Comparative biology comes into bloom: genomic and genetic comparison of flowering pathways in rice and Arabidopsis

Takeshi Izawa*, Yuji Takahashi† and Masahiro Yano†

Huge advances in plant biology are possible now that we have the complete genome sequences of several flowering plants. Now, genomes can be comprehensively compared and map-based cloning can be performed more easily. Association study is emerging as a powerful method for the functional identification of genes and molecular genetics has begun to reveal the basis of plant diversity. Taking the flowering pathways as an example, we discuss the potential of several approaches to comparative biology.

Introduction

Recently, two complete plant genome sequences, one from a dicot and one from a monocot, have been reported[1**,2**,3]. This progress has opened a floodgate of comparative genomics and molecular genetics in flowering plants. We review the use of the extensive new genomic information to reveal genes that are related to floral induction. We discuss the recent progress of molecular genetics in uncovering a flowering pathway that is conserved between rice, a short-day plant, and Arabidopsis, a long-day plant. We also review a new approach to identifying natural variations in flowering-time genes, which have contributed to the speciation and diversity of flowering plants.

What do genome sequences tell us about flowering pathways?

The molecular genetics of the long-day plant Arabidopsis have revealed several pathways that regulate floral induction and related flowering-time genes [4,5]. A long-day promotion pathway, a gibberellin-acid promotion pathway, and vernalization and autonomous pathways are well characterized. Several flowering pathway integrators, into whose expression multiple environmental stimuli are ‘integrated’, have also been identified. In addition, genes that are involved in determining chromatin structure are also involved in floral induction. We reciprocally compared whole-genome sequences using the public database of the indica rice genome draft [1**] and the München Information Center for Protein Sequences (MIPS) Arabidopsis proteome database (http://mips.gsf.de/proj/thal/) to find genes that are orthologous to previously reported flowering-time genes (Table 1). (As this review is focused on comparative analyses, see the original papers in the reference list for more information on the biological functions of flowering-time genes.)

Photoreceptors that are involved in floral induction include phytochromes (PHY) and cryptochromes (CRY). Arabidopsis contains five PHY and two CRY genes, whereas rice contains three PHY and three CRY genes (possibly two CRY1-type and one CRY2-type) [6,7]. PHYD and PHYE are missing in rice. As well as these PHY and CRY genes, circadian clock genes are conserved between the two plant species. Each genome includes a TIMING OF CHLOROPHYLL A/B BINDING PROTEIN (CAB) EXPRESSION 1 (TOC1) [8] and a GIGANTEA (GI) (or OsGI) [9,10,11]* orthologue. Orthologues of other members of the Arabidopsis PSEUDO RESPONSE REGULATOR (APRR) family, to which TOC1 belongs, also exist in rice [12]. There are two MYB-related genes in the Arabidopsis circadian clock system, LATE ELONGATED HYPOCOTYL (LHY) [13] and CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) [14], but only one orthologous gene,
OsLHY, in rice [15**]. At least one gene that is related to Arabidopsis EARLY FLOWERING3 (ELF3) [16] has been found in rice, but no apparent orthologue of ELF4 [17*] has been found in rice. Orthologues of both of the Arabidopsis F-box genes that function in the circadian clock, ZEITLUPE (ZTL) [18] and FLAVIN-BINDING, KELCH-REPEATS, F-BOX1 (FKF1) [19], have been found in rice, suggesting that each of these genes has a unique biological role in addition to its function in the circadian clock. These results imply that a conserved

<p>| Table 1 | Rice genes that are orthologous to flowering-time genes of Arabidopsis. |</p>
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*Genes are separated into several contigs. †Arabidopsis proteins were subjected to BLAST analysis with the MIPS Arabidopsis proteome database, indicating the values for the complete homology. ‡Arabidopsis proteins were subjected to BLAST analysis with the rice genomic contigs released by the Beijing group [1**]. Abbreviation: LKP2, LOV KELCH PROTEIN2.
Flowering pathways in rice and Arabidopsis

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flowering pathway is involved in photoreceptor and circadian-clock signaling rice and Arabidopsis, suggesting that this flowering pathway may exist in a large part of the plant kingdom.

The Arabidopsis genes CONSTANS (CO; a circadian-clock-related floral regulator [20]), CONSTANS-LIKE1 (COL1), and COL2 [21] belong to the same phylogenetic branch of a major quantitative trait locus (QTL) for flowering-time that is known as rice Heading date1 (Hd1) ([22]; Figure 1). COL1 and COL2 do not appear to be involved in floral induction, but may be involved in circadian clock systems. Therefore, these genes may have acquired specific biological functions other than floral induction. The Arabidopsis FLOWERING LOCUS T (FT) gene [23,24] is both one of the target genes of CO and one of the integrators. TWIN SISTER OF FT in Arabidopsis and ten FT-like genes [15**] in rice, including Hd3a [25**] (another flowering-time QTL), belong to the same branch in a phylogenetic tree. The redundancy of FT orthologues in rice suggests that they have novel functions, but this remains to be examined. Arabidopsis SUPPRESSOR OF OVEREXPRESSION OF CO 1 (SOC1) [26], another direct target gene of CO and another integrator, is a member of the large MADS-box family. At least one rice orthologue of SOC1 has been found on the basis of homology at the carboxy-end region as well as in the MADS and K domains. In addition, the RICE FLO/LEAFY (RFL) gene [27], which is present in the rice genome as a single copy, is orthologous to LEAFY (LFY), a single-copy gene that encodes another flowering pathway integrator in Arabidopsis.

FLOWERING LOCUS C (FLC) [28,29], a MADS-box gene, is a key regulator of the autonomous flowering and vernalization pathways in Arabidopsis. No apparent FLC orthologue has been found in rice. Neither has an orthologue of Arabidopsis FRIGIDA [30], the activator of FLC, been found in rice. Further, no orthologues of the recently identified VERNALIZATION1 (VRN1) and VRN2 genes [31**,32], which are required for vernalization in Arabidopsis, have been found in rice. It seems likely, therefore, that vernalization-related genes have been lost from the rice genome during evolution. This hypothesis is consistent with the fact that vernalization has not been reported in rice. FCA, an RNA-binding protein, is a component of the autonomous pathway that controls FLC expression [33]. A single orthologue of FCA has been found in the rice genome.

VRN2 belongs to the Polycomb group, whose members affect chromatin structure to repress gene expression. EMBRYONIC FLOWERING2 (EMF2) [34] and FERTILIZATION INDEPENDENT ENDOSPERM (FIE) [35*] also belong to the Polycomb group and affect floral induction in Arabidopsis. The LIKE HETEROCHROMATIN PROTEIN1 (LHP1) [36*] gene may be involved in heterochromatin formation and affects flowering time in Arabidopsis. Two orthologues of EMF2, two orthologues of FIE, and an orthologue of LHP1 have been found in
rice. These members of the Polycomb and heterochromatin protein groups affect the expression of multiple genes in a range of genomic regions. It will be interesting, therefore, to know whether the biological function of such chromatin-related genes is conserved among plant species, as gene order and chromosome structure are apparently not conserved between rice and *Arabidopsis*.

These comparisons of orthologous genes in rice and *Arabidopsis* provide many insights into the evolutionary conservation of flowering pathways in flowering plants. The functionality of many of these orthologues waits to be tested.

**Flowering pathways conserved between short- and long-day plants**

Recent progress in molecular genetics has provided evidence that supports the insights revealed by genomic comparison, revealing an evolutionarily conserved genetic pathway that regulates photoperiodic flowering in rice and *Arabidopsis*. Rice orthologues of the *Arabidopsis* genes *CO* and *FT* were recently identified as flowering-time QTLs named *Hd1* and *Hd3a*, respectively. The *PHOTOPERIOD SENSITIVITY5* (*SE5*) gene, which encodes a hemeoxygenase for phytochrome chromophore biosynthesis, is absolutely required for photoperiodic flowering in rice. The *Arabidopsis* orthologue *LONG HYPOCOTYL1* (*HY1*) is also required for full response to photoperiod in *Arabidopsis* [38]. In addition, the diurnal mRNA expression patterns of circadian clock genes — *LHY1* (or *CCA1*) of *Arabidopsis* and *OsLHY* of rice, and *GI* of *Arabidopsis* and *OsGI* of rice — are conserved [11*,15**]. The circadian-clock-regulated patterns of *CAB* gene expression in rice are similar to those in *Arabidopsis* [39], suggesting that the circadian clock system is conserved.

Recent detailed studies of the conserved flowering pathway have highlighted the molecular difference in how short- and long-day plants measure daylength (Figure 2; [15*,25**,40,42**,43*]). *CO* promotes flowering under long-day conditions, whereas *Hd1* promotes flowering under short-day conditions and inhibits it under long-day conditions.

![Figure 2: Comparison of gene interactions in the photoperiodic pathways of rice and Arabidopsis.](https://www.current-opinion.com/COPB/2003/6/113-120)

Comparison of gene interactions in the photoperiodic pathways of rice and Arabidopsis. Rice genes that have been assigned on the basis of sequence information only are shown in black. Rice genes assigned on the basis of mRNA expression analysis are shown in blue. The other rice genes (shown in red) are assigned on the basis of genetic evidence. Light has multiple actions on photoperiodic flowering. It is not clear whether *PHYB* affects *FT* mRNA expression in Arabidopsis. The transduction pathway for the external light signal that induces *LFY* and *SOC1* mRNA expression under long days remains unknown. Circadian clock mutants have not yet been found for rice. Os, *Oryza sativa*; RFL, RICE FLO/LFY; ZTL, ZEITLUPE.
conditions. The expression both CO and Hd1 mRNAs is mainly regulated by the circadian clock. It has recently been revealed that Hd1 functions as a repressor (activator) of mRNA expression of rice FT orthologues in interaction with (without) light-stable phytochrome signaling [15**]. On the other hand, CO promotes the expression of FT mRNA only in interaction with light signaling mediated by CRY2 (under white light) and PHYA, a light-unstable phytochrome, (under far-red-rich light) [42**]. These studies provide the first insight into the molecular nature of the external coincidence model proposed by Büning [44] and refined by Pittendrigh and Minis [45]. According to this model, light has two roles in allowing plants to measure daylength. First, light is involved in the entrainment of the circadian clock, which results in diurnal Hd1 and CO expression from dusk till dawn. Second, light modifies the activity of the transcription factors Hd1 and CO. The difference between rice and Arabidopsis largely comes from the differential action of external light signals on Hd1/CO activity. This differential action may be caused by domain differences between Hd1 and CO. Alternatively, different photoreceptor functions may be involved in the two species. In Arabidopsis, the CRY2 function for floral promotion requires PHYB action, whereas PHYB mainly inhibits flowering under short days [46,47]. Light-stable PHYB action may therefore control FT expression in both rice and Arabidopsis, although no effect of FT expression by PHYB has been reported in Arabidopsis [48].

Protein phosphorylation may also play a conserved role in photoperiodic flowering in rice and Arabidopsis. Hd6, another rice QTL, inhibits flowering under long days [49] and encodes the α subunit of casein kinase2 (CK2). Some lines of evidence indicate that CK2 is also involved in photoperiod response in Arabidopsis. Overexpression of CKB3 — a protein that interacts with the circadian clock component CCA1, which encodes an Arabidopsis CK2β — increases CK2 activity, shortens periods of circadian rhythms, and results in early flowering with a reduced photoperiod response [50,51]. These results indicate that CK2 affects floral transition in both rice and Arabidopsis, maybe partly through the regulation of the circadian clock. Antisense expression of the Arabidopsis CK2α gene ATHCK2A1 (or of an orthologue of Hd6) reduced CK2 activity and affected the expression of three light-regulated genes but did not significantly affect flowering time [52]. Further analysis will clarify the function of CK2 in both rice and Arabidopsis. It is now clear that the photoperiodic flowering pathway is evolutionarily conserved between rice and Arabidopsis. Whether other pathways, such as those for vernalization and gibberellin signaling, are conserved in these two species is the next obvious question for molecular geneticists.

Impacts of flowering-time QTLs

The analysis of natural allelic variation has contributed significantly to the exploration of genes that are involved in determining flowering time in rice [53]. Three QTLs for flowering time have been identified by map-based cloning [22,25**,49]. This work relied on standard processes for map-based cloning to identify gene function, including the construction of a physical map, chromosome walking, the sequencing of candidate genomic regions, and genetic complementation analysis. However, these processes are too time-consuming and laborious to be used by many researchers for the molecular identification of genes, especially at QTLs. The chromosome-aligned genome sequence information released by the International Rice Genome Sequencing Project allows us to skip several of the steps in map-based cloning [54].

A wide range of natural allelic variation exists in flowering-time genes because flowering time is a trait that adapts to environmental conditions such as photoperiod and temperature. For example, the Columbia and Landsberg erecta ecotypes of Arabidopsis, which are popular among molecular biologists, contain different alleles of the FLC and FRIGIDA floral regulators [29]. The introgression of new, naturally occurring alleles has contributed to the molecular analysis of flowering-times genes [29]. In addition, QTL analyses have provided clues to differences among functional alleles. A novel allele at CRY2 has been identified through the analysis of the tropical Cape Verde Islands ecotype of Arabidopsis [55**]. Functional variation of Hd1 alleles among rice cultivars has also been suggested [22]. Furthermore, map-based cloning of the flowering-time QTL Hd3a revealed a difference between two functional alleles at this locus. Nucleotide polymorphisms in non-coding sequences, such as introns and the 3′-untranslated region, may be involved in controlling the level of Hd3a transcript [25**].

The two subspecies of Oryza sativa (indica and japonica) and their wild relatives can be crossed to produce fertile progeny [56]. This situation provides the potential to mine a wide range of alleles using a map-based strategy [57].

Association study based on linkage disequilibrium

The use of whole-genome sequence information makes it easier to find plant genes on whose biological functions we can speculate. An alternative genomic approach, association study, can be used to identify the biological function of the candidate genes. Association studies are based on the linkage disequilibrium (LD) of candidate genes, that is, on the observation of a certain combination of alleles at different loci at a higher frequency than is predicted in a natural population. This approach has been widely used to study the complex genetics of many human diseases [58]. Association studies were thought to be limited to use in the identification of genes in artificially and naturally modified plant populations.
For instance, extensive LD was thought to prevent fine-scale mapping in self-pollinated plant species such as Arabidopsis and rice. However, recent studies in maize and Arabidopsis have demonstrated that the level of LD decays rapidly, suggesting that association study can achieve a resolution that is sufficient to define candidate genomic regions [59**,60**]. Association studies have also been used to identify the functions of genes in maize [61**], Arabidopsis [60**,62,63], and Brassica nigra [64**,65]. Moreover, this approach enabled researchers to finely localize quantitative trait nucleotides in candidate flowering-time genes [61**,64**].

In general, the level of LD depends on several factors, such as random genetic drift, and natural and artificial selection in crop species. More extensive surveys of local and genome-wide LD in crop plants will therefore be required to avoid the generation of false positives. Nevertheless, association study will be an effective approach for the functional identification of genes (or the high-resolution mapping of QTLs). It will also be an effective way to assess the contribution of particular candidate genes or functionally identified genes to the phenotypic variation among traits, such as flowering time, in naturally occurring plant populations.

Conclusions: ‘comparison’ starts to tell on the plant kingdom

The completion of rice genome sequencing and the comparison of genomic sequences within and between rice and Arabidopsis are providing great insights into the diversity among flowering plants. In addition, molecular genetic approaches such as forward, reverse, and transgene-based genetics can verify and refine these insights, as highlighted for photoperiodic flowering in this review. Furthermore, a gene-targeting approach that uses homologous recombination has been established recently in rice [66**]. This may become a powerful tool for the molecular identification of natural variations, which are often attributed to subtle nucleotide differences between functional alleles. Genome projects on other model plants, such as Lotus japonicus, Medicago sativa, and Physcomitrella patens, are ongoing. These will introduce us to a whole new world of genetic information on the plant kingdom.

Acknowledgements

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest


This study used the whole-genome shotgun method to sequence the rice genome. The indica rice cultivar ‘93-1’, the parent of the super-hybrid rice ‘Liang-You-Pei-Jiu’, was selected for this large project. In total, around 120 000 contigs were registered in the public database bases. The assembled sequence covers 92.0% of the genome. Free access to the database is essential to allow plant scientists to use the sequence information for the benefit of everyone.


This study also used the whole-genome shotgun method to sequence the rice genome. This project used the japonica cultivar ‘Nipponbare’, which is also being sequenced by the International Rice Genome Sequencing Project. The assembled sequence covers 93% of the genome. The resulting database, containing around 40 000 contigs in total, can be searched only by registration with the Torrey Mesa Research Institute.


This is the first report to explain how the short-day plant rice recognizes daylength at the molecular level. The evidence presented supports the external coincidence model, one of the most popular models for photo-
periodism. Daylengths other than 24 hours, such as 36 h light/12 h dark, were used to evaluate flowering-time mutants of rice.


Interestingly, the elf4 mutant exhibits rhythmic gene expression that has larger deviations than that of the wild-type. This suggests an important role for ELF4 in maintaining the circadian clock. This gene could be a central component of the circadian clock.


25. Kojima S, Takahashi Y, Kobayashi Y, Monna L, Sasaki T, Araki T, Yano M: Hd3a, a rice ortholog of the Arabidopsis FT gene, promotes transition to flowering downstream of Hd1 under short-day condition. Plant Cell Physiol 2002, 43:1096-1105. A QTL for heading date, £d3a, was isolated in rice by a map-based strategy. £d3a shows a high level of similarity to the Arabidopsis flowering-time gene FT. Using expression analysis, the authors showed that the amount of £d3a mRNA is upregulated by Hd1 under short days, suggesting that £d3a promotes heading under the control of Hd1. This work clearly demonstrates that photoperiod-response genes are conserved between long- and short-day plants.


31. Gendall AR, Levy YY, Wilson A, Dean C: The VERNALIZATION 2 gene mediates the epigenetic regulation of vernalization in Arabidopsis. Cell 2001, 107:225-235. VRN2, which is required for vernalization in Arabidopsis, encodes a protein that is homologous to Drosophila Su12. Arabidopsis FERTILIZATION INDEPENDENT SEED2 (FIS2), and EMF2. These genes are members of the Polycomb group. VRN2 maintains the repression of a floral repressor, FLC, but is not involved in initiating this repression. This evidence implies that FLC expression is epigenetically regulated through chromatin remodeling.


35. Kinosita T, Harada JJ, Goldberg RB, Fisher RL: Polycomb repression of flowering during early plant development. Proc Natl Acad Sci USA 2001, 98:14156-14161. Weak alleles of fmi mutants with light induced by it is causing a fusion protein of FIE in the fmi mutant. The phenotype of these mutants suggests that FIE represses flowering during the early development of Arabidopsis. FIE encodes a protein that is homologous to Drosophila Extra Sex Combs, a member of the Polycomb group.

36. Gaudin V, Libault M, Pouteau S, Juul T, Zhao G, Lefebvre D, Grandjean O: Mutations in LIKE HETEROCROMATIN PROTEIN I affect flowering time and plant architecture in Arabidopsis. Development 2001, 128:4847-4858. This study suggests that heterochromatin formation is involved in floral induction and flower architecture in Arabidopsis. This is the first genetic evidence that heterochromatin structure is involved in biological functions in plants. LHP1 can affect the expression of CO mRNA.


42. Yanovsky MJ, Kay SA: Molecular basis of seasonal time measurement in Arabidopsis. Nature 2002, 419:308-312. This paper describes how Arabidopsis, a long-day plant, recognizes daylength at the molecular level. The Arabidopsis toc1 mutant was used for this work as genetic modification in toc1 is likely to be specific to the circadian-clock system. The authors successfully separated the effect of the circadian clock from diurnal light cycles. It is interesting to compare this work with that by Izawa et al. [15**], who described how rice, a short-day plant, recognizes daylength.

43. Roden LC, Song H-R, Jackson S, Morris K, Carre IA: Floral responses to photoperiod are correlated with the timing of rhythmic expression relative to dawn and dusk in Arabidopsis. Proc Natl Acad Sci USA 2002, 99:13313-13318. The authors performed extensive physiological experiments. Non-24-h light/dark cycles were used to examine the photoperiodic control of flowering in Arabidopsis. The results support the external coincidence model.