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综 述

基于转录特征的水稻 WRKY 转录因子功能注释

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摘要: 转录水平的变化是转录因子功能发挥的重要体现形式，高通量测序技术的发展和应用揭示了丰富的转录数据，对转录数据的深度分析有助于基因的注释和功能研究。本文以水稻 WRKY 转录因子家族为对象，在总结 *WRKY* 基因功能的基础上，对生物和非生物胁迫、发育、营养和激素处理等不同生物学过程中的转录数据进行了系统的整理和挖掘，获得了不同反应中转录变化的特定 *WRKY* 基因清单，丰富了水稻 WRKY 转录因子家族成员的注释信息，以期这些信息为后续的功能研究提供有价值的参考。

关键词: WRKY 转录因子；转录特征；水稻；注释；转基因

Functional annotation of rice WRKY transcription factors based on their transcriptional features

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Abstract: Transcription factors regulate alteration of transcription levels. Recently, huge amount of transcriptomic data are accumulated *via* the application of high throughput sequencing technology, and it is reasonable to postulate that in-depth analysis of transcription data could be used to enhance gene annotation. In this study, we chose the gene family of rice WRKY transcription factors. Based on literature search, the transcriptional data under different biological processes, including biotic and abiotic stress, development, and nutrient absorption and hormone treatments were analyzed systematically. To the end, we summarize the list of differentially expressed *WRKY* genes. We also expect that such information will enrich their functional annotation and also provide direct clues for subsequent functional studies.

Keywords: WRKY transcription factor; transcriptional feature; rice; annotation; transgenic plants

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转录因子是植物生长发育和逆境应答过程中基因表达的核心调控枢纽。目前在水稻(*Oryza sativa* L.)、拟南芥(*Arabidopsis thaliana* L.)等植物中相继克隆了众多的 *WRKY* 基因, 并发现 WRKY 转录因子是植物所特有的[1]。水稻是重要的粮食作物，2000 年第一个水稻 *WRKY* 基因的克隆[2]和 2002 年水稻全基因组测序工作的完成使人们可以全面了解 WRKY 家族的组成[1,3~5]。近年来，高通量测序技术的广泛应用揭示了丰富的 *WRKY* 基因的转录信息。在此基础上, 本文对水稻 WRKY 转录因子家族的功能及其转录特征进行汇总分析, 试图对 WRKY 家族有一个整体了解, 借此丰富水稻 WRKY 转录因子家族成员的注释信息，以期这些信息对后续的功能研究提供有价值的参考。

1　水稻 WRKY 转录因子的结构特点和分类

WRKY 蛋白质的氨基端都有一段高度保守的多肽序列，其中 WRKY 序列基本上是不变的，WRKY 也由此得名[1]。根据 WRKY 结构域的数量及锌指结构的特征，WRKY 转录因子一般分为 3 类。第Ⅰ类有两个 WRKY 结构域和两个 C2H2 锌指结构域；第Ⅱ类有一个 WRKY 结构域和一个 C2H2 锌指结构域；第Ⅲ类有一个 WRKY 结构域和一个 C2HC 锌指结构域。水稻 WRKY 蛋白质的分类也大致遵循上述原则, 其中第Ⅰ类被分成二个亚类，Ⅰa 成员含有 2 个 C2H2 锌指结构域，Ⅰb 成员含有 2 个 C2HC 锌指结构域；锌指结构域缺失或不完整的 WRKY 蛋白质被列为第Ⅳ类，包括二个亚类，Ⅳa 成员含有不完整的 CX4C(C2XX，C2HX，C2-)锌指结构域，Ⅳb 成员则缺少锌指结构域[4,6]。

根据基因组注释结果, 在水稻品种日本晴(粳稻)和 9311(籼稻)中分别有 98 和 102 个 *WRKY* 基因, 比拟南芥的 *WRKY* 基因数(74 个)略多[4]。由于不同研究组对水稻 *WRKY* 基因分别进行了命名[4,6~10]，造成了名称的不统一，因此，基因符号、命名和连锁关系委员会(The committee on gene symbolization, nomenclature and linkage, CGSNL)的水稻 *WRKY* 基因工作组协商统一了水稻 *WRKY* 的命名[11]。本文使用的是 CGSNL 的命名，为方便读者查阅还尽可能同时列出了原文献中的编号。

2　水稻 *WRKY* 基因转录数据的来源

本文采用的水稻 *WRKY* 基因的转录信息主要来源于发表的文献和数据库，包括 RiceSRTFDB (The Rice Stress-Responsive Transcription Factor Database, http://www.nipgr.res.in/RiceSRTFDB.html)、GEO (Gene Expression Omnibus, http://www.ncbi.nlm.nih.gov/geo/)、MPSS (Massively Parallel Signature Sequencing, http://mpss.udel.edu/rice/)和 RiceXPro (Rice gene coexpression database, http://ricexpro.dna.affrc.go.jp/)等。通过人工阅读文献和检索数据库，将不同数据平台产生的水稻 *WRKY* 基因的原始转录数据汇总，根据原文的描述和具体的转录数据，将 *WRKY* 基因的转录水平记作表达(Expression, E)或不表达(No expression, NE)、上调(Up)或下调(Down, Dn)；对于同一个 *WRKY* 基因，如果不同数据平台的分析结果不一致，则同时记录；原文中只标注为差异表达基因，而未具体指明上调或下调，则标注为 DE(Differential expression)。

3　水稻 *WRKY* 基因的转录特征

水稻 *WRKY* 基因与逆境胁迫、生长发育、激素处理、营养吸收以及衰老和损伤修复等过程有关，水稻 *WRKY* 基因家族在不同生物学反应中的转录变化信息见附表 1，这种基于转录的注释提供了一个全基因家族水平的整体视野。

3.1　*WRKY* 基因与生物胁迫

WRKY 家族成员广泛参与植物的抗病及防卫反应，全基因组基因芯片和 Deep-seq 测序数据表明，当水稻受到病原菌等侵染时，多个 *WRKY* 基因的转录水平发生显著变化(表 1)。在细菌性病害中，白叶枯病菌(*Xanthomonas oryzae* pv.*oryzae*)侵染后鉴定到 28 个 *WRKY* 基因的转录水平发生变化[9,12~20]，条斑病菌(*X. oryzae* pv.*oryzicola*)[13,15,17]和鞘腐病菌(*Pseudomonas syringae* pv. tomato)[21]侵染后，分别有 13 个和 1 个 *WRKY* 基因发生转录水平变化。在真菌性病害中，稻瘟病菌(*Magnaporthe oryzae*)侵染后鉴定到 49 个 *WRKY* 基因的转录水平发生变化[2,9,17,22~30]，

表 1 生物胁迫诱导差异转录的 *WRKY* 基因

Table 1 Differentially expressed rice *WRKY* genes under biotic stresses

生物胁迫	*WRKY* 基因	数目	参考文献
白叶枯病菌(*Xanthomonas oryzae* pv.*oryzae*)	4, 7, 10, 11, 12, 13, 30, 32, 40, 42, 45, 50, 51, 52, 53, 57, 62, 65, 67, 69, 70, 71, 76, 81, 88, 90, 96, 119	28	[9, 12~20]
条斑病菌(*X. oryzae* pv.*oryzicola*)	1, 8, 9, 19, 20, 23, 28, 45, 50, 72, 76, 95, 109	13	[13, 15, 17]
鞘腐病菌(*Pseudomonas syringae* pv. tomato)	77	1	[21]
稻瘟病菌(*Magnaporthe oryzae*)	2, 4/122, 7, 10, 11, 12, 13, 14, 15, 19, 21, 22, 23, 24, 26/59, 28, 30, 39, 40, 45, 47, 50, 51, 53, 55, 56, 62, 64, 65, 67, 69, 70, 71, 72, 73, 74, 76, 77, 79, 81, 89, 94, 95, 96, 104, 107, 108, 111, 118	49	[2, 9, 17, 22~30]
纹枯病菌(*Rhizoctonia solani*)	30, 45, 89	3	[25, 31]
白粉病菌(*Blumeria graminis*)	24, 47	2	[22]
稻曲病菌(*Ustilaginoidea virens*)	72	1	[32]
水稻矮缩病毒(Rice dwarf virus)	1, 3, 6, 7, 8, 11, 12, 13, 14, 19, 28, 32, 35, 40, 45, 49, 53, 55, 57, 62, 64, 65, 71, 73, 74, 76, 77, 79, 80, 82, 95, 102, 104, 107, 108, 111	36	[33, 34]
水稻条纹叶枯病毒(Rice stripe virus)	28, 45, 53, 62, 71	5	[13, 31]
白背飞虱(*Sogatella furcifera*)	45, 68, 71, 95, 104	5	[29]
褐飞虱(*Nilaparvata lugens*)	79	1	[35]
稻纵卷叶螟(*Cnaphalocrocis medinalis*)	53, 70	2	[37]
二化螟(*Chilo suppressalis*)	70	1	[36]

注：下划线表示在不同病原菌侵染后共同表达的基因。

纹枯病菌(*Rhizoctonia solani*)侵染后鉴定到 3 个 *WRKY* 基因的转录水平发生变化[25,31]，白粉病菌(*Blumeria graminis*)侵染后有 2 个 *WRKY* 基因表达上调[22]，稻曲病菌(*Ustilaginoidea virens*)侵染后有 1 个 *WRKY* 基因的转录水平发生变化[32]。在病毒病害中，矮缩病毒侵染后 36 个 *WRKY* 基因的转录水平发生变化[33,34]，与条纹病毒侵染相关的有 5 个 *WRKY* 基因[13,31]。*WRKY* 基因还参与了虫害的防御，在白背飞虱(*Sogatella furcifera*)、褐飞虱(*Nilaparvata lugens*)、稻纵卷叶螟(*Cnaphalocrocis medinalis Guenee*)和二化螟(*Chilo suppressalis*)的侵染过程中也都有 *WRKY* 基因转录水平变化的报道[29,35~37]。此外，激发子[23]和寄生杂草独脚金(*Striga*)等[13]也能诱导水稻 *WRKY* 基因表达(附表 1)。因此可以推测，在水稻受到生物逆境胁迫时，通常有多个 *WRKY* 基因协同发挥调控作用。

稻瘟病、白叶枯病和纹枯病是水稻三大主要病害，汇总表 1 的数据可见在水稻受到病原菌侵染过程中分别有 49、28 和 3 个 *WRKY* 基因发生转录水平的改变，其中 *WRKY30* 和 *WRKY45* 在 3 大病害中的表达都发生了变化。综合比较还发现，在细菌、真菌、病毒和害虫侵染后，*WRKY13*、*WRKY 30*、*WRKY 45*、*WRKY 53* 和 *WRKY 71* 基因的转录水平均发生了变化(表 1，下划线表示)。由此可见，一个 *WRKY* 基因可参与多个水稻-病原物互作过程，对数据的综合分析可为转录因子的功能研究提供线索。

转基因实验提供了 *WRKY* 基因在抗病反应中发挥作用的直接证据。超表达 *WRKY13*[27]、*WRKY45-2*[17]、*WRKY71*[19]基因以及同时超表达 4 个 *WKRY* (*62*、*28*、*71* 和 *76*)基因[38]都能提高水稻对白叶枯病的抗性，而单独超表达 *WRKY45-1*、*WRKY62* 或 *WRKY76*[17,18]基因的水稻对白叶枯病的抗性降低。超表达 *WRKY22*[14]、*WRKY45-1*、*WRKY45-2*[17]、*WRKY47*[24]、*WRKY53*[28]、*WRKY55*(原文编号为 *WRKY31*)[26]或 *WRKY104*(原文编号为 *WRKY89*)[29]基因提高了水稻对稻瘟病的抗性，而 *WRKY28*[23]和 *WRKY76*[39]基因的超表达使水稻更易感稻瘟病。另外超表达 *WRKY30* 的转基因水稻同时提高了对稻瘟病和纹枯病的抗性[25]。超表达 *WRKY45* 基因的水稻对稻瘟病的抗性增强，但减弱了对纹枯病的抗性[30]。

3.2 *WRKY* 基因与非生物胁迫

植物在生长过程中经常要面对多种非生物逆境的胁迫，本文对干旱、高盐、高温/低温、极端 pH 和重金属等条件下的差异转录 *WRKY* 基因进行了汇

总(表 2)。通过控制土壤中的可利用水分(Available water content)和土壤可蒸发水分(Fraction of transpirable soil water)进行缺水处理，在耐旱和不耐旱水稻材料中发现了多个差异表达的 *WRKY* 基因[40,41]。利用聚乙二醇和甘露醇[8,35,42,43]进行拟旱处理也分别鉴定到多个 *WRKY* 基因参与。干旱胁迫共涉及 62 个 *WRKY* 基因(表 2)[8,13,35,40,41,44~49]。超表达 *WRKY30* 基因增加了水稻的抗旱性[47]，对 *WRKY47* 基因的超表达和敲除实验证明了该基因是水分胁迫的负调控因子[50]。此外在淹水条件下有 7 个 *WRKY* 基因发生转录水平的变化[35]。

土壤盐渍化是限制作物产量的因素之一。用高浓度的 NaCl 处理水稻幼苗，鉴定到 35 个 *WRKY* 基因的转录水平发生变化(表 2)[13,22,42~44,46,51,52]。转基因实验表明，超表达 *WRKY13*[16,46]或 *WRKY45-2*[52]基因的水稻对高盐更敏感。

合适的温度是植物生长发育过程中最为重要的环境条件之一。目前的数据表明, 高温(37℃、40℃和 42℃)导致 15 个 *WRKY* 基因的转录水平发生改变[13,43,49,53]，低温(4℃和 10℃)条件下有 31 个 *WRKY* 基因的转录水平发生改变(表 2)[13,35,42,51,53]。在 4℃处理时, *WKRY42* 和 *WRKY* 77 基因的转录水平明显上调，*WRKY28*、*WRKY 47*、*WRKY 71* 和 *WRKY 95* 则明显下调(附表 1)[35]。

此外，在 pH[35]、光照[20,54]、紫外线[29]、机械损伤[19,20,31]、甲醇[55]、臭氧[35]、过氧化氢[35,53]、阿魏酸[54]、联二-N-甲基吡啶[44,56]和重金属[57,58]等胁迫处理中的相关 *WRKY* 基因见表 2。

利用生物信息学对水稻基因表达数据进行分析，发现特定胁迫处理后表达发生变化的 *WRKY* 基因成员可能处于同一调控网络中[8]。另外植物在应对不同的逆境胁迫时，也有共同的转录因子参与，例如 *WRKY45* 基因在干旱、盐、水淹、冷、热和 pH 等胁迫下均发生表达变化(表 2)，提示其功能的重要性。

3.3　激素处理诱导的差异转录 *WRKY* 基因

激素对植物的生长、发育、衰老、休眠和抗逆性等具有调节作用。目前，已有多篇关于在不同激素处理下水稻 *WRKY* 基因转录特征的报道(表 3)。生

表 2　非生物胁迫诱导差异转录的 *WRKY* 基因

Table 2　Differentially expressed rice *WRKY* genes under abiotic stresses

非生物胁迫	*WRKY* 基因	数目	参考文献
干旱或模拟干旱	1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 14, 19, 20, 23, 24, 26/59, 28, 29, 30, 35, 42, 43, 45, 46/91, 47, 49, 50, 51 53, 58, 61/103, 62, 67, 68, 69, 70, 71, 72, 74, 75, 76, 77, 79, 81, 82, 84, 88, 89, 90, 94, 95, 96, 97, 102, 105, 113, 114, 115, 117	62	[8, 13, 35, 40, 41, 44~49]
水淹	1, 28, 42, 45, 47, 76, 95	7	[35]
氯化钠	3, 5, 7, 8, 10, 12, 13, 23, 24, 28, 45, 46/91, 47, 49, 50, 53, 55, 61/103, 62, 67, 69, 70, 71, 72, 82, 87, 88, 89, 94, 95, 96, 104, 107, 113, 121	35	[13, 22, 42~44, 46, 51, 52]
热(37℃、40℃、42℃)	7, 11, 12, 13, 17, 24, 28, 42, 45, 53, 71, 72, 89, 95, 104	15	[13, 43, 49, 53]
冷(4℃、10℃)	1, 12, 17, 21, 24, 26/59, 28, 39, 42, 45, 47, 50, 51, 53, 55, 62, 66, 67, 68, 71, 72, 74, 76, 77, 79, 82, 87, 95, 102, 104, 113	31	[13, 35, 42, 51, 53]
酸度(pH)	2, 12, 19, 21, 28, 30, 45, 57, 62, 76, 77	11	[35]
光照	12, 23	2	[20, 54]
紫外线	104	1	[29]
损伤	12, 30, 71, 90, 104	5	[19, 20, 31]
甲醇	7, 14, 19, 26/59, 28, 72	6	[55]
臭氧	1, 19, 24, 28, 39, 57, 68, 69, 71, 72, 76, 77, 79	13	[35]
过氧化氢	8, 17, 24, 42, 71	5	[35, 53]
阿魏酸	4/122, 10, 14, 19, 24, 28, 29, 37, 49, 50, 62, 66, 71, 72, 74, 79, 87, 88, 104	19	[54]
联二-N-甲基吡啶	9, 62, 76, 109	4	[44, 56]
汞	24, 30, 53, 70	4	[57]
铬	6, 9, 11, 14, 19, 23, 37, 66, 72, 76, 84, 104	12	[58]

表 3 激素处理诱导差异转录的 *WRKY* 基因

Table 3 Differentially expressed rice *WRKY* genes under different phytohomone treatments

激素	*WRKY* 基因	数目	参考文献
生长素、萘乙酸、2,4-二氯苯氧乙酸	1, 8, 9, 10, 17, 19, 34, 45, 47, 50, 62, 64, 67, 72, 76, 79, 84	17	[41~43]
赤霉素	3, 11, 12, 24, 34, 50, 51, 53, 58, 61/103, 62, 68, 70, 71, 76, 104, 113, 117	18	[6, 7, 31, 41, 42, 59, 60]
脱落酸	8, 9, 10, 11, 12, 17, 23, 24, 29, 30, 34, 39, 42, 43, 45, 46/91, 51, 53, 55, 58, 68, 70, 71, 72, 74, 84, 87, 88, 95, 102, 105, 107, 113	33	[6, 41~43, 48, 49, 52, 59, 60]
1-氨基环丙烷-1-羧酸、乙烯利	12, 13, 45, 71, 104	5	[19, 20, 31]
油菜素内酯	45	1	[61]
水杨酸、2,6-二氯异烟酸、苯并噻二唑 S-甲基酯	1, 10, 11, 12, 13, 15, 19, 21, 23, 24, 26/59, 28, 29, 30, 40, 42, 43, 45, 46/91, 49, 50, 51, 53, 54, 58, 61/103, 62, 64, 67, 69, 71, 72, 74, 76, 77, 79, 94, 95, 96, 97, 102, 104, 105, 113, 114, 117	46	[9, 19~21, 30, 41, 42, 48, 54, 62]
茉莉酸、茉莉酸甲酯	1, 7, 9, 10, 11, 12, 13, 15, 24, 26/59, 28, 29, 30, 40, 42, 43, 45, 49, 50, 53, 58, 61/103, 62, 64, 71, 72, 76, 84, 89, 94, 95, 96, 102, 104, 105, 113, 114, 117	38	[9, 19, 31, 41, 42, 63]

注：下划线表示 ABA、SA 和 JA 途径中共同表达的基因。

长素、萘乙酸(1-Naphthaleneacetic acid, NAA)和 2,4-二氯苯氧乙酸(2,4-Dichlorophenoxyacetic acid 2,4-D)处理引起 17 个 *WRKY* 基因的转录水平发生变化[41~43]。赤霉素处理后有 18 个水稻 *WRKY* 基因的转录水平发生变化[6,7,31,41,42,59,60]，*WRKY71* 基因是赤霉素信号传导过程中的转录抑制因子[7]。脱落酸(Abscisic acid, ABA)处理后有 33 个水稻 *WRKY* 基因的转录水平发生变化[6,41~43,48,49,52,59,60]，在 ABA 信号途径中，*WRKY45-1* 是负调控因子，而 *WRKY45-2* 是正调控因子[52]；水稻糊粉层细胞中的 *WRKY24*、*WRKY51*、*WRKY71* 和 *WRKY72* 受 ABA 诱导表达[6]。利用乙烯(Ethylene, ET)生物合成的前体 1-氨基环丙烷-1-羧酸(1-aminocyclopropane-1-carboxylic acid, ACC)或乙烯利(Ethrel)处理水稻，发现 5 个 *WRKY* 基因发生了转录水平的变化[19,20,31]。油菜素内酯(Brassinosteroids, BRs)处理后 *WRKY45* 的表达下调[61]。

水杨酸(Salicylic acid, SA)和茉莉酸(Jasmonic acid, JA)等信号分子能够激活植物体内防御基因的表达，从而使植物表现出对生物胁迫的抗性反应。研究发现，46 个 *WRKY* 基因在 SA、苯并噻二唑 S-甲基酯(Benzothiadiazole, BTH)或 2,6-二氯异烟酸(2,6-dichloroisonicotinic acid, INA)处理后转录水平发生改变[9,19~21,30,41,42,48,54,62]。茉莉酸及其甲酯(Methyl jasmonate, MeJA)是存在于高等植物体内的内源生长调节物质，38 个 *WRKY* 基因在 JA 或 MeJA 处理后转录水平发生变化[9,19,31,41,42,63]。

在植物防御信号网络中，SA 和 JA/ET 信号路径之间存在紧密联系。比较 SA 和 JA/ET 信号转导途径中的 *WRKY* 基因，发现大多数 *WRKY* 基因共同参与了上述两个途径，表明 SA 和 JA/ET 信号转导途径之间存在关联(Crosstalk)。ABA 是生物与非生物胁迫反应交叉的重要调控者，在 ABA、SA 和 JA/ET 途径中共同表达的 WRKY 基因有 16 个(表 3，下划线标示)。其他激素也与 SA 和 JA/ET 途径相连，参与调控植物-病原菌互作。

3.4 *WRKY* 基因与水稻的生长发育

对水稻的转录谱研究发现，在根中表达的 *WRKY* 基因有 19 个[12,19,31,41,48,49,54]，茎中有 8 个[12,19,31,41,48]，叶片中有 22 个[19,31,41,43,46,64]，穗子中有 19 个[19,31,41]，籽粒中有 5 个[31,48,59](表 4)。比较可见，在根和叶片中共同表达的 *WRKY* 基因有 9 个(表 4，下划线标示)，*WRKY30* 和 *WRKY71* 存在于根、茎、叶片、穗子和种子中[19,31]，*WRKY42*、*WRKY43* 和 *WRKY105* 在根、茎、叶和穗子中都表达[41]。由此可见，在水稻正常生长发育的各个环节均有 *WRKY* 基因参与，有些 *WRKY* 基因同时参与多个组织的生长发育调控。

部分 *WRKY* 基因的表达具有组织特异性，如 *WRKY79* 只在穗子中表达，在根、茎和叶片中不表达，而 *WRKY58* 则相反[41]，提示它们可能只参与营

表 4　水稻 *WRKY* 基因在生长发育过程中的表达特征

Table 4　Transcription features of rice *WRKY* genes at different growth and development processes

组织	*WRKY* 基因	数目	参考文献
根	9, 11, 12, 15, 21, 22, 23, 30, 37, 42, 45, 58, 66, 71, 88, 89, 96, 113, 116	19	[12, 19, 31, 41, 48, 49, 54]
茎	30, 34, 36, 42, 58, 71, 89, 102	8	[12, 19, 31, 41, 48]
叶	1, 8, 12, 13, 23, 24, 30, 42, 43, 45, 50, 53, 55, 58, 69, 71, 72, 74, 81, 89, 108, 113	22	[19, 31, 41, 43, 46, 64]
穗子	3, 22, 29, 30, 34, 36, 42, 55, 66, 68, 71, 75, 79, 88, 89, 96, 102, 115, 116	19	[19, 31, 41]
籽粒	30, 51, 71, 87, 89	5	[31, 48, 59]

注：下划线表示在根和叶片中共同表达的基因。

表 5　在水稻营养吸收过程中差异转录的 *WRKY* 基因

Table 5　Differentially expressed rice *WRKY* genes in nutrient absorption processes

营养元素	*WRKY* 基因	数目	参考文献
N	1, 8, 10, 13, 16, 21, 23, 25/44, 45, 46/91, 53, 62, 67, 71, 74, 76, 95, 104, 109	19	[50, 73]
P	7, 10, 11, 14, 19, 23, 24, 26/59, 28, 42, 45, 49, 53, 62, 66, 67, 70, 71, 72, 76,79, 108, 109, 113, 125	25	[73, 74]
K	7, 10, 19, 28, 50, 64, 65, 67, 76, 105	10	[73]
Fe	11, 17, 19, 23, 27, 28, 35, 40, 45, 46/91, 55, 62, 64, 71, 72, 73, 90, 97, 113	19	[45]

注：下划线表示 N、P、K 吸收过程中共同表达的基因。

养生长或生殖生长的调控。在水稻品种明恢 63 中，*WRKY*22 和 *WRKY116* 在根中特异表达，*WRKY66* 则在穗中高表达[41]。*WRKY72* 在幼苗根部表达较强而在成株期根部几乎不表达，提示该基因在生长旺盛的部位表达较强[42]。*WRKY24*、*WRKY 51* 和 *WRKY 71* 均存在于糊粉层细胞中, 参与种子的发育(附表 1)[6]。调查水稻旗叶从基部到叶尖不同部位的基因表达谱, 发现有 15 个 *WRKY* 基因在叶片中呈现梯度表达[65]。*WRKY* 基因在幼苗中的表达受昼夜节律的影响[66], *WRKY* 基因还与水稻落粒[67]、向重力性[68]和种子萌发[69]有关。总之，*WRKY* 基因具有表达的时空特异性，在多个生长发育过程中发挥重要作用。

转基因实验也提供了 *WRKY* 基因在水稻生长发育中的功能的数据，水稻 *WRKY11* 的超表达突变体呈现卷叶表型、抽穗时间晚[70]，超表达 *WRKY13* 的转基因水稻开花时间延迟、株高降低[16]，超表达 *WRKY55*(原文编号为 *WRKY31*)的转基因水稻侧根数目减少[26]，*WRKY87*(原文编号为 *WRKY78*)超表达的水稻植株茎秆伸长[71]，超表达 *WRKY104*(原文编号为 *WRKY89*)的转基因水稻生长迟缓、株高降低[29]。

衰老是植物生长发育的最终阶段，*WRKY42* 在幼嫩的叶片中不表达，在衰老的叶片中表达上调，超表达 *WRKY42* 的水稻植株表现为叶片早衰，并伴随着活性氧积累和叶绿素下降[64]。*WRKY23* 主要在水稻衰老叶片中表达[54], *WRKY4* 和 *WRKY89* 在水稻旗叶衰老早期被诱导表达[72]。

3.5　*WRKY* 基因与营养吸收

氮、磷、钾是植物营养的三大主要元素，是植物正常生长和代谢过程不可缺少的。当水稻缺乏氮、磷、钾时，发现分别有 19 个[50,73]、25 个[73,74]和 10 个[73]*WRKY* 基因的转录水平发生变化, 其中 *WRKY10*、*WRKY67* 和 *WRKY76* 共同参与了氮、磷、钾营养的调控(表 5，下划线标示)。在氮饥饿的叶鞘中有 12 个 *WRKY* 表达上调，根中则没有[50]。铁是植物必需营养元素，过量 Fe^{2+}处理水稻幼苗，有 19 个 *WRKY* 基因的转录水平发生变化[45]。

此外，*WRKY* 还参与多个代谢途径的调控。在糖代谢中，水稻 *WRKY24*、*WRKY51*、*WRKY71* 与 α-淀粉酶基因的转录有关[6,7], *WRKY62*、*WRKY67* 和 *WRKY45* 在蔗糖饥饿时的转录水平发生变化[75]，*WRKY87*(原文编号为 *WRKY34*)与支链淀粉合成有关(附表 1)[76]。在水稻-固氮螺菌(*Azospirillum ligoferum*)的互作中，鉴定到多个转录水平改变的 *WRKY* 基因(附表 1)[77]。

4 WRKY 转录因子的表达调控

WRKY 转录因子能够特异地与下游靶基因的调控元件结合，进而激活其转录。W-box(即(T)(T)TGAC(C/T)序列)，在受病原菌诱导或与植物防卫反应有关的基因中出现频率较高[1]。WRKY71 可与 W-box 特异结合，超表达 *WRKY71* 能提高白叶枯病抗性[19]。WRKY53 特异性结合 W-box，在受稻瘟病菌侵染后超表达 *WRKY53* 的植株中 *PBZ1(PR10a)*的表达量升高[28]。WRKY13 与 *PR1a* 的 W-box 特异结合，超表达植株对白叶枯病的抗性提高[27]。WRKY70(原文编号为 WRKY52)与 *PR1a* 的 W-box 特异结合，且在稻瘟病菌侵染后诱导表达[78]。另外与抗病相关的 WRKY28[23]、WRKY42[12]、WRKY51(原文编号为 WRKY6)[62]和 WRKY104(原文编号为 WRKY89)[63]都能与 W-box 特异性结合，而当 W-box 的碱基被改变时其与 W-box 的结合能力减弱甚至丧失。由此可见，WRKY 作为植物防御反应中的重要转录因子，通过与下游基因的顺式元件结合从而发挥其抗病调控功能。

WKRY 与 W-box 的结合还能调控其它的生物学过程。如水稻 WRKY24 和 WRKY71 都能与 α-淀粉酶基因 *Amy32b* 的 W-box 序列特异结合，抑制该基因的转录[7]。WRKY14 结合到色氨酸合成酶基因 *TSa* 和色氨酸脱羧酶基因 *TDC1* 启动子区域的 W-box 序列，在 Trp 及其次生衍生物的生物合成中发挥关键作用[55]。WRKY42 与金属硫蛋白基因 *OsMT1d* 中的 W-box 结合，抑制其介导的活性氧清除系统的表达，从而加速了叶片的衰老[64]。总之，WRKY 作为转录因子，其功能发挥往往是通过与下游元件的相互作用发生的。

值得指出的是，一些 *WRKY* 基因自身的启动子上游也存在 W-box 或类 W-box 序列，如 *WRKY10*、*WRKY13*、*WRKY14*、*WRKY24*、*WRKY42*、*WRKY45*、*WRKY51*、*WRKY53*、*WRKY68*、*WRKY71* 和 *WRKY74* 等基因[12,27,53]。WRKY13 通过结合到其自身的类 W-box(TTGAC)上抑制其自身基因表达，说明 *WRKY13* 通过自我转录抑制，使其基因在叶片中维持低表达水平[27,46]。*WRKY53* 有 3 个串联的 W-box 序列，它们都参与了激发子诱导的或基础启动子的活性调节[79]。在水稻-稻瘟病菌互作过程中，*WRKY45-2* 转录激活 *WRKY13*，*WRKY13* 可以抑制 *WRKY42*，而 *WRKY42* 通过抑制 JA 途径相关基因，负调控水稻抗稻瘟病的抗性[80]。这些结果显示，在植物的防御系统中，WRKY 不仅与下游基因相互作用，而且 *WRKY* 基因之间甚至自身也可以自我调节，实现对抗病过程的调控。

WRKY 作为抗病信号转导途径的重要成员，位于 MAPK 的下游。有研究表明，WRKY19 表达受 MAPK3/6 磷酸化的调控[81]，WRKY30 被 MPK3、MPK7 和 MPK14 磷酸化[47]，WRKY45 在体外被 MPK4 和 MPK6 磷酸化[82]，WRKY53 被 MPK1 磷酸化[83]，WRKY81(原文编号为 WRKY33)被 BWMK1(MAPK)磷酸化后参与 SA 介导的抗病反应[84]。

5 结语与展望

WRKY 是一类重要的水稻转录因子，了解 WRKY 家族成员的功能及其调控网络是科研人员长期工作的目标。目前的高通量测序技术和转录数据的积累为人们提供了有价值的信息，但是 WRKY 的转录谱数据分布于不同的文献和数据库中，基于转录信息的注释需要人工介入，该过程耗时且效率不高，而且不同实验室、不同水稻品种和不同技术平台采集的数据难以直接比较。如能建立共同的内参或数据质量控制标准，对数据进行有效且自动的归一化，将有助于数据的客观比较。另外受水稻转化效率的影响，目前高通量测序获得的数据的生物学意义还难以逐一验证。

随着高通量测序技术的进步，转录数据的积累将呈几何级数增加，为了清晰地展示结果，需要生物信息学专家设计专门的软件承载这些数据并进行自动化的挖掘和比较，而分子生物学家可以在此基础上更有目的性地采用反向遗传学策略展开功能研究。

附 录：

附表 1 见电子版 www.chinagene.cn。

参考文献(References)：

[1] Eulgem T, Rushton PJ, Robatzek S, Somssich IE. The WRKY superfamily of plant transcription factors. *Trends Plant Sci*, 2000, 5(5): 199–206.[DOI]

[2] Kim CY, Lee SH, Park HC, Bae CG, Cheong YH, Choi YJ, Han CD, Lee SY, Lim CO, Cho MJ. Identification of rice blast fungal elicitor-responsive genes by differential display analysis. *Mol Plant Microbe Interact*, 2000, 13(4): 470–474. [DOI]

[3] Cheng HT, Wang SP. WRKY-type transcription factors: a significant factor in rice-pathogen interactions. *Sci Sin Vitae*, 2014, 44(8): 784–793.
成洪涛, 王石平. 水稻-病原互作中的重要角色: WRKY 类转录因子. 中国科学: 生命科学, 2014, 44(8): 784–793. [DOI]

[4] Ross CA, Liu Y, Shen QJ. The *WRKY* gene family in rice (*Oryza sativa*). *J Int Plant Biol*, 2007, 49(6): 827–842. [DOI]

[5] Tian Y, Lu XY, Peng LS, Fang J. The structure and function of plant WRKY transcription factors. *Hereditas (Beijing)*, 2006, 28(12): 1607–1612. [DOI]
田云, 卢向阳, 彭丽莎, 方俊. 植物 WRKY 转录因子结构特点及其生物学功能. 遗传, 2006, 12(12): 1607–1612.

[6] Xie Z, Zhang ZL, Zou XL, Huang J, Ruas P, Thompson D, Shen QJ. Annotations and functional analyses of the rice *WRKY* gene superfamily reveal positive and negative regulators of abscisic acid signaling in aleurone cells. *Plant Physiol*, 2005, 137(1): 176–189. [DOI]

[7] Zhang ZL, Xie Z, Zou XL, Casaretto J, Ho THD, Shen QJ. A rice *WRKY* gene encodes a transcriptional repressor of the gibberellin signaling pathway in aleurone cells. *Plant Physiol*, 2004, 134(4): 1500–1513. [DOI]

[8] Berri S, Abbruscato P, Faivre-Rampant O, Brasileiro ACM, Fumasoni I, Satoh K, Kikuchi S, Mizzi L, Morandini P, Pè ME, Piffanelli P. Characterization of WRKY co-regulatory networks in rice and *Arabidopsis*. *BMC Plant Biol*, 2009, 9: 120. [DOI]

[9] Ryu HS, Han M, Lee SK, Cho JI, Ryoo N, Heu S, Lee YH, Bhoo SH, Wang GL, Hahn TR, Jeon JS. A comprehensive expression analysis of the *WRKY* gene superfamily in rice plants during defense response. *Plant Cell Rep*, 2006, 25(8): 836–847. [DOI]

[10] Qiu YP, Jing SJ, Fu J, Li L, Yu DQ. Cloning and analysis of expression profile of 13 *WRKY* genes in rice. *Chin Sci Bull*, 2004, 49(18): 1860–1869.
仇玉萍, 荆邵娟, 付坚, 李璐, 余迪求. 13 个水稻 WRKY 基因的克隆及其表达谱分析. 科学通报, 2004, 49(18): 1860–1869. [DOI]

[11] Rice WRKY Working Group. Nomenclature report on rice WRKY's - Conflict regarding gene names and its solution. *Rice*, 2012, 5: 3. [DOI]

[12] Miao LY, Zhou L, Yang S, Li LY, Li XJ, Fan W, Lan JP, Shi JN, Liu LJ, Liu GZ. Characterization of transcription, expression and binding properties with W-box of rice transcription factor *WRKY42* gene. *Prog Biochem Biophys*, 2014, 41(7): 682–692.
缪刘杨, 周亮, 杨烁, 李莉云, 李雪姣, 范伟, 兰金苹, 史佳楠, 刘丽娟, 刘国振. 水稻转录因子 *WRKY42* 的转录、表达及其与 W-box 的结合特征分析. 生物化学与生物物理进展, 2014, 41(7): 682–692. [DOI]

[13] Narsai R, Wang C, Chen J, Wu JL, Shou HX, Whelan J. Antagonistic, overlapping and distinct responses to biotic stress in rice (*Oryza sativa*) and interactions with abiotic stress. *BMC Genomics*, 2013, 14: 93–113. [DOI]

[14] Abbruscato P, Nepusz T, Mizzi L, Del Corvo M, Morandini P, Fumasoni I, Michel C, Paccanaro A, Guiderdoni E, Schaffrath U, Morel JB, Piffanelli P, Faivre-Rampant O. *OsWRKY22*, a monocot *WRKY* gene, plays a role in the resistance response to blast. *Mol Plant Pathol*, 2012, 13(8): 828–841. [DOI]

[15] Grewal RK, Gupta S, Das S. *Xanthomonas oryzae* pv *oryzae* triggers immediate transcriptomic modulations in rice. *BMC Genomics*, 2012, 13: 49. [DOI]

[16] Qiu DY, Xiao J, Xie WB, Liu HB, Li XH, Xiong LZ, Wang SP. Rice gene network inferred from expression profiling of plants overexpressing OsWRKY13, a positive regulator of disease resistance. *Mol Plant*, 2008, 1(3): 538–551. [DOI]

[17] Tao Z, Liu HB, Qiu DY, Zhou Y, Li XH, Xu CG, Wang SP. A pair of allelic *WRKY* genes play opposite roles in rice-bacteria interactions. *Plant Physiol*, 2009, 151(2): 936–948. [DOI]

[18] Peng Y, Bartley LE, Chen XW, Dardick C, Chern M, Ruan R, Canlas PE, Ronald PC. OsWRKY62 is a negative regulator of basal and *Xa21*-mediated defense against *Xanthomonas Oryzae* pv. *Oryzae* in rice. *Mol Plant*, 2008, 1(3): 446–458. [DOI]

[19] Liu XQ, Bai XQ, Wang XJ, Chu CC. OsWRKY71, a rice transcription factor, is involved in rice defense response. *J Plant Physiol*, 2007, 164(8): 969–979. [DOI]

[20] Liu XQ, Bai XQ, Qian Q, Wang XJ, Chen MS, Chu CC. OsWRKY03, a rice transcriptional activator that functions in defense signaling pathway upstream of OsNPR1. *Cell Res*, 2005, 15(8): 593–603. [DOI]

[21] Lan A, Huang J, Zhao W, Peng Y, Chen Z, Kang D. A salicylic acid-induced rice (*Oryza sativa* L.) transcription factor OsWRKY77 is involved in disease resistance of *Arabidopsis thaliana*. *Plant Biol*, 2013, 15(3): 452–461. [DOI]

[22] Shaik R, Ramakrishna W. Genes and co-expression modules common to drought and bacterial stress responses in *Arabidopsis* and rice. *PLoS One*, 2013, 8(10): e77261. [DOI]

[23] Chujo T, Miyamoto K, Shimogawa T, Shimizu T, Otake Y, Yokotani N, Nishizawa Y, Shibuya N, Nojiri H, Yamane H, Minami E, Okada K. OsWRKY28, a PAMP-responsive transrepressor, negatively regulates innate immune responses in rice against rice blast fungus. *Plant Mol Biol*, 2013, 82(1–2): 23–37. [DOI]

[24] Wei T, Ou B, Li JB, Zhao Y, Guo DS, Zhu YY, Chen ZL, Gu HY, Li CY, Qin GJ, Qu LJ. Transcriptional profiling of rice early response to *Magnaporthe oryzae* identified OsWRKYs as important regulators in rice blast resistance. *PLoS One*, 2013, 8(3): e59720. [DOI]

[25] Peng XX, Hu YJ, Tang XK, Zhou PL, Deng XB, Wang HH, Guo ZJ. Constitutive expression of rice *WRKY30* gene increases the endogenous jasmonic acid accumulation, *PR* gene expression and resistance to fungal pathogens in rice. *Planta*, 2012, 236(5): 1485–1498. [DOI]

[26] Zhang J, Peng YL, Guo ZJ. Constitutive expression of pathogen-inducible *OsWRKY31* enhances disease resistance and affects root growth and auxin response in transgenic rice plants. *Cell Res*, 2008, 18(4): 508–521. [DOI]

[27] Qiu DY, Xiao J, Ding XH, Xiong M, Cai M, Cao YL, Li XH, Xu CG, Wang SP. OsWRKY13 mediates rice disease resistance by regulating defense-related genes in salicylate- and jasmonate-dependent signaling. *Mol Plant Microbe Interact*, 2007, 20(5): 492–499. [DOI]

[28] Chujo T, Takai R, Akimoto-Tomiyama C, Ando S, Minami E, Nagamura Y, Kaku H, Shibuya N, Yasuda M, Nakashita H, Umemura K, Okada A, Okada K, Nojiri H, Yamane H. Involvement of the elicitor-induced gene OsWRKY53 in the expression of defense-related genes in rice. *Biochim Biophys Acta*, 2007, 1769(7–8): 497–505. [DOI]

[29] Wang HH, Hao JJ, Chen XJ, Hao ZN, Wang X, Lou YG, Peng YL, Guo ZJ. Overexpression of rice WRKY89 enhances ultraviolet B tolerance and disease resistance in rice plants. *Plant Mol Biol*, 2007, 65(6): 799–815. [DOI]

[30] Shimono M, Sugano S, Nakayama A, Jiang CJ, Ono K, Toki S, Takatsuji H. Rice WRKY45 plays a crucial role in benzothiadiazole-inducible blast resistance. *Plant Cell*, 2007, 19(6): 2064–2076. [DOI]

[31] Peng XX, Tang XK, Zhou PL, Hu YJ, Deng XB, He Y, Wang HH. Isolation and expression patterns of rice WRKY82 transcription factor gene responsive to both biotic and abiotic stresses. *Agric Sci China*, 2011, 10(6): 893–901. [DOI]

[32] Chao JQ, Jin J, Wang D, Han R, Zhu RS, Zhu YG, Li SQ. Cytological and transcriptional dynamics analysis of host plant revealed stage-specific biological processes related to compatible rice-*Ustilaginoidea virens* interaction. *PLoS One*, 2014, 9(3): e91391. [DOI]

[33] Yang L, Du ZG, Gao F, Wu KC, Xie LH, Li Y, Wu ZJ, Wu JG. Transcriptome profiling confirmed correlations between symptoms and transcriptional changes in RDV infected rice and revealed nucleolus as a possible target of RDV manipulation. *Virol J*, 2014, 11: 81. [DOI]

[34] Satoh K, Shimizu T, Kondoh H, Hiraguri A, Sasaya T, Choi IR, Omura T, Kikuchi S. Relationship between symptoms and gene expression induced by the infection of three strains of *rice dwarf virus*. *PLoS One*, 2011, 6(3): e18094. [DOI]

[35] Satoh K, Saji S, Ito S, Shimizu H, Saji H, Kikuchi S. Gene response in rice plants treated with continuous fog influenced by pH, was similar to that treated with biotic stress. *Rice*, 2014, 7(1): 10. [DOI]

[36] Li R, Zhang J, Li JC, Zhou GX, Wang Q, Bian WB, Erb M, Lou YG. Prioritizing plant defence over growth through WRKY regulation facilitates infestation by non-target herbivores. *Elife*, 2015, 4: e04805. [DOI]

[37] Ye M, Song YY, Long J, Wang RL, Baerson SR, Pan ZQ, Zhu-Salzman K, Xie JF, Cai KZ, Luo SM, Zeng RS. Priming of jasmonate-mediated antiherbivore defense responses in rice by silicon. *Proc Natl Acad Sci USA*, 2013, 110(38): E3631-E3639. [DOI]

[38] Peng Y, Bartley LE, Canlas P, Ronald PC. OsWRKY iIa Transcription factors modulate rice innate immunity. *Rice*, 2010, 3(1): 36–42. [DOI]

[39] Yokotani N, Sato Y, Tanabe S, Chujo T, Shimizu T, Okada K, Yamane H, Shimono M, Sugano S, Takatsuji H, Kaku H, Minami E, Nishizawa Y. WRKY76 is a rice transcriptional repressor playing opposite roles in blast disease resistance and cold stress tolerance. *J Exp Bot*, 2013, 64(16): 5085–5097. [DOI]

[40] Huang LY, Zhang F, Zhang F, Wang WS, Zhou YL, Fu BY, Li ZK. Comparative transcriptome sequencing of tolerant rice introgression line and its parents in response to drought stress. *BMC Genomics*, 2014, 15: 1026. [DOI]

[41] Nuruzzaman M, Sharoni AM, Satoh K, Kumar A, Leung H, Kikuchi S. Comparative transcriptome profiles of the *WRKY* gene family under control, hormone-treated, and drought conditions in near-isogenic rice lines reveal differential, tissue specific gene activation. *J Plant Physiol*, 2014, 171(1): 2–13. [DOI]

[42] Ramamoorthy R, Jiang SY, Kumar N, Venkatesh PN, Ramachandran S. A comprehensive transcriptional profiling of the *WRKY* gene family in rice under various abiotic and phytohormone treatments. *Plant Cell Physiol*, 2008, 49(6): 865–879. [DOI]

[43] Song Y, Chen LG, Zhang LP, Yu DQ. Overexpression of Os*WRKY72* gene interferes in the abscisic acid signal and auxin transport pathway of *Arabidopsis*. *J Biosci*, 2010, 35(3): 459–471. [DOI]

[44] Guo MX, Wang RC, Wang J, Hua K, Wang YM, Liu XQ, Yao SG. ALT1, a Snf2 family chromatin remodeling ATPase, negatively regulates alkaline tolerance through enhanced defense against oxidative stress in rice. *PLoS One*, 2014, 9(12): e112515. [DOI]

[45] Ricachenevsky FK, Sperotto RA, Menguer PK, Fett JP. Identification of Fe-excess-induced genes in rice shoots reveals a WRKY transcription factor responsive to Fe, drought and senescence. *Mol Biol Rep*, 2010, 37(8): 3735–3745. [DOI]

[46] Xiao J, Cheng HT, Li XH, Xiao JH, Xu CG, Wang SP. Rice WRKY13 regulates cross talk between abiotic and biotic stress signaling pathways by selective binding to different cis-elements. *Plant Physiol*, 2013, 163(4): 1868–1882. [DOI]

[47] Shen HS, Liu CT, Zhang Y, Meng XP, Zhou X, Chu CC, Wang XP. OsWRKY30 is activated by MAP kinases to confer drought tolerance in rice. *Plant Mol Biol*, 2012, 80(3): 241–253. [DOI]

[48] Peng XX, Hu YJ, Tang XK, Zhou PL, Deng XB, Wang HH. Isolation and expression profiles of rice WRKY30 induced by jasmonic acid application and fungal pathogen infection. *Sci Agric Sin*, 2011, 44(12): 2454–2461.
彭喜旭, 胡耀军, 唐新科, 周平兰, 邓小波, 王海华. 茉莉酸和真菌病原诱导的水稻 WRKY30 转录因子基因的分离及表达特征. 中国农业科学, 2011, 44(12): 2454–2461. [DOI]

[49] Qiu YP, Yu DQ. Over-expression of the stress-induced *OsWRKY45* enhances disease resistance and drought tolerance in *Arabidopsis*. *Environ Exp Bot*, 2009, 65(1): 35–47. [DOI]

[50] Raineri J, Wang SH, Peleg Z, Blumwald E, Chan RL. The rice transcription factor *OsWRKY47* is a positive regulator of the response to water deficit stress. *Plant Mol Biol*, 2015, 88(4–5): 401–413. [DOI]

[51] Ray S, Dansana PK, Giri J, Deveshwar P, Arora R, Agarwal P, Khurana JP, Kapoor S, Tyagi AK. Modulation of transcription factor and metabolic pathway genes in response to water-deficit stress in rice. *Funct Integr Genomics*, 2011, 11(1): 157–178. [DOI]

[52] Tao Z, Kou YJ, Liu HB, Li XH, Xiao JH, Wang SP. *OsWRKY45* alleles play different roles in abscisic acid signalling and salt stress tolerance but similar roles in drought and cold tolerance in rice. *J Exp Bot*, 2011, 62(14): 4863–4874. [DOI]

[53] Mittal D, Madhyastha DA, Grover A. Genome-wide transcriptional profiles during temperature and oxidative stress reveal coordinated expression patterns and overlapping regulons in rice. *PLoS One*, 2012, 7(7): e40899. [DOI]

[54] Jing SJ, Zhou X, Song Y, Yu DQ. Heterologous expression of *OsWRKY23* gene enhances pathogen defense and dark-induced leaf senescence in *Arabidopsis*. *Plant Growth Regul*, 2009, 58(2): 181–190. [DOI]

[55] Kang K, Park S, Natsagdorj U, Kim YS, Back K. Methanol is an endogenous elicitor molecule for the synthesis of tryptophan and tryptophan-derived secondary metabolites upon senescence of detached rice leaves. *Plant J*, 2011, 66(2): 247–257. [DOI]

[56] Chi WC, Chen YA, Hsiung YC, Fu SF, Chou CH, Trinh NN, Chen YC, Huang HJ. Autotoxicity mechanism of *Oryza sativa*: transcriptome response in rice roots exposed to ferulic acid. *BMC Genomics*, 2013, 14: 351–363. [DOI]

[57] Chen YA, Chi WC, Trinh NN, Huang LY, Chen YC, Cheng KT, Huang TL, Lin CY, Huang HJ. Transcriptome profiling and physiological studies reveal a major role for aromatic amino acids in mercury stress tolerance in rice seedlings. *PLoS One*, 2014, 9(5): e95163. [DOI]

[58] Dubey S, Misra P, Dwivedi S, Chatterjee S, Bag SK, Mantri S, Asif MH, Rai A, Kumar S, Shri M, Tripathi P, Tripathi RD, Trivedi PK, Chakrabarty D, Tuli R. Transcriptomic and metabolomic shifts in rice roots in response to Cr (VI) stress. *BMC Genomics*, 2010, 11: 648. [DOI]

[59] Xie Z, Zhang ZL, Zou XL, Yang GX, Komatsu S, Shen QJ. Interactions of two abscisic-acid induced *WRKY* genes in repressing gibberellin signaling in aleurone cells. *Plant J*, 2006, 46(2): 231–242. [DOI]

[60] Zhang LY, Gu LK, Ringler P, Smith S, Rushton PJ, Shen QJ. Three WRKY transcription factors additively repress abscisic acid and gibberellin signaling in aleurone cells. *Plant Sci*, 2015, 236: 214–222. [DOI]

[61] De Vleesschauwer D, Van Buyten E, Satoh K, Balidion J, Mauleon R, Choi IR, Vera-Cruz C, Kikuchi S, Höfte M. Brassinosteroids antagonize gibberellin- and salicylate-mediated root immunity in rice. *Plant Physiol*, 2012, 158(4): 1833–1846. [DOI]

[62] Hwang SH, Yie SW, Hwang DJ. Heterologous expression of *OsWRKY6* gene in *Arabidopsis* activates the expression of defense related genes and enhances resistance to pathogens. *Plant Sci*, 2011, 181(3): 316–323. [DOI]

[63] Wang HH, Hao ZN, Xie K, Wu KL, Guo ZJ. Leucine zipper like structure in rice WRKY89 enhances its affinity for binding with W box elements. *Chin Sci Bull*, 2005, 50(10):

980–989. [DOI]

[64] Han M, Kim CY, Lee J, Lee SK, Jeon JS. *OsWRKY42* represses *OsMT1d* and induces reactive oxygen species and leaf senescence in rice. *Mol Cells*, 2014, 37(7): 532–539. [DOI]

[65] Li N, Chen YR, Ding ZH, Li PH, Wu Y, Zhang A, Yu S, Giovannoni JJ, Fei ZJ, Zhang W, Xiang JZ, Xu CM, Liu B, Zhong SL. Nonuniform gene expression pattern detected along the longitudinal axis in the matured rice leaf. *Sci Rep*, 2015, 5: 8015. [DOI]

[66] Xu WY, Yang RD, Li MN, Xing Z, Yang WQ, Chen G, Guo H, Gong XJ, Du Z, Zhang ZH, Hu XM, Wang D, Qian Q, Wang T, Su Z, Xue YB. Transcriptome phase distribution analysis reveals diurnal regulated biological processes and key pathways in rice flag leaves and seedling leaves. *PLoS One*, 2011, 6(3): e17613. [DOI]

[67] Htun TM, Inoue C, Chhourn O, Ishii T, Ishikawa R. Effect of quantitative trait loci for seed shattering on abscission layer formation in Asian wild rice *Oryza rufipogon*. *Breed Sci*, 2014, 64(3): 199–205. [DOI]

[68] Hu LW, Mei ZL, Zang AP, Chen HY, Dou XY, Jin J, Cai WM. Microarray analyses and comparisons of upper or lower flanks of rice shoot base preceding gravitropic bending. *PLoS One*, 2013, 8(9): e74646. [DOI]

[69] Wei T, He ZL, Tan XY, Liu X, Yuan X, Luo YF, Hu SN. An integrated RNA-Seq and network study reveals a complex regulation process of rice embryo during seed germination. *Biochem Biophys Res Commun*, 2015, 464(1): 176–181. [DOI]

[70] Cai YH, Chen XJ, Xie K, Xing QK, Wu YW, Li J, Du CH, Sun ZX, Guo ZJ. Dlf1, a WRKY transcription factor, is involved in the control of flowering time and plant height in rice. *PLoS One*, 2014, 9(7): e102529. [DOI]

[71] Zhang CQ, Xu Y, Lu Y, Yu HX, Gu MH, Liu QQ. The WRKY transcription factor OsWRKY78 regulates stem elongation and seed development in rice. *Planta*, 2011, 234(3): 541–554. [DOI]

[72] Liu L, Zhou Y, Zhou G, Ye RJ, Zhao LN, Li XH, Lin YJ. Identification of early senescence-associated genes in rice flag leaves. *Plant Mol Biol*, 2008, 67(1–2): 37–55. [DOI]

[73] Takehisa H, Sato Y, Antonio BA, Nagamura Y. Global transcriptome profile of rice root in response to essential macronutrient deficiency. *Plant Signal Behav*, 2013, 8(6): e24409. [DOI]

[74] Oono Y, Kawahara Y, Yazawa T, Kanamori H, Kuramata M, Yamagata H, Hosokawa S, Minami H, Ishikawa S, Wu JZ, Antonio B, Handa H, Itoh T, Matsumoto T. Diversity in the complexity of phosphate starvation transcriptomes among rice cultivars based on RNA-Seq profiles. *Plant Mol Biol*, 2013, 83(6): 523–537. [DOI]

[75] Wang HJ, Wan AR, Hsu CM, Lee KW, Yu SM, Jauh GY. Transcriptomic adaptations in rice suspension cells under sucrose starvation. *Plant Mol Biol*, 2007, 63(4): 441–463. [DOI]

[76] Zhang MZ, Fang JH, Yan X, Liu J, Bao JS, Fransson G, Andersson R, Jansson C, Åman P, Sun CX. Molecular insights into how a deficiency of amylose affects carbon allocation-carbohydrate and oil analyses and gene expression profiling in the seeds of a rice waxy mutant. *BMC Plant Biol*, 2012, 12: 230–247. [DOI]

[77] Drogue B, Sanguin H, Chamam A, Mozar M, Llauro C, Panaud O, Prigent-Combaret C, Picault N, Wisniewski-Dye F. Plant root transcriptome profiling reveals a strain-dependent response during *Azospirillum*-rice cooperation. *Front Plant Sci*, 2014, 5: 607. [DOI]

[78] Wang HH, Xie K, Wu KL, Guo ZJ. Isolation of a rice WRKY gene OsWRKY52, whose expression is induced by *Magnaporthe grisea*. *Prog Biochem Biophys*, 2005, 10(32): 937–946. [DOI]

[79] Chujo T, Sugioka N, Masuda Y, Shibuya N, Takemura T, Okada K, Nojiri H, Yamane H. Promoter analysis of the elicitor-induced WRKY gene *OsWRKY53*, which is involved in defense responses in rice. *Biosci Biotechnol Biochem*, 2009, 73(8): 1901–1904. [DOI]

[80] Cheng HT, Li HB, Deng Y, Xiao JH, Li XH, Wang SP. The WRKY45-2 WRKY13 WRKY42 transcriptional regulatory cascade is required for rice resistance to fungal pathogen. *Plant Physiol*, 2015, 167(3): 1087–1099. [DOI]

[81] Kim SH, Oikawa T, Kyozuka J, Wong HL, Umemura K, Kishi-Kaboshi M, Takahashi A, Kawano Y, Kawasaki T, Shimamoto K. The bHLH rac immunity1 (RAI1) is activated by osrac1 via OsMAPK3 and osmapk6 in rice immunity. *Plant Cell Physiol*, 2012, 53(4): 740–754. [DOI]

[82] Ueno Y, Yoshida R, Kishi-Kaboshi M, Matsushita A, Jiang CJ, Goto S, Takahashi A, Hirochika H, Takatsuji H. MAP kinases phosphorylate rice WRKY45. *Plant Signal Behav*, 2013, 8(6): e24510. [DOI]

[83] Yoo SJ, Kim SH, Kim MJ, Ryu CM, Kim YC, Cho BH, Yang KY. Involvement of the OsMKK4-OsMPK1 cascade and its downstream transcription factor OsWRKY53 in the wounding response in rice. *Plant Pathol J*, 2014, 30(2): 168–177. [DOI]

[84] Koo SC, Moon BC, Kim JK, Kim CY, Sung SJ, Kim MC, Cho MJ, Cheong YH. OsBWMK1 mediates SA-dependent defense responses by activating the transcription factor OsWRKY33. *Biochem Biophys Res Commun*, 2009, 387(2): 365–370. [DOI]

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