

Nomenclature for Two-Component Signaling Elements of Rice

Plants make use of two-component systems for signal transduction, and these are involved in vital cellular processes such as the responses to cytokinins, ethylene, red/far-red light, and osmosensing (Schaller et al., 2002). Two-component systems were originally identified in bacteria, and in their simplest form involve a His kinase and a response regulator that participate in a phosphorelay (Mizuno, 1997). Of particular relevance to plants is a permutation on the two-component system known as the multistep phosphorelay, which incorporates an additional protein called a His-containing phosphotransfer protein into the phosphorelay (Schaller et al., 2002).

In plants, two-component signaling has been studied most extensively in the dicot *Arabidopsis thaliana* (Schaller et al., 2002). But in the past several years, as the rice (*Oryza sativa*) genome has been sequenced (Feng et al., 2002; Goff et al., 2002; Sasaki et al., 2002; Yu et al., 2002; Rice Chromosome 10 Sequencing Consortium, 2003; International Rice Genome Sequencing Program, 2005), publications have begun to appear on the two-component signaling elements of rice (Murakami et al., 2003; Doi et al., 2004; Han et al., 2004; Yau et al., 2004; Murakami et al., 2005; Ito and Kurata, 2006; Jain et al., 2006; Pareek et al., 2006). Given the broad impact that the two-component signaling systems have on plant growth and development, the number of publications describing their action in rice is likely to increase rapidly in the coming years. It is thus necessary that a uniform nomenclature be adopted to facilitate scientific communication.

Unfortunately, because publications on two-component signaling elements of rice appeared from multiple

laboratories within a short period of time, it was not possible to coordinate the terminology being used. This resulted in multiple designations being applied to the same gene, different criteria being used for classifying genes into families, and some redundancy with previously used gene symbols. Now with a high-quality rice genome sequence available and most if not all of the two-component signaling elements identified, it is timely to implement a standardized nomenclature for the rice two-component signaling elements.

In assigning gene symbols, we followed the rules for gene symbols in rice adapted from the 1986 report of the Committee on Gene Symbolization, Nomenclature, and Linkage (the November 7, 2005 draft document is available at <http://www.gramene.org/documentation/nomenclature/>). Thus all gene symbols are given in italics with the first letter capitalized. Although not shown in the tables, the protein symbol should be identical to the adopted gene symbol, the only difference being that it is written using all uppercase characters in italics followed by the numeric locus identifier. Precedence of publication was the primary determinant of the gene symbol and, whenever possible, we used the same gene symbol for all related genes. Additional symbols for the same gene were assigned as synonyms. A rice designation (e.g. *Os*) is not part of the gene symbol but may be added when needed to differentiate between similar genes of other species.

For the His kinases, the ethylene receptor family retains the original designations from Yau et al. (2004), which are consistent with gene symbols used in other plant species. The other rice His kinases use the gene

Table 1. His kinase-like proteins of rice

Gene Symbol	Synonyms	Chromosome Locus	Features ^a	Family
<i>Ers1</i> ^b		Os03g49500	C ₂ H ₄ , HK	Ethylene receptor
<i>Ers2</i> ^b		Os05g06320	C ₂ H ₄ , HK	Ethylene receptor
<i>Etr2</i> ^b		Os04g08740	C ₂ H ₄ , HKL, Rec	Ethylene receptor
<i>Etr3</i> ^b		Os02g57530	C ₂ H ₄ , HKL, Rec	Ethylene receptor
<i>Etr4</i> ^b		Os07g15540	C ₂ H ₄ , HKL, Rec	Ethylene receptor
<i>Hk1</i> ^c		Os06g44410	HK, Rec	AtCK12 like
<i>Hk2</i> ^c	<i>Ohk1</i> ^d	Os06g08450	HK, Rec	AtCK11 like
<i>Hk3</i> ^c	<i>Cr12</i> ^e , <i>Ohk2</i> ^d	Os01g69920	CHASE, HK, Rec	Cytokinin receptor
<i>Hk4</i> ^c	<i>Cr11b</i> ^e , <i>Ohk4</i> ^d	Os03g50860	CHASE, HK, Rec	Cytokinin receptor
<i>Hk5</i> ^c	<i>Cr13</i> ^e , <i>Ohk3</i> ^d	Os10g21810	CHASE, HK, Rec	Cytokinin receptor
<i>Hk6</i> ^c	<i>Cr11a</i> ^e , <i>Ohk5</i> ^d	Os02g50480	CHASE, HK, Rec	Cytokinin receptor

^aFeatures noted are conserved His-kinase domain (HK), diverged His-kinase-like domain (HKL), receiver domain (Rec), CHASE domain for cytokinin binding (CHASE), and ethylene-binding domain (C₂H₄). ^bYau et al. (2004). ^cPareek et al. (2006). ^dIto and Kurata (2006). ^eHan et al. (2004).

Table II. *His-containing phosphotransfer proteins of rice*

Gene Symbol	Synonyms	Chromosome Locus	Features ^a
<i>Ahp1</i>	<i>Hpt2^b</i> , <i>Ohp1^c</i>	Os08g44350	HPt
<i>Ahp2</i>	<i>Hpt3^b</i> , <i>Ohp2^c</i>	Os09g39400	HPt
<i>Php1</i>	<i>Hpt1^b</i>	Os01g54050	Pseudo-HPt
<i>Php2</i>	<i>Hpt4^b</i>	Os05g09410	Pseudo-HPt
<i>Php3</i>	<i>Hpt5^b</i>	Os05g44570	Pseudo-HPt

^aFeatures indicate whether the proteins contain a conserved His-containing phosphotransfer domain (HPt) or a pseudo-HPt lacking the His that is phosphorylated. ^bPareek et al. (2006). ^cIto and Kurata (2006).

symbol *Hk*, including the four members of the cytokinin receptor family (Pareek et al., 2006).

The His-containing phosphotransfer proteins are given the gene symbol *Ahp* (authentic His-containing

Table III. *Response regulators of rice*

Gene Symbol	Synonyms	Chromosome Locus	Features ^a	Family
<i>Rr1^b</i>	<i>Rra9^c</i>	Os04g36070	Rec	Type A
<i>Rr2^b</i>	<i>Rra10^c</i>	Os02g35180	Rec	Type A
<i>Rr3^b</i>	<i>Rra7^c</i>	Os02g58350	Rec	Type A
<i>Rr4^b</i>	<i>Rra3^c</i>	Os01g72330	Rec	Type A
<i>Rr5^b</i>	<i>Rra4^c</i>	Os04g44280	Rec	Type A
<i>Rr6^b</i>	<i>Rra6^c</i>	Os04g57720	Rec	Type A
<i>Rr7^b</i>	<i>Rra5^c</i>	Os07g26720	Rec	Type A
<i>Rr8^b</i>	<i>Rra13^c</i>	Os08g28900	Rec	Type A
<i>Rr9^b</i>	<i>Rra1^c</i>	Os11g04720	Rec	Type A
<i>Rr10^b</i>	<i>Rra2^c</i>	Os12g04500	Rec	Type A
<i>Rr11^d</i>	<i>Rra8^c</i>	Os02g42060	Rec	Type A
<i>Rr12^d</i>	<i>Rra11^c</i>	Os08g28950	Rec	Type A
<i>Rr13^d</i>	<i>Rra12^c</i>	Os08g26990	Rec	Type A
<i>Rr21</i>	<i>Rrb1^c</i> , <i>Orr1^d</i>	Os03g12350	Rec, Myb	Type B
<i>Rr22</i>	<i>Rrb4^c</i> , <i>Orr2^d</i>	Os06g08440	Rec, Myb	Type B
<i>Rr23</i>	<i>Rrb5^c</i> , <i>Orr3^d</i>	Os02g55320	Rec, Myb	Type B
<i>Rr24</i>	<i>Rrb2^c</i> , <i>Orr4^d</i>	Os02g08500	Rec, Myb	Type B
<i>Rr25</i>	<i>Rrb3^c</i> , <i>Orr5^d</i>	Os06g43910	Rec, Myb	Type B
<i>Rr26</i>	<i>Rrb6^c</i> , <i>Orr6^d</i>	Os01g67770	Rec, Myb	Type B
<i>Rr27</i>	<i>Rra16^c</i>	Os05g32880	Rec, Myb	Type B
<i>Rr28</i>	<i>Rra22^c</i>	Os04g28160	Rec, Myb	Type B
<i>Rr29</i>	<i>Rrb7^c</i>	Os04g28130	Rec, Myb	Type B
<i>Rr30</i>	<i>Ehd1^e</i>	Os10g32600	Rec, Myb	Type B
<i>Rr31</i>		Os08g35650	Rec, Myb	Type B
<i>Rr32</i>		Os08g17760	Rec, Myb	Type B
<i>Rr33</i>	<i>Rra19^c</i>	Os08g35670	Rec, Myb	Type B
<i>Rr41</i>	<i>Rra14^c</i>	Os03g53100	Rec	Type C
<i>Rr42</i>	<i>Rra15^c</i>	Os04g13480	Rec	Type C
<i>Prr1^f</i>		Os02g40510	Rec(D-E), CCT	Clock
<i>Prr37^f</i>	<i>Prr4^c</i>	Os07g49460	Rec(D-E), CCT	Clock
<i>Prr73^f</i>	<i>Prr3^c</i>	Os03g17570	Rec(D-E), CCT	Clock
<i>Prr59^f</i>	<i>Prr5^c</i>	Os11g05930	Rec(D-E), CCT	Clock
<i>Prr95^f</i>	<i>Prr2^c</i>	Os09g36220	Rec(D-E), CCT	Clock
<i>Prr10</i>	<i>Rra18^c</i>	Os05g32890	Rec(D-E), Myb	
<i>Prr11</i>		Os04g28150	Rec(D-E)	
<i>Prr12</i>	<i>Rra17^c</i>	Os04g28120	Rec(D-A)	

^aFeatures include receiver domain (REC) with change in phosphorylated Asp indicated if differing from the conserved sequence, Myb-like DNA-binding domain (Myb), and CCT motif found in clock proteins. ^bJain et al. (2006). ^cPareek et al. (2006). ^dIto and Kurata (2006). ^eDoi et al. (2004). ^fMurakami et al. (2003).

phosphotransfer protein) if they contain the conserved His residue that is phosphorylated, and the gene symbol *Php* (pseudo His-containing phosphotransfer protein) if they lack the conserved His. These new symbols are in accordance with nomenclature for genes encoding response regulators (see below), and will simplify discussion of the His-containing phosphotransfer proteins because the symbols carry information related to function.

The rice response regulators are given the gene symbol *Rr* if they contain the conserved Asp that serves as the phosphorylation site (Jain et al., 2006), and the gene symbol *Prr* if they lack the conserved Asp (Murakami et al., 2003). The rice response regulators are numbered according to type (the gene symbols for type A starting from *Rr1*, type B starting from *Rr21*, and type C starting from *Rr41*), such that if additional response regulators of each type are found in annotation of the genome, they may still be numbered in sequence with their more closely related sequences. Note that we are using the same definition of the type A response regulators as that employed for Arabidopsis (short N- and C-terminal extensions in addition to the receiver domain, related at the sequence level based on phylogenetic analysis, and induced by cytokinin). The type B response regulators are transcriptional regulators with C-terminal extensions containing a Myb-like DNA-binding domain, although it should be pointed out that there is substantial sequence variation among the rice Myb-like motifs. We also introduce the term type C response regulator to refer to *OsRr41* and 42 (along with *AtARR22* and 24) which, although the proteins lack long C-terminal extensions, are not closely related to the type A response regulators based on phylogenetic analysis (Schaller et al., 2002).

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