberrima</i> locus ID
<i>Hd3A</i>	LOC_Os06g06320	Florigen under SD	ORGLA06g0035400
<i>RFT1</i>	LOC_Os07g30250	Florigen under LD	Not found
<i>OsFD1</i>	LOC_Os09g36910	Interactor of the florigens	ORGLA09g0142900
<i>OsGF14C</i>	LOC_Os08g33370	Floral repressor (<i>Hd3a</i> interactor)	ORGLA08g0135700
<i>RFL</i>	LOC_Os04g51000	homolog of <i>FLO/LFY</i>	ORGLA04g0204600
<i>OsGI</i>	LOC_Os01g08700	Circadian clock protein	Not found
<i>Hd1</i>	LOC_Os06g16370	Activator in SD, repressor in LD	Deleted in CG14
<i>Ehd1</i>	LOC_Os10g32600	Floral activator	ORGLA10g0110500
<i>Ehd2</i>	LOC_Os10g28330	Floral activator	ORGLA10g0088000
<i>OsMADS51</i>	LOC_Os01g69850	Floral promoter	ORGLA01g0361900
<i>OsMADS14</i>	LOC_Os03g54160	Inflorescence meristem identity factor	ORGLA03g0314900
<i>OsMADS15</i>	LOC_Os07g01820	Inflorescence meristem identity factor	ORGLA07g0005200
<i>OsMADS18</i>	LOC_Os07g41370	Inflorescence meristem identity factor	ORGLA07g0222800
<i>OsPRR37</i>	LOC_Os07g49460	Floral repressor under LD	ORGLA07g0218800
<i>Ghd7</i>	LOC_Os07g15570	Floral repressor under LD	ORGLA07g0080500

Abbreviations: LD, long days; SD, short days.

(Linares, 2002), mainly caused by the male and female components of the *S1* locus [discussed in (Garavito et al., 2010)].

To overcome the problems related to the reduced viability and fertility of the hybrids, the Programme of West African Rice Development Association (WARDA) elegantly applied the embryo rescue techniques during the breeding process. Since then, WARDA researchers have been generating novel varieties, named 'New Rice for Africa' (NERICA), through interspecific crossing (Ndjondjop et al., 2008). Compared to traditional varieties, NERICA lines have a shorter life cycle, double grain yields and better tolerate abiotic and biotic stresses. For example, the line NERICA-L-44 subjected to heat stress (42°C) shows higher survival rates of seedlings and greater reproductive success, mainly due to increased antioxidant abilities that reduce membrane damages and maintain photosynthetic capacity (Bahuguna et al., 2015). Thus, the cultivation of rice hybrids successfully generated under the frame of this programme can be a useful 'weapon' to fight against decreasing food production and increasing population in sub-Saharan Africa.

Interspecific crosses can also be used to identify variants that associate with alteration in *Hd*. Actually, association analysis of the progeny produced by crossing Asian (cv. WAB56-104) and African rice (cv. CG14) detected a SNP in the fourth exon of *Hd3a* (causing an amino acid change) that correlates with late heading, and a 3 bp insertion in the third exon of *Ehd2* (causing an amino acid insertion) that correlates with early heading (Badro et al., 2020).

8 | COEVOLUTION OF HUMANS AND PLANTS OVER MILLENNIA

Humans and plants show interlaced evolutionary pathways since they have been acting and interacting with each other's for millennia. In prehistoric times, humans were completely dependent on the environment for their subsistence as wild plants constituted the major proportion of their nutrition. Over time, the development of agricultural societies brought to tremendous modifications of the natural landscape and exploitation of natural resources for food production.

During the domestication process of the *Oryza* genus, ancient Asian and African farmers artificially selected—in different times and places—common traits beneficial for cultivation. Comparative analysis of domestication genes between Asian and African rice revealed that the two species went through an independent but convergent evolutionary process. The successive diversification of domesticated rice species led to the generation of locally adapted varieties that were also selected for their taste, nutritional value or culinary preferences. Through centuries, rice cultivation has expanded globally—also thanks to human migration and international trades—and to date, rice constitutes the main ingredient of several traditional dishes worldwide (Figure 3).

In the last 50 years, rice production has doubled following the adoption of scientific advances including novel semidwarf



FIGURE 3 Popular rice-based dishes worldwide. Arroz con frioles in central America and Arroz con huevos in south America; paella in Spain (cv Bomba) and risotto in Italy (cv Arborio); Jollof rice in West Africa; Chicken biryani in India; rice bowl in China; rice for sushi in Japan. [Color figure can be viewed at wileyonlinelibrary.com]

high-yield varieties and innovative agricultural practices (e.g., mechanization, irrigation, fertilization). What will happen in the next 50 years? Rice yields are being progressively affected by extreme weather events such as sudden changes in ambient temperatures, heat waves, drought and flooding. Facing environmental degradation and changing climate, mitigation and adaptation strategies should rely on cutting-edge technologies (e.g., precision farming) as well as genetic improvement aimed at obtaining climate-smart varieties.

Global warming represents one of the major concerns for plant productivity. In fact, elevated ambient temperatures are severely affecting rice yields in southern China (Song et al., 2022). However, the impact of heat is greater on early maturing varieties than on late maturing varieties, considering that hot days are more frequent in early summer than late summer (Song et al., 2022). Therefore, targeting regulators of the floral transition in breeding programmes could be a good strategy to modulate heading and guarantee reproductive success in a warmer planet.

Climate change represents a great challenge for agriculture not only because adverse conditions have a negative impact on different developmental stages but also because alterations in the environment can change the range of pests (viruses, insects, bacteria, fungi), undermining food security. Thus, efforts should be made towards multifactorial stresses and development of crops able to maintain high yield even in the presence of biotic and abiotic stresses.

By 2050, man and women of the future will be needing innovative crops for space gardens in the case of long missions to the outer space, construction of lunar bases or colonization of Mars (Kordyum & Hasenstein, 2021). In this scenario, space agriculture will require super rice varieties also able to cope with microgravity, UV radiation and absence of diurnal changes.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in PubMed.

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