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Anotação da família WRKY de soja [*Glycine max* (L.) Merril] e caracterização funcional de genes envolvidos na resposta a *Phakopsora pachyrhizi*, agente causador da Ferrugem Asiática

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À minha querida família e ao meu grande amor, dedico.

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Resumo

Fatores de transcrição WRKY de soja têm sido identificados e relacionados em resposta a estresses bióticos e abióticos. No entanto, em estudos anteriores, a família WRKY estava subestimada. Recentemente, o envolvimento dos genes *WRKY* em resposta a *Phakopsora pachyrhizi,* o agente causador de uma importante doença da soja, a Ferrugem Asiática, foi sugerido a partir de análise de dados de expressão gênica global. No presente estudo, a anotação completa da família WRKY de soja e a análise funcional de genes envolvidos na resposta à infecção por *P. pachyrhizi* foram realizada. A partir de buscas em bancos de dados do genoma da soja, genes *WRKY* foram anotados e aqueles envolvidos na resposta a *P. pachyrhizi* foram identificados usando quatro experimentos de expressão gênica global: superSAGE, RNA-Seq de lesões microdissecadas e dois microarranjos. O padrão de expressão gênica foi confirmado por RT-qPCR para oito genes. Embriões somáticos de soja foram transformados, visando a superexpressão ou silenciamento gênico, e plantas transgênicas foram desafiadas com *P. pachyrhizi*. Cento e setenta e oito genes *WRKY* foram anotados e 74 identificados como diferencialmente expressos durante a infecção pelo fungo. Em resposta a *P. pachyrhizi,* oito genes apresentaram expressão mais inicial e⁄ou mais forte no genótipo resistente quando comparado com o suscetível. Todos os oito genes analisados mostraram o pico de expressão nas primeiras 24 horas após a inoculação. Comparando a mineração de dados em resposta à infecção por *P. pachyrhizi* com o resultado do cladograma, um padrão de expressão similar pode ser observado em genes relacionados. Plantas superexpressando Glyma15g00570 não foram recuperadas. Provavelmente a expressão constitutiva deste gene afeta a regeneração das plantas. A participação de quatro genes homólogos em resposta ao patógeno foi demonstrada usando a técnica de RNAi. Quando infectada por *P. pachyrhizi*, folhas da linhagem silenciada mostraram maior número de lesões do que plantas não-transformadas. Em conclusão, neste trabalho a família WRKY de soja completa foi anotada e a participação de alguns membros em resposta a *P. pachyrhizi* foi demonstrada.

Abstract

Soybean WRKY transcription factors have been identified and related with the response to biotic and abiotic stresses. However the soybean WRKY family was underrepresented in previous studies. Recently, the involvement of *WRKY* genes in response to *Phakopsora pachyrhizi*, the causal agent of an important soybean disease - Asian Soybean Rust (ASR)- has been suggested by the analyses of global gene-expression data. In the present study a genome-wide annotation of soybean WRKY family and the functional analyzes of genes involved in response to *P. pachyrhizi* were performed. Following a search in the soybean genomic databases, *WRKY*-encoding genes were annotated and those involved in response to *P. pachyrhizi* were identified using global gene-expression experiments: superSAGE, RNA-Seq of microdissected lesions and two microarrays. Gene expression pattern was validated by RT-qPCR. Soybean somatic embryos were transformed aiming *WRKY* overexpression or silencing, and transgenic plants were challenged with *P. pachyrhizi*. One hundred-seventy-eight *WRKY* genes were annotated and 74 identified as differentially expressed during fungus infection. In response to *P. pachyrhizi*, eight genes were expressed earlier and⁄or stronger in a resistant genotype when compared to a susceptible one. All the eight analyzed genes showed the expression peak at the first 24 hours after inoculation. By comparing data mining in response to *P. pachyrhizi* infection with the clustering result, similar expression pattern could be observed in closely related genes. Plants overexpressing Glyma15g00570 were not recovered. Probably the constitutive overexpression of the gene may affect the regeneration of plants. The participation of four homologous genes in response to pathogen was demonstrated using RNAi approach. When infected by *P. pachyrhizi*, leaves of silenced transgenic line showed higher number of lesions than wild-type plants. In conclusion, the complete soybean WRKY family was annotated and the participation of some members in response to *P. pachyrhizi* was demonstrated.

Lista de Abreviaturas

ASR: Ferrugem Asiática ("Asian Soybean Rust")

At: *Arabidopsis thaliana*

AVR: efetor/ produto de avirulência ("effector/avirulence products")

Bn: *Brassica napus*

BP filter: "Band Pass filter"

CaMV: vírus do mosaico da couve-flor ("Cauliflower mosaic virus")

cDNA: DNA complementar

CDS: sequência codificante ("coding sequence")

DNA: ácido desoxirribonucleico ("desoxyribonucleic acid")

dai: dias após a inoculação ("days after inoculation")

EgfpER: promoter da protein fluorescente verde ("Enhanced green fluorescent protein")

ESTs: etiquetas de sequências expressas ("Expressed Sequence Tags")

ETI: efetor deencadeia a imunidade ("Effector Triggered Immunity")

FPKM: "Fragments Per Kilobase or exon per million fragments Mapped"

GFP: proteína fluorescente verde ("Green Fluorescent Protein")

Gm: *Glycine max*

hai: horas após a inoculação ("hours after inoculation")

hpt: higromicina fosfotransferase

Hv: *Hordeum vulgare*

ICS1: "Isochorismate Synthase 1"

JA: ácido jasmônico ("Jasmonic Acid")

LCM: "Laser Capture Microdissection"

LRR-RLK: "Leucine-Rich Repeats – Receptor-like Kinase"

LRR-RLP: "Leucine-Rich Repeats – Receptor-like Protein"

MAMPs:" Microbes-associated Molecular Patterns"

MAPK: "Mithogen-activated Protein Kinase"

MKKK: "Mithogen-activated Protein Kinase Kinase Kinase"

MS: meio de cultura de Murashinge e Skoog

NCBI: "National Center for Biotechnology Information"

NMR: "Nuclear Magnetic Resonance"

NPR1: "Nonexpressor of PR genes 1"

Nt: *Nicotiana tabacum*

PAMPs: "Pathogen-associated Molecular Patterns"

P35S: promotor 35S do CaMV

pb: pares de bases

ORF: "Open Reading Frame"

Os: *Oryza sativa*

PCR: Reação em Cadeia da Polimerase

PIG: "Particle Inflow Gun"

pH: potencial hidrogeniônico

PM: "Plasmatic Membrane"

ProlD: "rooting loci promoter" de *Agrobacterium rhizogenes*

PRs: "Pathogenesis-Related proteins"

PTI: "Pathogen triggered Immunity"

R genes: "Resistence genes"

RB: Reddish Brown"

RLK: "Receptor-like Kinase"

RNA: ácido ribonucleico

RNAi: RNA de interferência

RNA-Seq: Whole transcriptome shotgun sequencing

RT-PCR: ("Reverse Transcription-Polymerase Chain Reaction")

RT-qPCR: PCR quantitativa precedida de transcrição reversa

SA: ácido salicílico ("Salicilic Acid")

SAR: resistência sistêmica adquirida ("Systemic Acquired Resistance")

SuperSAGE: Serial analysis of gene expression

T35S: terminador 35S do CaMV

T-DNA: DNA de transferência de *Agrobacterium tumefaciens*

TIR-NB-LRR: "Toll/Interleukin1 Receptor – Nucleotide Binding – Leucine-Rich Repeats"

TGA: "TGA transcription factor"

TTSS: Sistema de Secreção Tipo III ("Type III Secretion System")

U: "Units"

WT: selvagem ("Wild-type")

Sumário

INTRODUÇÃO GERAL

1. INTRODUÇÃO GERAL

1.1. Soja

A soja (*Glycine max*), pertencente à família Fabaceae, é a espécie de leguminosas de maior importância econômica no mundo. Atualmente, são produzidas, por ano, cerca de 260 milhões de toneladas deste grão. O Brasil aparece como o segundo maior produtor — com uma produção de 75,32 milhões de toneladas na safra 2010/11 — aproximadamente ¼ de toda a produção mundial (CONAB, 2012; Embrapa, 2010).

A relevância dessa espécie na agricultura é decorrente de sua capacidade de fixação de nitrogênio atmosférico pela simbiose com microrganismos, do seu alto teor proteico e lipídico, de ser utilizada há milênios na alimentação humana e animal e, mais recentemente, da possibilidade de utilização do óleo de soja para a produção de biocombustíveis (Reetz *et al*. 2008; Varshney *et al*. 2009).

Devido a sua grande importância econômica, a comunidade científica internacional que trabalha com leguminosas recomendou a soja como planta modelo para estudos genéticos e moleculares, na conferência "Cross-Legume Advances through Genomics" realizada em 2004 (Gepts *et al*., 2005). Desde então, muitos estudos têm sido desenvolvidos. Um exemplo é o sequenciamento do genoma da cultivar Williams 82 (Schmutz *et al*., 2010). Em 1997, foi criado o Consórcio Internacional do genoma da soja entre pesquisadores da China, Japão, Coréia do Sul, Estados Unidos e Brasil. O projeto GENOSOJA (Consórcio Nacional do Genoma da Soja) é parte integrante do consórcio internacional. O GENOSOJA integra diversos grupos de pesquisa do país, tem como objetivo a caracterização do genoma da soja por intermédio de estudos da estrutura física do genoma e de expressão de genes e proteínas. Dessa forma, propõe-se a auxiliar na compreensão da função de genes e dos mecanismos moleculares envolvidos em processos do desenvolvimento da planta e em resposta a situações de estresse tais como a ocorrência de secas, doenças e pragas, que afetam a produtividade da cultura no país. O Brasil faz parte, ainda, do projeto BIOTECSUR (Projeto de Cooperação Bi-regional entre a União Européia & MERCOSUL), que tem por objetivo a caracterização de genes e desenvolvimento de tecnologias para agregar valor ao cultivo da soja.

1.2. Estresses ambientais que afetam a produtividade da cultura da soja

Entre os fatores que limitam o rendimento das culturas de soja estão os estresses ambientais tais como fungos, bactérias, nematoides, vírus, plantas invasoras, insetos, seca, inundações, temperaturas extremas, salinidade e toxicidade de minerais (Dita *et al.*, 2006). Normalmente, estes fatores não ocorrem isoladamente: plantas sob condições de estresse abiótico tornam-se ainda mais suscetíveis aos danos causados por pragas e doenças, aumentando consideravelmente as perdas (Dita *et al.*, 2006). Em função das mudanças climáticas, muitos esforços têm sido dirigidos para o desenvolvimento de cultivares mais tolerantes às adversidades abióticas (Tollefson, 2010).

Além dos estresses abióticos, as doenças estão entre os fatores mais importantes e difíceis de controlar. A expansão das culturas para novas áreas, a monocultura e a utilização de práticas inadequadas de manejo têm aumentado o número de doenças causadas por fungos, bactérias, vírus e nematoides, além de outras anormalidades desconhecidas (Suzuki & Yuyama, 2005). Apesar do uso de fungicidas e outras técnicas que visam o controle ou à eliminação dos patógenos, as moléstias fúngicas são responsáveis por grandes prejuízos nas colheitas todos os anos.

Diversos fungos atacam as culturas de soja. Os patógenos mais comumente envolvidos com podridão de sementes e morte de plântulas são: *Pythium* sp., *Phytophtora sojae*, *Rhizoctonia solani* e *Fusarium* sp. Estes dois últimos, juntamente com *Macrophomina phaseoli*, *Sclerotium rolfsii* e *S. sclerotiorum*, são também responsáveis por podridões radiculares e da haste (Reis & Casa, 2002). Os autores salientam que, em soja, não há fonte de resistência a esses fungos, sendo este um grande desafio para os programas de melhoramento.

A Ferrugem Asiática (ASR, *Asian Soybean Rust*), doença causada pelo fungo biotrófico *Phakopsora pachyrhizi* Sydow, é responsável por grandes perdas na produtividade de soja no mundo (Goellner *et al.*, 2010). Sob condições de desenvolvimento favoráveis para o fungo, a infecção pode resultar em perdas de 10% a 80% na produção (Ogle *et al.*, 1979; Bromfield, 1984; Patil *et al.*, 1997; Yorinori *et al.*, 2005). O patógeno coloniza primeiro os tecidos foliares e, em menor extensão, hastes e vagens. (Miles *et al.*, 2006). O desenvolvimento da infecção resulta na desfolhação prematura e na redução drástica no rendimento dos grãos. As estimativas apontam que a doença tenha causado perdas econômicas de mais de 2,2 bilhões de dólares durante a safra de 2006/2007, no Brasil (Nunes, 2009).

Atualmente, não há cultivares resistentes à Ferrugem Asiática e a tentativa de controle por meio de fungicidas se mostra cara e, por vezes, ineficiente, devido à agressividade do fungo e à dificuldade de detecção nos estágios iniciais da infecção. Além disso, o controle químico causa forte impacto ambiental e pode resultar na resistência do patógeno (Sconyers *et al*., 2006; Calvo *et al*., 2008).

1.3. Mecanismos de resposta da planta à infecção por patógenos

Quando entra em contato com a planta hospedeira, o patógeno precisa sobrepor diversas barreiras físicas pré-existentes como a cutícula e tricomas presentes nas folhas, ou barreiras induzidas (ex. fechamento dos estômatos, deposição de calose). Com o sucesso na penetração ele deve persistir no espaço apoplástico, que possui pH baixo, componentes antimicrobianos e enzimas de degradação. Além disso, a parede celular limita os micróbios ao espaço apoplástico. Uma vez que acessam o citosol, precisam suprimir as respostas de defesa e absorver nutrientes das plantas. Bactérias possuem um sistema de secreção do tipo III (TTSS- *Type III Secretion System*) que penetra através da parede celular e membrana plasmática para injetar moléculas efetoras no citoplasma e ganhar acesso aos nutrientes. Alguns fungos e oomicetos formam um apressório e forçam a penetração da hifa pela pressão de turgor através da parede celular. Em seguida, estruturas de alimentação (haustórios) são formadas e efetores secretados por exocitose (Bent *et al*., 2007; Göhre & Robattzek, 2008).

As plantas possuem sistemas de reconhecimento que induzem respostas de defesa desencadeadas após o contato com moléculas diferentes das suas (Figura 1). Padrões Moleculares Associados a Patógenos (PAMPs, do inglês, *Pathogen-Associated Molecular Patterns*) ou Padrões Moleculares Associados a Micróbios (MAMPs, do inglês, *Microbe-Associated Molecular Patterns*) são estruturas moleculares bem conservadas, presentes somente em micróbios, como flagelinas bacterianas, quitinas fúngicas e lipopolissacarídeos de oomicetos. *Pattern Recognition Receptors* (PRRs) são receptores presentes na membrana plasmática vegetal, tais como as LRR-RLKs (*Leucine-rich Repeat Receptor Like Kinase*), que reconhecem PAMPs e desencadeiam a imunidade basal - PTI (*Plant Triggered Immunity*). Alguns patógenos desenvolveram fatores de virulência (efetores) que suprimem essa resposta de defesa. No entanto, as plantas acabaram por desenvolver proteínas de resistência (R) que reconhecem os efetores e desencadeiam a ETI (*Effector-Triggered Immunity*). A ETI está associada

com a resposta de hipersensibilidade (morte celular programada) e à Resistência Sistêmica Adquirida (SAR, do inglês, *Systemic Acquire Resistance*). Porém, esta resistência pode ser também sobreposta por patógenos que eliminaram ou modificaram seus efetores, escapando à detecção pela planta (Bent *et al.*, 2007; Göhre & Robattzek, 2008).

As respostas a ataques por patógenos requerem uma ampla reprogramação transcricional e uma sinalização interconectada envolvendo o balanço entre os hormônios ácido salicílico (AS, do inglês, *Salicilic Acid*) e ácido jasmônico (JÁ, do inglês, *Jasmonic Acid*) na célula vegetal.
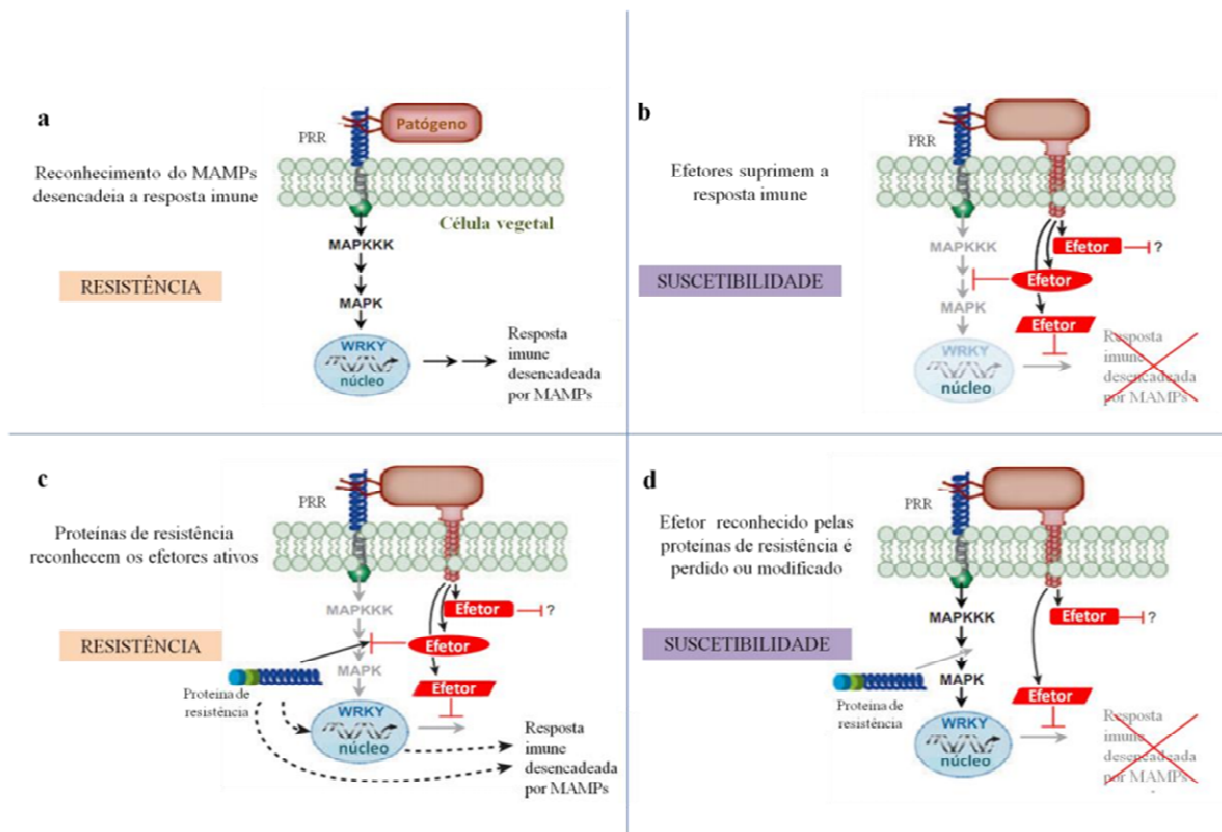
Figura 1. Modelo evolutivo da interação planta-patógeno (adaptado a partir de Bent & Mackey, 2007).

1.3. Resistência à *P. pachyrhizi* em soja

O ciclo de vida de *P. pachyrhizi*, sob condições adequadas, começa com a germinação de esporos 1 ou 2 horas após a inoculação (hai). A formação de um apressório sobre a epiderme do tecido vegetal ocorre nas primeiras 12 hai. A hifa de infecção penetra nas células da epiderme em até 24 hai (Schneider *et al.*, 2011). Quando a hifa de penetração emerge no espaço intercelular abaixo da epiderme, um septo é formado produzindo a hifa primária. O haustório, órgão especializado com o qual o fungo obtém nutrientes e secreta efetores, é formado entre a parede celular e a membrana plasmática, entre 24 e 48 hai. Completados esses eventos com sucesso, o fungo coloniza os espaços intercelulares do mesófilo esponjoso produzindo a hifa secundária e haustórios adicionais (Yang *et al.*, 1991). Novos esporos são formados de 7 a 9 dias após a inoculação (daí) (Marchetti *et al.*, 1975), sendo disseminados por até 4 semanas (Mortel *et al.*, 2007).

Foram descritos três tipos de infecção causados pelo fungo em genótipos de soja (Figura 2): (1) reação suscetível caracterizada por lesões marrons (TAN), com esporulação total das pústulas; (2) reação de hipersensibilidade caracterizada por lesões avermelhadas (Reddish Brown –RB), com pouca ou moderada esporulação; e (3) reação resistente com pouca ou nenhuma esporulação, conferindo o fenótipo imune (Bromfield, 1984; Bromfield & Hartwig, 1980). Cinco locus de *Glycine max* que conferem o fenótipo de imunidade (*Rpp1*) ou de resistência (*Rpp1b*, *Rpp2*, *Rpp3*, *Rpp4* e *Rpp5*) foram identificados (Cheng and Chan, 1968; Hidayat & Somaatmadja, 1977; Singh & Thapliyal, 1977; Bromfield & Hartwig, 1980; McLean and Byth, 1980; Hartwig & Bromfield, 1983; Hartwig, 1986; Monteros *et al.*, 2007; Garcia et al., 2008). A efetividade desses genes é limitada por isolados virulentos do fungo, os quais são capazes de sobrepor os mecanismos de resistência conferidos pelos genes (Bonde *et al.*, 2006; Miles *et al.*, 2006).

Como não há resistência durável contra *P. pachyrhizi* e a variabilidade genética apresentada pelas cultivares de soja existentes é baixa (Camargo & Yuyama, 2001), a identificação de espécies, genótipos ou genes que possibilitem a construção de um "arsenal" contra os diferentes estresses ambientais no germoplasma comercial pode contribuir enormemente na busca por cultivares mais resistentes/tolerantes aos limites impostos pelo ambiente.

Como alternativas efetivas, que visam contribuir para o desenvolvimento de

estratégias que permitam minimizar a suscetibilidade da soja a limitações bióticas e abióticas, conta-se com estudos de genômica e engenharia genética, que abrem novas possibilidades para o melhoramento da soja. O emprego destas abordagens torna possível a identificação de novos genes e fornece recursos para maior compreensão das respostas fisiológicas e bioquímicas, bem como das redes regulatórias dos genes envolvidos, abrindo a perspectiva para o desenvolvimento, a longo prazo, de novas estratégias para a melhoria de características de interesse agronômico.
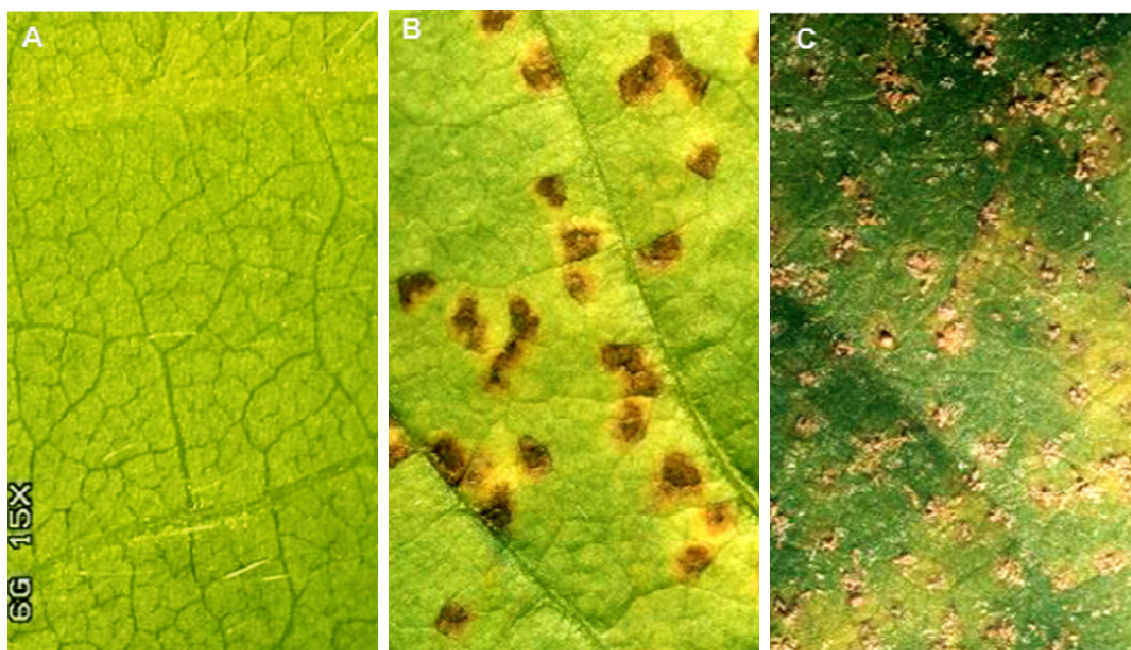
**Figura 2.** Tipos de reação da soja à infecção por *P. pachyrhizi*. (A) Reação imune, sem sintomas visíveis; (B) reação de hipersensibilidade, com lesões avermelhadas - RB; e (C) reação suscetível, com lesões marrons (TAN) (Miles *et al*., 2006).

1.5. A família de fatores de transcrição WRKY

Estudos do perfil de expressão gênica global têm demonstrado a modulação da expressão de vários genes de soja em resposta à infecção causada por *P. pachyrhizi* (Mortel *et al*., 2007; Panthee *et al*., 2007; Choi *et al*., 2008; Panthee *et al*., 2009; Tremblay *et al*., 2010; Schneider *et al*., 2011). No estudo realizado por Mortel *et al*. (2007), o perfil de expressão de genes em folhas de um genótipo resistente (PI970230), portador do gene de resistência *Rpp2*, e de um genótipo suscetível (Embrapa 48), em resposta à infecção por *P. pachyrhizi*, foi comparado com o perfil de expressão em folhas não infectadas. Por meio de hibridizações de microarranjo de DNA, foi identificado um grande número de genes diferencialmente expressos, em especial genes da família WRKY. Schneider *et al*. (2011) analisaram o perfil de expressão gênica global da cultivar de soja Ankur (PI462312), que porta o gene de resistência *Rpp3*, inoculada com um isolado avirulento (Hawaii 94-1) e um virulento (Taiwan 80-2) de *P. pachyrhizi*. Nos dados obtidos da análise, genes WRKY também estavam representados. Esses resultados demonstram a importância dos fatores de transcrição da família WRKY na reprogramação transcricional durante a infecção da soja por *P. pachyrhizi*. Os genes *WRKY* devem regular a expressão de genes de defesa, modulando genes–alvo *downstream* ou ativando/reprimindo outros fatores de transcrição (Pandey & Somssich, 2009).

Os fatores de transcrição WRKY pertencem a uma das maiores famílias de proteínas regulatórias no reino vegetal. A característica que dá nome à família é o domínio WRKY, uma região altamente conservada que contém o heptapeptídeo WRKYGQK e um motivo "dedo-de-zinco" C_2H_2 ou C_2HC. Estudos anteriores identificaram 72 genes *WRKY* em Arabidopsis (Eugelm *et al*., 2000) e cerca de 100 membros em arroz (Xie *et al*., 2005; Zhang & Wang, 2005; Wu *et al*., 2005; Ross *et al*., 2007).

A família é classificada em três grupos de acordo com o número de domínios WRKY e o tipo de motivo "dedo-de-zinco" (Eugelm *et al*., 2000). Genes com dois domínios pertencem ao grupo I, enquanto que os grupos II e III possuem somente um domínio. Proteínas que contém dois domínios têm maior atividade de ligação ao DNA no domínio C-terminal. A função do domínio N-terminal permanece não determinada (Eulgem *et al*., 1999; Maeo *et al*., 2001). Os grupos I e II possuem "dedos-de- zinco" do tipo $C_2–H_2$ ($C–X_{4–5}–C–X_{22–23}–H–X_1–H$). O grupo II é subdividido em cinco subgrupos

(a-e) baseados em aminoácidos adicionais presentes no domínio. O motivo "dedo-de-zinco" do grupo III é do tipo C_2–HC (C–X_7–C–X_{23}–H–X_1–C).

A presença dessas proteínas em eucariotos primitivos revela a ampla ocorrência das proteínas WRKY (Ülker & Somssich, 2004). O grupo I parece ser o mais basal, uma vez que é o único presente na alga *Chlamydomonas reinhardtii*. Surpreendentemente, cinco genes do grupo III foram identificados no musgo *Physcomitrella patens*. Anteriormente, pensava-se que este era o grupo mais derivado devido a sua expansão nas monocotiledônias. Os grupos IIa e IIe parecem ser os mais derivados, porque são os únicos que estão ausentes em *P. patens*. O grupo I foi encontrado também em eucariotos não fotossintetizantes (*Dictyostelium discoideum*) e no protista unicelular *Giardia lamblya* (Rushton *et al*., 2010).

A análise por ressonância magnética nuclear (NMR, do inglês, *Nuclear Magnetic Resonance*) de um domínio WRKY C-terminal de uma proteína de Arabidopsis (*AtWRKY4*) mostrou que a sequência conservada WRKYGQK está diretamente envolvida na ligação ao DNA (Yamasaki *et al*., 2005). A maior parte das proteínas WRKY já caracterizadas ligam-se ao elemento W-box (C/T)TGAC(C/T), presente no promotor de genes-alvo (Eugelm & Somssich, 2007). Exceções são o fator de transcrição WRKY de cevada SUSIBA2 e o de tabaco *NtWRKY12*, que se ligam a regiões diferentes (Sun *et al*, 2003; van Verk *et al*., 2008). A especificidade é parcialmente dependente de sequências de DNA adjacentes ao W-box e o envolvimento das proteínas WRKY em complexos pode ser o critério mais importante para determinar essa especificidade (Ciolkowski *et al*., 2008). Tanto a assinatura WRKYGQK quanto o motivo dedo de zinco são requeridos para ligação ao DNA (Maeo *et al*., 2001). No entanto, até o momento, não foi determinada a estrutura cristalizada de um domínio WRKY associado com seu sítio de ligação ao DNA ou de uma proteína WRKY completa (Pandey & Somssich, 2009).

As proteínas WRKY têm sido descritas como reguladores transcricionais em vários processos, desde a defesa contra patógenos (Eugelm *et al*., 1999; Chen & Chen, 2000; Dong *et al*., 2003; Ryu *et al*., 2006), senescência foliar (Hinderhofer *et al*., 2001; Miao *et al*., 2004), desenvolvimento de tricomas (Johnson *et al*., 2002) e semente (Luo *et al*., 2005), até na sinalização por açúcar (Sun *et al*., 2003), remodelagem da cromatina (Kim *et al*., 2008) e na resposta a estresses abióticos (Rushton *et al*., 2010). Na Figura 3

está apresentado um modelo hipotético da rede de interação entre WRKYs de *A. thaliana*, que estariam envolvidos nas respostas ao ataque por patógenos.

Em soja, a identificação de 64 genes WRKY expressos em diversos tecidos e em resposta a estresses abióticos foi realizada por RT-PCR (Zhou *et al*., 2008). No entanto, devido ao método de análise e ao sequenciamento do genoma da soja estar incompleto na época, os próprios autores consideraram que a família estava sendo subestimada. Além disso, a nomenclatura que vem sendo utilizada para genes *WRKY* em soja não tem um consenso na literatura. O banco de dados Phytozome nomeia os genes de acordo com os ortólogos em Arabidopsis, enquanto Zhou *et al*. (2008) numeraram aleatoriamente os 64 membros identificados por seu grupo (depositados no NCBI). Em estudos com genes individuais (Zhang *et al*., 2008; Kang *et al*., 2009), os mesmos foram nomeados de forma diferente da proposta por Zhou *et al*. (2008).
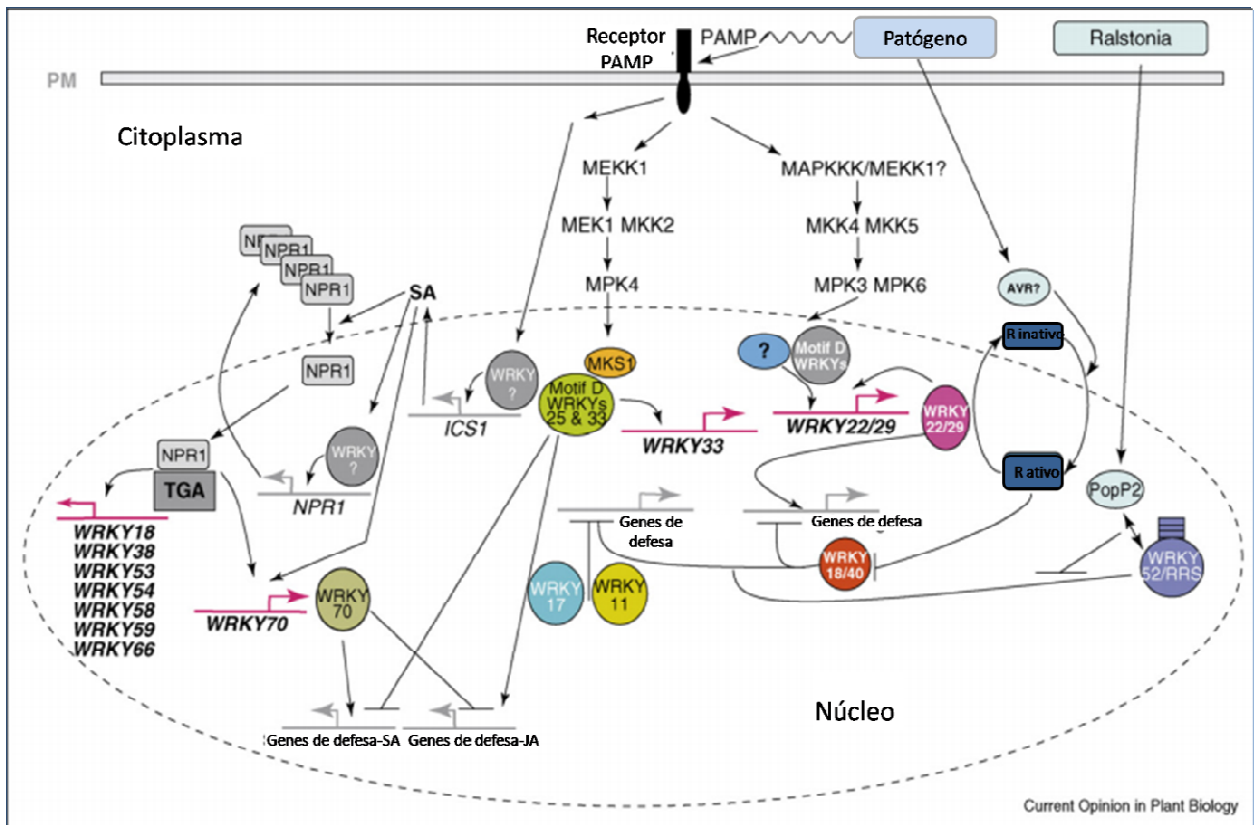
Figura 3. Modelo hipotético de rede de interação entre WRKYs de *A. thaliana* envolvidos nas respostas ao ataque por patógenos (adaptado a partir de Eugelm & Somssich, 2007).

2. OBJETIVOS

2.1. Objetivo geral

O presente estudo teve como objetivo a anotação completa dos genes *WRKY* de soja, a identificação daqueles envolvidos na resposta à infecção pelo fungo *P. pachyrhizi* e a análise funcional de genes selecionados, através de superexpressão e silenciamento gênico em soja.

2.2. Objetivos específicos

a) Anotação da família WRKY em soja;

b) Classificação dos genes

c) Identificação dos genes *WRKY* responsivos ao ataque de *P. pachyrhizi* pela análise de dados da literatura (microarranjo), da análise *in silico* e de experimento de microdissecção de lesões (RNA-Seq);

d) Seleção dos genes que apresentaram expressão diferencial em mais de uma das situações analisadas no item c para determinar o perfil de expressão em resposta ao fungo *P. pachyrhizi* através de PCR quantitativa precedida de Transcrição reversa (RT-qPCR);

e) Construção de vetores de transformação vegetal para superexpressão e silenciamento gênico (via RNAi);

f) Obtenção de linhagens transgênicas de soja com as construções descritas no item anterior;

g) Caracterização das linhagens estavelmente transformadas em nível molecular;

h) Desafio das plantas transgênicas com o agente patogênico.

CAPÍTULO I

Genome-wide annotation of the soybean WRKY family and functional characterization of genes involved in the response to *Phakopsora pachyrhizi*

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Genome-wide annotation of the soybean WRKY family and functional characterization of genes involved in the response to *Phakopsora pachyrhizi*

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Summary

- Soybean WRKY transcription factors have been identified and related with the response to biotic and abiotic stresses. The involvement of *WRKY* genes in response to *Phakopsora pachyrhizi*, the causal agent of an important soybean disease -Asian Soybean Rust (ASR)- has been suggested by several studies involving global gene-expression data. In the present study, a genome-wide annotation of soybean WRKY family and the functional analyzes of genes involved in response to *P. pachyrhizi* were performed.

- Following a search in the soybean genomic databases, *WRKY*-encoding genes were annotated and those involved in the response to *P. pachyrhizi* were identified using global gene-expression experiments: superSAGE, RNA-Seq of microdissected lesions and microarrays. Gene expression pattern of eight genes was validated by RT-qPCR. For functional analysis, soybean was transformed aiming WRKY overexpression or silencing, and transgenic plants were challenged with *P. pachyrhizi*.

- One hundred-seventy-eight *WRKY* genes were annotated and 74 identified as differentially expressed during fungus infection. The expression of eight genes in response to *P. pachyrhizi* was earlier and∕or stronger in a resistant genotype when compared to a susceptible one. When infected by *P. pachyrhizi*, leaves of silenced transgenic line showed higher number of lesions than wild-type plants.

- The complete soybean WRKY family was annotated and the participation of some members in response to *P. pachyrhizi* was demonstrated.

Key-words: *Glycine max*, genetic transformation, fungus resistance, transcription factors, Asian Soybean Rust, RNAi, overexpression, functional analysis

Introduction

WRKY transcription factors comprise one of the largest families of regulatory proteins found in plants, whose most prominent feature is the WRKY domain, a highly conserved 60 amino acid region characterized by the hallmark heptapeptide WRKYGQK followed by a C_2H_2- or C_2HC- zinc finger motif. Previous studies identified 72 *WRKY*-encoding genes in Arabidopsis (Eugelm *et al.*, 2000) and about 100 members in rice (Xie *et al.*, 2005; Zhang & Wang, 2005; Wu *et al.*, 2005; Ross *et al.*, 2007). Presence in primitive eukaryotes (Ülker & Somssich, 2004) reveals the widespread occurrence of WRKY proteins. As deduced from nuclear magnetic resonance (NMR) analysis of the C-terminal WRKY domain of one Arabidopsis protein (*At*WRKY4), the conserved WRKYGQK sequence is directly involved in DNA binding (Yamasaki *et al.*, 2005). Most of the characterized WRKY proteins bind to the W-box element (C/T)TGAC(C/T) in the promoter of target genes (Eugelm & Somssich, 2007). Exceptions are the barley WRKY factor SUSIBA2 and the tobacco *Nt*WRKY12, which have additional DNA-binding sites (Sun *et al*, 2003; van Verk *et al.*, 2008). Specificity of binding site is partly dependent on the adjacent DNA sequences outside of the W-box core and the involvement of WRKY factors in protein complexes may be the major criteria in determining promoter selectivity (Ciolkowski *et al.*, 2008). Both WRKY residues as well as the zinc finger motif are required for proper DNA binding of the protein (Maeo *et al.*, 2001).

Significant advances regarding WRKY proteins have occurred since the publication of the first report of WRKY transcription factor, SPF1 from sweet potato (Ishiguro & Nakamura, 1994). Such studies are not restricted to *Arabidopsis thaliana* - model plant - but have been expanded particularly to crop species like barley (Mangelsen *et al.*, 2008), tobacco (van Verk *et al.*, 2008), rice (Xie *et al.*, 2005; Wu *et al.*, 2005; Ramamoorthy *et al.*, 2008) and canola (Yang *et al.*, 2009). WRKY proteins have been described as transcriptional regulators in various processes such as pathogen defense (Eugelm *et al.*, 1999; Chen & Chen, 2000, 2002; Dong *et al.*, 2003; Eugelm, 2006; Ryu *et al.*, 2006), leaf senescence (Hinderhofer *et al.*, 2001; Miao *et al.*, 2004), as well as trichome (Johnson *et al.*, 2002) and seed development (Luo *et al.*, 2005). They

have been also implicated in sugar signaling (Sun *et al.*, 2003), chromatin remodeling (Kim *et al.*, 1998) and in response to abiotic stresses (Rushton *et al.*, 2010).

Soybean (*Glycine max*) is one of the most important crops in the world. At present, one of the major diseases affecting soybean production is Asian Soybean Rust (ASR), caused by *Phakopsora pachyrhizi,* an obligate biotrophic plant-pathogenic fungus which colonizes primarily leaf tissue and, to a lesser extent, stems and pods (Miles *et al.*, 2006). Under favorable conditions for the fungus, infection can result in yield losses ranging from 10% to 80% (Ogle *et al.*, 1979; Bromfield, 1984; Patil *et al.*, 1997).

Three infection types have been described on soybean accessions after inoculation with *P. pachyrhizi*: (1) susceptible reaction characterized by tan lesions with many uredinia and prolific esporulation; (2) resistant reaction typified by reddish brown lesions with few uredinia and little to moderate esporulation and; (3) resistant reaction with no visible lesions or uredinia, conferring the immune phenotype (Bromfield & Hartwig, 1980; Bromfield, 1984). Five *Glycine max* loci that confer either immunity - *Rpp1* - or resistance phenotype with little or no esporulation -*Rpp1b*, *Rpp2*, *Rpp3*, *Rpp4* and *Rpp5* - have been identified (Cheng & Chan, 1968; Hidayat & Somaatmadja, 1977; Singh & Thapliyal, 1977; Bromfield & Hartwig, 1980; McLean & Byth, 1979; Hartwig & Bromfield, 1983; Hartwig, 1986; Monteros *et al.*, 2007; Garcia *et al.*, 2008). The effectiveness of these genes is limited by virulent ASR isolates that are able to overcome the resistance mechanism conferred by each of them (Bonde *et al.*, 2006; Miles *et al.*, 2006). For this reason, the most successful control method so far is the application of fungicides that are costly, have a negative impact to the environment, can develop pathogen resistance and in severe cases are ineffective (Sconyers *et al.*, 2006).

Many studies have reported the involvement of soybean WRKY transcription factors in the response to *P. pachyrhizi* infection (Mortel *et al.*, 2007; Panthee *et al.*, 2007, 2009; Choi *et al.*, 2008; Tremblay *et al.*, 2010; Schneider *et al.*, 2011). *WRKY* genes may regulate expression of defense genes, modulating immediate downstream target genes or activating/repressing other transcriptional factors (Pandey & Somssich, 2009). Understanding the molecular basis of the soybean defense against fungal infection and growth, identifying genes involved in susceptible or resistant response and characterizing their individual roles are key steps for engineering durable and

quantitative disease resistance. In this context, genetic transformation represents a powerful tool for functional studies by genes overexpression and silencing.

The identification of 64 *WRKY* genes expressed in various soybean tissues and in response to abiotic stress was already accessed by RT-PCR (Zhou *et al.*, 2008). However, due to the analysis method and the unavailability of the whole soybean genome sequence at that time, the number of members of this gene family identified so far is certainly underrepresented. The present study reports a genome-wide annotation of soybean WRKY family and the functional analyzes of genes involved in response to *P. pachyrhizi* infection.

Materials and Methods

Database Search and Sequence Annotation

Predicted *Glycine max WRKY*-encoding gene were downloaded from three different public databases: Plant Transcription Factor Database - Planttfdb (http://planttfdb.cbi.pku.edu.cn/), SoyDB (http://casp.rnet.missouri.edu/soydb/) and Soybean Transcription Factor Knowledge Base - Plntfdb (http://systemsbiology.usm.edu/Soybean/). Each database has used different criteria to classify soybean WRKYs. Coding sequences (CDS) were blasted against Phytozome database (www.phytozome.org**)** to retrieve any additional *WRKY* gene. WRKY domain was identified using Pfam v2.5 with default parameters (*e*-value 1^{-10}) implemented by the HMMER v3.0 program (Finn *et al.*, 2011). Gene structures were provided by Phytozome database. WRKY automated predicted genes containing incorrect gene models (wrong start/ stop codons or truncated protein) were reannotated using GENSCAN (http://genes.mit.edu/GENSCAN.html**)** and FEGENESH (http://linux1.softberry.com/) predictors, considering 2, 5 or 10 kb DNA sequence from Gbrowse. Sequences were aligned (ClustalX v2.1) and the domains manually checked. Genes without conserved WRKYGQK domain signature were discarded. Annotated genes were classified in groups and subgroups proposed by Eugelm *et al.* (2000) for *Arabidopsis thaliana.* Structure of four soybean *WRKY*-encoding genes, as well as the structure of their alternative transcripts, were analyzed using Fancy Gene v1.4 (http://host13.bioinfo3.ifom-ieo-campus.it/fancygene/).

Clustering analysis

Multiple sequence alignments were performed with full-length *Gm*WRKY protein sequences using ClustalX tool. The best-fit model of protein evolution was determined using ProTest (Abascal *et al*., 2005) which selected the JTT model for protein matrix substitution. Clustering were obtained using PhyML3.0 program (Guindon *et al*., 2003). The support for the clustering topologies was checked by performing 100 re-sampled bootstraps. The clustering was visualized and edited using the software FigTree v.1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

Gene expression data mining

In order to confirm gene expression, *Gm*WRKY CDSs were first blasted against Soybase EST database (Severin *et al*., 2010). In addition, expression profiles of the identified *WRKY* genes in response to *P. pachyrhizi* infection were obtained from four different sources.

a) SuperSAGE: SuperSAGE library was constructed using leaves of a soybean resistant genotype (PI561356) infected with *P. pahyrhizi* vs. uninfected leaves (mock inoculation/control) collected and bulked in 12, 24 and 48 hai. This library was carried out as part of the GenoSoja project (Brazilian Soybean Genome Consortium) and results are available in LGE (Laboratório de Genômica e Expressão UNICAMP) Soybean Genome database (http://www.lge.ibi.unicamp.br/soja/**)** for members of the consortium.

b) RNA-Seq of lesion: spores of a Brazilian population of *P. pachyrhizi* were collected and ressuspended in 0.05% Tween20 (v/v) solution to a final concentration of 13×10^4 spores/mL. This suspension was pulverized over soybean resistant (PI561356) and susceptible BRS231 (Ribeiro *et al*., 2007) genotypes at V2 growth stage. Solution without spores was used as mock inoculation/control. The experiment followed a complete randomized design with three replicates (pots) per treatment and three plants per pot. Immediately after inoculation plants were covered with humid plastic bags for two days. Ten days after inoculation TAN and RB lesions were observed on abaxial leaf surface of BRS231 and PI561356 inoculated plants, respectively. At this time, it was possible to collect foliar segments showing rust lesion for laser capture microdissection proceeding. Briefly, eight leaf segments of 1cm^2 were randomly sampled from the third trifoliate infected leaf and immediately fixed on ice in Farmer's solution (Kerk *et al*., 2003). Dehydration and paraffin inclusion was done as described by Cai & Lashbrook (2006). Serial sections of 12 μm were made with a rotary microtome and transferred to

microscope membrane slides. Then, sections were deparaffinized, dehydrated and stained with acid fucsin and fast green. Twenty sections containing a variable number of rust lesions were prepared for each biological replicate/treatment. PixCell II LCM system (Arcturus, Sunnyvale, CA) and CapSure Macro LCM (Arcturus, Sunnyvale, CA) were used to collect foliar cells within the lesion. RNA extraction using the PicoPure RNA isolation (Arcturus, Sunnyvale, CA) was performed on cells collected in a variable number of infection sites for each biological replicate, thus each genotype was represented by RNA extracted from 4500–6000 cells. Synthesis of cDNA was carried out and high performace paired end (108 bp) sequencing was done on the Illumina genome analyzer GAAllx. Low quality RNA-Seq reads were discarded. Reads (a total of 86,301,242) were aligned against the soybean genome and corresponding genes were predicted using the TopHat (Trapnell *et al*., 2009) and SOAP2 (Li *et al*., 2009) aligners. Gene expression was calculated using the FPKM (Fragments Per Kilobase of exon per Million fragments mapped) value (Mortazavi *et al*., 2008). To identify differential expressed genes a pair-wise comparison between the FPKM values of both genotypes was done using a *t*-test considering 99% of confidence rate. This library was carried out as part of the Biotecsur Consortium (Apoyo al desarrolo de las biotecnologias en el Mercosur) and results are available in site http:bionfo.cnpso.embrapa.br/biotecsoja.

c) Microarray (Mortel *et al*., 2007): expression profiles of *WRKY* genes in leaves of resistant genotype (PI970230), which carries the *Rpp2* gene, and in susceptible genotype (Embrapa 48) in response to *P. pachyrhizi* infection were compared to that of uninfected leaves (mock inoculation/control). In the present study data obtained at 12 and 120 hai were considered since these time points exhibited higher gene expression. The 46 probes previously described as WRKYs were checked. The specificity of probes was analyzed using the Soybase and Phytozome databases. Only probes with significant *e*-values (<0.05) were considered.

d) Microarray (Schneider *et al*., 2011): global expression profile of soybean cultivar Ankur (PI462312), which carries the *Rpp3* resistance gene, inoculated with avirulent (Hawaii 94-1) and virulent (Taiwan 80-2) isolates of *P. pachyrhizi* was analyzed. Affy probe sets were searched using the tools available in Soybase database. In the present study only the WRKY probes that hybridize to single locus in the soybean genome were selected. Data obtained at 12 and 120 hai were considered since these time points

exhibited higher gene expression. Genes with a p-value <0.05 were considered as differentially expressed.

P. pachyrhizi bioassay for gene expression analysis

Soybean plants were grown in a pot-based system maintained under greenhouse conditions at 28±1ºC with 16/8 h light/dark at a light intensity of 22.5 $\mu Em^{-2}s^{-1}$ in Embrapa Soja, Londrina, PR, Brazil. The Embrapa-48 genotype which develops a Tan lesion (Mortel *et al.*, 2007) was used as a susceptible standard, and the PI561356 genotype which carries the resistance to soybean rust mapped on linkage group G (P.O. Camargo *et al.*, unpublished) was used as the resistant standard. Spores were harvested from leaves exhibiting sporulating uredinia and diluted in distilled water with 0.05% Tween-20 to a final concentration of 3 x 10^5 spores/mL. The spore suspension was sprayed onto plantlets at the V2 developmental stage. The same solution without spores was used for mock inoculation/control. Following inoculation, water-misted bags were placed over each individual pot for one day. One trifoliate leaf from each plant was collected at 12 and 192 hai, frozen in liquid nitrogen, and stored at -80 °C. Three biological replicates from each genotype were analyzed for both treatments.

Expression pattern analysis using reverse transcription and quantitative, real-time PCR (RT-qPCR)

Total RNA was extracted using the TRIzol reagent (Invitrogen) and further treated with DNAse (Promega) according to the manufacturer's instruction. The first-strand cDNAs were obtained with approximately 2 μg of DNA-free RNA in the M-MLV reverse transcriptase system (Invitrogen) with a 24-polyVT primer. RT-qPCR was conducted in StepOne Applied Biosystem real-time cycler^{TM}. The PCR-cycling conditions were implemented as follows: 5 min at 94 °C, followed by 40 repetitions of 10 s at 94°C, 15 s at 60°C and 15 s at 72°C, and ending with 2 min at 40°C. A melting curve analysis was performed at the end of the PCR run over a range of 55–99°C, increasing the temperature stepwise by 0.1°C every 1 s. Each 25 μL reaction comprised 12.5 μL of diluted DNA template, 1x PCR buffer (Invitrogen), 2.4 mM of $MgCl_2$, 0.024 mM of dNTPs, 0.1 μM of each primer, 2.5 μL of SYBR-Green (1:100000 - Molecular Probes Inc.) and 0.03 U of Platinum Taq DNA polymerase (Invitrogen). cDNA (1:100) templates were evaluated. All PCR reactions were carried out in technical quadruplicates. Reactions lacking templates were used as negative controls.

PCR amplifications were performed using gene-specific primers (Table 1). Primer-pairs designed to amplify an FBox protein and a Metalloprotease sequences were used as internal controls to normalize the amount of mRNA present in each sample. These genes were confirmed as good reference genes in previous reports (Jian *et al*. 2008; Libault *et al*., 2008). All expression data analyses were performed after comparative quantification of amplified products using the $2^{-\Delta\Delta Ct}$ method as previously described (Livak & Schmittgen, 2001). Results were statistically compared by variance analysis with three-factor factorial treatments: genotypes, time and pathogen presence. The data were transformed using the weighted least squares method. Means were compared using Tukey multiple comparison test.

Silencing and overexpression vector construction

The open reading frame (ORF) of Glyam15g00570 (Gm*WRKY27*) was amplified from MGBR-46 Conquista soybean cultivar, using a high-fidelity Taq DNA Polimerase (*Pfu* − Fermentas). The Gateway® System (Invitrogen) was used to recombine PCR product into the overexpression pH7WG2D,1 vector (Karimi *et al*., 2002). The T-DNA region of the resulting pH7WG2D-Glyma15g00570 vector contained the Glyma15g00570 gene ORF under control of the CaMV *35S* promoter, the hygromycin-phosphotransferase marker gene (*hpt*) and the green fluorescent protein reporter gene (*gfp*) (Fig. 1a). A RNAi silencing vector was constructed using pH7GWIWG2(II),0 (Karimi *et al*., 2002). The T-DNA region of the resulting pH7GWIWG2 (II),0-Glyma15g00570 vector contained inverted repeat fragments (176 pb) of Glyma15g00570, separated by a intron of *Arabidopsis*, under the control of CaMV *35S* promoter and the hygromycin-phosphotransferase marker gene (*hpt*) (Fig. 1b). Both constructions were confirmed by DNA sequencing.

Soybean transformation and plant regeneration

Pods containing immature seeds of 3-5 mm in length from soybean cultivars MGBR 46 (Conquista), BRSMG 68 (Vencedora), IAS5 and Bragg were harvested from field grown plants. Somatic embryogenesis was induced from immature cotyledons and proliferated as described by Droste *et al*. (2002). Proliferating embryogenic tissues were submitted to transformation by particle bombardment using the particle inflow gun (PIG; Finer *et al*., 1992) following the procedure described by Droste *et al*. (2002) or by the combined DNA-free particle bombardment and *Agrobacterium* system as previously

described (Wiebke-Strohm *et al*., 2010). After three months in hygromycin-B selection medium, hygromycin-resistant embryogenic soybean tissues were visually selected, counted and individually cultured for the establishment of lines corresponding to putative independent transformation events.

Embryo histodifferentiation, conversion into plants and acclimation were carried out as described by Droste *et al*. (2002). All plants derived from an independent piece of hygromycin-resistant tissue were considered as being cloned plants. Plants derived from non-transformed embryogenic tissues submitted to the same culture conditions were recovered and used as controls for molecular characterization and bioassay.

The cultivars Bragg, BRSMG68 Vencedora and MGBR-46 Conquista were selected to Biobalistic transformation experiments due to their competence to somatic embryogenesis (Droste *et al*., 2000, 2002, 2010). IAS5 soybean cultivar was chosen to transformation via Biobalistc/*Agrobacterium* integrated system, due to their competence to somatic embryogenesis as well as their high susceptibility to *Agrobacterium tumefaciens* wild-type strains (Droste *et al*., 2010).

Screening for transgenic embryos and plants

Total DNA was extracted (Doyle & Doyle, 1987) from plant leaves. Putative transgenic plants were PCR-screened for the presence of the complete T-DNA using different primers combinations (Table 2). The PCR mixture consisted of 200 ng of template DNA, 0.4 mM of dNTPs, 0.4 μM of each primer, 2.5 mM of $MgCl_2$, 1x Taq Buffer, 1 U of Taq DNA Polymerase (Invitrogen), and autoclaved distilled water in a final volume of 25 μl. The reactions were heated at the beginning (5 min at 94°C) and subjected to 30 cycles as follows: 45 s at 94°C, 45 s at 58 °C and 1 min at 72°C. After electrophoresis in a 1% agarose gel containing ethidium bromide (0.01 mg/L), the PCR-products were visualized under ultraviolet light.

GFP expression was detected under blue light using an Olympus[®] fluorescence stereomicroscope equipped with a BP filter set containing a 488 nm excitation filter and a 505-530 nm emission filter. Images were captured using the software QCapture Pro™ 6 (QImaging[®]).

Gene overexpression or silencing was confirmed by RT-qPCR. RNA extraction, cDNA synthesis and qPCR were carried out as described above.

Fungal bioassay

A detached leaf method was used to evaluate soybean plant infection by *P. pachyrhizi* (Twizeyimana *et al.*, 2006). Three fully expanded leaves from one transgenic and two wild-type plants (2-month-old) were collected, rinsed on sterile distilled water and cut in 5 cm × 5 cm pieces. Each leaf piece was inoculated by dripping 1 mL of a uredospores suspension (10^5 spores/mL) and placed with abaxial side upwards in a Petri dish covered with wet filter paper. The material was incubated at 20°C with a 12/12 h light/dark cycle. Number of lesions and pustules were recorded 12 days after inoculation. A non-parametric Student's *t* -test, was carried out to compare the effect of *P. pachyrhizi* on transgenic and non-transgenic plants. The results with $p < 0.05$ were considered significant.

Results

Annotation, *in silico* characterization and clustering

A total of 198 soybean *WRKY*-encoding genes was identified in the Planttfdb, SoyDB and Plntfdb databases. Using HMMER with Pfam, 11 sequences were discarded: Glyma06g41910, Glyma07g20510, Glyma08g32740, Glyma12g20900, Glyma12g31860, Glyma13g34250, Glyma14g35150, Glyma14g36450, Glyma15g21570, Glyma18g48460, Glyma20g16010. Another three genes (Glyma05g38200, Glyma13g05720 and Glyma20g03820) were also excluded as they did not contain the conserved WRKYGQK domain signature. Forty-six out of 184 predicted *GmWRKY* genes presented incorrect gene models: 44 wrong start/stop codons and two truncated proteins. Most sequences were manually corrected (Supplementary Fig. 1). However, even after correction, four sequences (Glyma08g08290, Glyma14g12290, Glyma17g24700 and Glyma17g24710) did not fit gene models and two sequences (Glyma07g13610, Glyma12g29970) with a lower *e*-value were discarded. Therefore, a final number of 178 potentially *WRKY*-encoding genes were identified and annotated in the present work (Table 3). Transcripts of 140 annotated WRKY genes were detected.

The *GmWRKY* genes are distributed over the 20 soybean chromosomes with protein sequences ranging from 363 to 2,286 amino acids (Table 3). There is an average of 8.9 *WRKY* genes per chromosome, with the higher amount of members (15 genes) found in chromosome 6, whereas only two members were detected in chromosome 20.

By the number of WRKY domains and the pattern of zing-finger motives, proteins were assigned to three major groups and subgroups, according to Eugelm *et al.* (2000). Genes with two WRKY domains belong to group I, whereas genes of group II and III contained only a single WRKY domain. Proteins containing two WRKY domains have the major DNA-binding activity in the C-terminal domain, whereas the function of N-terminal domain remains unclear (Eulgem *et al.*, 1999; Maeo *et al.*, 2001). Both group I and II have a C_2–H_2-type zinc finger motif (C–$X_{4–5}$–C–$X_{22–23}$–H–X_1–H). Group II was further divided into subgroups (a-e) based upon additional amino acid motifs present in WRKY domain. The zinc finger motif of group III contains a C_2–HC motif (C–X_7–C–X_{23}–H–X_1–C). Group I, II and III contain 33, 121 and 23 soybean WRKY members, respectively (Table 3). Glyma10g31410 could not be consistently classified and therefore remain unassigned. Thirteen, 31, 39, 16 and 22 proteins were assigned to subgroup IIa, IIb, IIc, IId and IIe, respectively.

Although the WRKYGQK signature is highly conserved in the soybean WRKYs, 16 proteins with amino acid substitutions in the signature of the C-terminal domain were identified. These variant proteins are distributed in all groups, except subgroup IId. WRKYGKK is the most common variant shared by 11 members. Other atypical sequences (WRKYGEK, WRKYEDK, WKKYGQK, CRKYGQK and WHQYGKK) occurred in single proteins. Thirteen WRKY proteins contained incomplete and/or amino acid substitutions in the zinc finger sequence (Table 3). Some of these proteins contain patterns of zinc finger motifs that have not been reported in the literature. Expression was detected for ten genes presenting modifications in WRKY signature and two in zinc finger motif, indicating that they may be functional. Lacking expression of variant genes suggests they could be pseudogenes. Furthermore, another highly conserved domain, the Zinc Cluster, was identified right upstream of the WRKY domain in IId members.

Clustering of the full-length proteins clearly split up the *Gm*WRKY members into three groups, which corresponds to the WRKY domain classification (groups I, II and III). Group II was further divided in the five distinct subgroups (IIa-e) (Fig. 2). Group IIa and IIb genes form two closely related clades, as well as group IId and IIe genes. The exceptions were the presence of Glyma10g31420, Glyma07g16040, Glyma18g39970 and Glyma14g37960 (IIc) in a separated branch. Furthermore, clustering suggests that most of *WRKY* genes are present as double or quadruple copies.

Gene expression data

An overview of differential expressed soybean *WRKY* genes in response to *P. pachyrhizi* infection is presented in Table 4. Four different experiments were considered: a SuperSAGE, a RNA-Seq of microdissected lesions and two different microarrays. Seventy-four members showed differential expression in at least one experiment, whereas 16 in more than one experiment. Genes from all three groups seem to respond to this stress condition.

Some genes presenting differential expression profiles in response to the fungus were selected for more detailed analyses. Glyma15g00570 and Glyma09g41050 were differentially expressed in three out of the four experiments, while Glyma08g23380, Glyma07g02630 and Glyma08g02580 in the two microarrays. Glyma13g44730, Glyma05g36970, Gyma18g44560 were also analyzed since they are closely related to at least one of the genes above. Curiously none of these genes was expressed inside rust infection lesions ten days after fungus inoculation (RNA-Seq of lesion LCM).

Differential expression of these genes was confirmed by RT-qPCR. Transcript levels during the course of fungus infection in a resistant genotype (PI561356) and in a susceptible genotype (Embrapa-48) were compared to that of mock inoculated plants (Fig. 3).

Interaction among genotypes, time-course and pathogen presence was highly significant ($p<0.0001$). Expression of some genes (Glyma15g00570, Glyma05g36970, Glyma09g41050 and Glyma18g44560) in mock-inoculated plants was continuous in both genotypes, while for other genes (Glyma13g44730, Glyma08g23380, Glyma07g02630 and Glyma08g02580) a slight modulation in expression pattern was observed. In the inoculated plants the eight genes showed an earlier expression in PI561356 (resistant host) when compared with Embrapa 48 (susceptible host). In the Embrapa 48 the expression peaks were higher 24 and/or 96 hai, while in PI561356 these peaks varied from one to 24 hai. Furthermore Glyma08g23380, Glyma07g02630, Glyma08g02580 and Glyma09g41050 presented a stronger response in the resistant genotype. Interestingly the homologous genes (Glyma15g00570 and Glyma13g44730, Glyma09g41050 and Glyma18g44560) did not overlap their expression peaks in the resistant genotype. Glyma15g00570 and Glyma18g44560 showed higher expression levels one hai followed by a decrease, whereas Glyma13g44730 and Glyma09g41050 presented higher transcript levels 12 hai.

Glyma15g00570 overexpression and silencing in soybean plants

Glyma15g00570 was selected for further functional characterization because it was one of the genes which shows differential expression in different experiments evaluated in the present study. Furthermore it was also showed that this gene is involved in different abiotic stresses (Zhou *et al.*, 2008). In order to determine the functional role of the Glyma15g00570 in response to *P. pachyrhizi*, soybean somatic embryos were transformed aiming gene overexpression or silencing. In overexpression experiment, GFP expression was detected in hygromycin resistant globular embryos (Supplementary Fig. 2a and b). Histodifferentiated embryos of nine independent transgenic lines (seven from Biobalistic and two from bombardment/*Agrobacterium*) were obtained. The presence of the T-DNA in embryo genomes was confirmed by PCR and the Glyma15g00570 expression was significantly higher in embryos of four transgenic independent lines (Supplementary Fig. 1c). However, development of transgenic embryos overexpressing Glyma15g00570 did not proceed. As a consequence those embryos were not able to convert into plants.

For gene silencing, a vector carrying a 176 pb inverted-repeat fragment from Glyma15g00570 was constructed. This fragment shares 94% similarity with the homologous region of Glyma13g44730 and 76% with both Glyma08g23380 and Glyma07g02630. This data reflects the close relationship among the genes revealed by the clustering analysis (Fig. 2). Based on the high sequence similarity we could predict that the silencing construct would target the four homologous genes.

In light of the above results a more detailed structural analysis of the four homologous genes was performed. WRKYGQK signature, zinc finger motif and other residues into the domain are highly conserved in all four corresponding proteins (Fig. 4a). The identity of the complete proteins varied from 74% up to 94% (Table 5). The four soybean genes are putative orthologous of *AtWRKY40, AtWRKY18* and *AtWRKY60* Arabidopsis genes. The gene structure of Glyma15g00570, Glyma13g44730, Glyma08g23380 and Glyma07g02630 is very similar, with the WRKY domain present in the fourth exon (Fig. 4b). Interestingly, Glyma08gg23380 has four alternative transcripts, one of them lacking the WRKY domain.

Two independent transgenic lines (cultivar BRSMG 68 Vencedora) carrying the silencing construct were obtained. Molecular analysis showed that one of the repeats (176 pb fragment) was lost in the first line. Therefore the pos-transcriptional silencing was not triggered, which was confirmed by non-reduction of transcript levels in RT-

qPCR (data not shown). In the second transgenic line (P3-2) the complete cassette was successfully integrated (Fig. 5a). As anticipated, RT-qPCR analysis showed that the expression of the four homologous genes was significantly reduced (Fig. 5b). Transgenic line exhibited no major visible altered phenotype when compared to control plants.

Silenced line was shown to be more susceptible to *P. pachyrhizi*

In order to confirm the involvement of Glyma15g00570, Glyma13g44730, Glyma08g23380 and Glyma07g02630 in soybean response to *P. pachyrhizi*, a detached leaf assay was carried out. As previously described, there is a high correlation of the susceptibility to *P. pachyrhizi* between detached leaf and intact plant bioassays (Twizeyimana *et al*., 2006). In the present study, tan lesions could be observed in all detached leaves of both transgenic and wild-type samples 12 days after *P. pachyrhizi* inoculation. However the number of lesions was significantly higher in leaves of the transgenic line (Fig. 6). No visible difference was observed on the timing of lesion and pustule formation or pustule eruption (data not shown).

Discussion

Soybean WRKY genes

The whole genome sequence (Schmutz *et al*., 2010) has allowed the accurate annotation of soybean gene families. In this study we present the annotation of 178 members of WRKY transcription factors in soybean. Transcripts of most genes (140) were detected, suggesting they can be expressed in protein level. Specific conditions must be necessary for transcription of the remaining genes. Some of these genes might represent pseudogenes.

The terminology of soybean WRKY members has not a consensus in the literature. Phytozome database assign names from Arabidopsis orthologous, while Zhou *et al*. (2008) numbered randomly the 64 soybean WRKY genes (deposited in NCBI) identified by his research group. In addition, studies with individual genes (Zhang *et al*., 2008; Kang *et al*., 2009) have assigned numbers different from that proposed by Zhou *et al*. (2008). With the aim of unifying the terminology, we are proposing a nomenclature based on Phytozome gene ID.

The number of *WRKY* genes identified in soybean was higher than that previously described for other species, such as rice and Arabidopsis (Eugelm *et al*.,

2000; Wu *et al*., 2005; Xie *et al*., 2005; Zhang & Wang, 2005; Ross *et al*., 2007). Clustering analysis suggests that most of the soybean *WRKY* genes are present as double or quadruple copies. This pattern is expected, since two duplication events occurred in soybean genome (Schmutz *et al*., 2010). The duplication events are vastly overretained specifically in the case of transcription factors because they are too costly to be removed (Freeling, 2009). According to the author, the functional redundancy is a common feature in plant species. Homologous genes might diverge in function or subfunctionalize, providing a source of evolutionary novelty (Carretero-Paulet *et al*., 2010).

Clustering analysis of WRKY domain sequences of rice (Zhang & Wang, 2005) and tobacco (Rushton *et al*., 2008) has divided WRKY family members into I, IIa+IIb, IIc, IId+IIe and III groups. The cladogram of soybean *WRKY* genes, constructed with full-length protein sequences, resulted in the separation of the members in the same five groups. The use of full-length sequences adds more accuracy and reliability to tree resolution (Amoutzias *et al*., 2004), once the WRKY domain is a short and highly conserved sequence. Some genes that did not clustered properly were exceptions and might reflect similarities/differences outside the WRKY domain. Anyway, the features of the domain appear to have the most important contribution to shape the WRKY family clustering.

In soybean all members of group I contain domains formed by a C_2H_2-type zinc finger motif. The same characteristic is observed in Arabidopsis, while in rice the WRKY domains of group I members include two types of zinc finger motifs: a C_2H_2 and C_2HC (Wu *et al*., 2005; Xie *et al*., 2005).

Although the WRKYGQK signature is highly conserved among soybean WRKY proteins, variants were identified into 20 genes. Zhou *et al*. (2008) have already described that Glyma08g15050 (*GmWRKY6*) and Glyma04g39650 (*GmWRKY21*) contain the variant WRKYGKK rather than the conserved WRKYGQK motif. Slight variations into this region have been also reported in Arabidopsis, rice, tobacco, barley, canola and sunflower (Zhang *et al*., 2005; Xie *et al*., 2005; Mangelsen *et al*., 2008; van Verk *et al*., 2008; Yang *et al*., 2009; Giacomelli *et al*., 2010). Compared to Arabidopsis, which contain four WRKYGKK variants, the number of genes with mutated motif is greater in soybean.

Some unusual *GmWRKY*-encoding genes (i.e. with modified WRKY signature and/or zinc finger motif) produced mRNA (Table 4). Further analyses are necessary to

show if these genes are functional as transcription factors or they trigger post-transcriptional regulation by RNAi, as previously suggested (Pandey & Somssich, 2009). Variant proteins may have abolished or decreased their ability to bind to the W-box (Maeo *et al*., 2001; Ciolkowski *et al*., 2008). It has been suggested that WRKY proteins without the canonical WRKYGQK motif may have different binding sites (Ciolkowski *et al*., 2008; van Verk *et al*., 2008), target genes and possibly divergent roles (Yang *et al*., 2009).

Functional analysis

Despite the fact that identification or prediction of many WRKY genes from different species have been done, only a small number of them have been functionally characterized. Information about the role of soybean genes (Glyma13g00380, Glyma04g39650, Glyma10g01450 and Glyma18g44560) during abiotic stresses has been based in heterologous expression systems (Zhang *et al*., 2008; Zhou *et al*., 2008). Involvement of *WRKY* genes in response to biotic stresses is mainly supported by expression data (Mortel *et al*., 2007; Kang *et al*., 2009). Global expression profiling studies have demonstrated the importance of *WRKY*-encoding genes in transcriptional reprogramming during soybean infection by *P. pachyrhizi* (Choi *et al*., 2007; Mortel *et al*., 2007; Panthee *et al*., 2007; Panthee *et al*., 2009; Tremblay *et al*., 2010; Schneider *et al*., 2011).

In order to determine which soybean *WRKY* genes are involved in plant defense against *P. pachyrhizi*, we performed a series of analysis to investigate their expression pattern after infection. Firstly we compared microarray data available in the literature (Mortel *et al*., 2007; Schneider *et al*., 2010) with results obtained from two other experiments: SuperSAGE and RNA-Seq of lesion LCM (Laser Capture Microdissection). Many genes were differentially expressed in only one library, while few of them showed differential expression in more than one. Modulation in the transcript levels of eight genes was validated, showing the reliability of data mining. *WRKY* genes which respond to *P. pachyrhizi* were distributed among all classification groups (I, II and III). By comparing data mining in response to *P. pachyrhizi* infection with the cladogram, similar expression pattern could be observed in closely related genes, such as Glyma06g15220 and Glyma04g39650, Glyma14g11920 and Glyma17g33920, Glyma07g02630 and Glyma08g23380, Glyma04g40130 and Glyma06g14720. Similar expression pattern suggests that genes may share similar

functions in disease resistance. The redundant function of *GmWRKY* genes may be beneficial in protecting the cell or organism under various stress conditions and in eliciting multiple pathways that lead to the wide array of physiological responses that occur following infection with pathogens (Ryu *et al.*, 2006).

Global expression data have suggested that timing and the degree of induction of a defense pathway are determinant to induce soybean resistance to *P. pachyrhizi* (Mortel *et al.*, 2007; Choi *et al.*, 2008; Goellner *et al.*, 2010; Schneider *et al.*, 2011). In our study, the expression induction of Glyma18g44560, Glyma15g00570, Glyma13g44730, Glyma09g41050, Glyma08g23380, Glyma08g02680, Glyma07g02630 and Glyma05g36970 in response to *P. pachyrhizi* was earlier and∕or stronger in the resistant genotype. Since the eight analyzed genes showed the expression peak at the first 24 hai, we assume they might be involved in a non-specific defense response. Mortel *et al.* (2007) and Schneider *et al.* (2011) reported that *P. pachyrhizi* induce a biphasic global expression. A first peak of gene expression occurred at 12 hai, which corresponded to the early infection processes of appressoria formation and epidermal cells penetration. The authors suggested that this peak corresponded to a non-specific defense response similar to Pathogen Triggered Immunity (PTI). A second phase of gene expression, which starts 72 hai and continues until 288 hai, is coincident with the haustoria formation and effector secretion. The authors suggested that this response is consistent with the activation of *RPP2* and *RPP3*-mediated resistance. It has been shown that gene expression is faster and of greater magnitude in the incompatible interaction (Mortel *et al.*, 2007, Panthee *et al.*, 2007; Schneider *et al.*, 2011).

The closely related genes Glyma15g00570, Glyma13g44730, Glyma08g23380 and Glyma07g02630 are putative orthologous of *AtWRKY40, AtWRKY18* and *AtWRKY60* Arabidopsis genes. In both species these genes were classified into group IIa. The three Arabidopsis WRKY are involved in stress responses, for instance, against the bacteria *Pseudomonas syringae* and fungus *Botrytis cinerea* (Xu *et al.*, 2006; Chen *et al.*, 2010). *AtWRKY18* is a salicylic acid-induced gene that positively regulates SAR (Yu *et al.*, 2001; Wang *et al.*, 2006), modulates PR gene expression and its overexpression increases the resistance to *P. syringae* (Chen & Chen, 2002). *At*WRKY40 and *At*WRKY60 proteins antagonize *At*WRKY18 during *P. syringae* infection. Gain or loss of gene function in single, double or triple combination resulted in higher susceptibility to *B. cinerea* (Xu *et al.*, 2006). Some *Oryza sativa, Hordeum*

vulgare and *Brassica napus* WRKY members from group IIa are also involved in response to fungal and bacterial pathogens, as demonstrated by expression studies. O*sWRKY62* and *OsWRKY76* are upregulated in *Magnaporthe grisea* infected-leaves *and* downregulated in *Xanthomonas oryzae* inoculated leaves (Ryu *et al*., 2006). *HvWRKY1* and *HvWRKY2* play an important role in response to *Blumeria graminis* (Mangelsen *et al*., 2008), and *BnWRKY18 and BnWRKY40* in response to *Sclerotinia sclerotiorum* and *Alternaria brassicae* (Yang *et al*., 2009).

Most available information on gene function is based in heterologous expression systems. However, as activity of many promoters or proteins frequently depends on specific interactions only found in homologous backgrounds, the present study was based on an homologous expression system. RNA interference approach was used for silencing of four soybean homologous genes (Glyma15g00570, Glyma13g44730, Glyma08g23380 and Glyma07g02630). The quadruple silencing is an advantage since single knockout of transcription factors rarely exhibit altered phenotypes because of functional redundancy among closely related members (Chen & Chen, 2002). The transgenic RNAi line presented significant reduction in transcript levels of the four target genes. When infected by *P. pachyrhizi* the transgenic line showed higher susceptibility to the fungus. This result together with expression data strongly suggest that at least one of the four genes must be involved in the soybean resistance phenotype.

Glyma15g00570 was selected for overexpression study. Histodifferentiated embryos overexpressing this gene were obtained from four independent transformation experiments. However, plants were not recovered. The most likely explanation is that the constitutive overexpression of the Glyma15g00570 may affect the regeneration of plants. The use of constitutive promoters in investigation of genes whose constant overexpression has deleterious effects on the plant is a major limitation (Zuo *et al*., 2000). Chen & Chen (2002) reported that high levels of *At*WRKY18 cause severe abnormality in plant growth. Even at moderate levels, individual or in combination overexpression of *AtWRKY18*, *AtWRKY40* and *AtWRKY60* lead to development of smaller plants or to death after germination (Xu *et al*., 2006). The deleterious effect of excessive production of these WRKYs on plant growth suggested that expression of the gene might require proper regulation during the activation of plant defense responses. However in healthy plants, expression of those genes is negatively regulated, as demonstrated by Chen & Chen (2002) for the *AtWRKY18*.

To a certain extent, the lethality problems observed in the present study could be partially overcomed by using tissue-specific, developmentally-regulated or inducible promoters. Although the number of tissue-specific promoters has increased in recent years, soybean leaf-specific promoters are not available so far.

In conclusion, in the present study 178 soybean WRKY transcription factors were annotated. Seventy-four genes were identified as involved in soybean response to *P. pachyrhizi*. The participation of four of those genes in response to that pathogen was demonstrated using RNAi approach. Further investigations are required to provide clues regarding the function of the individual genes.

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Table 1. Primer set designed for RT-qPCR**.**

Target	Orientation	Tm*	Primer Sequence	PCR product size (pb)
Glyma1844560 transcripts	Forward	60	5´-TCCCTCAACTTCCTCCAATC-3´	170
	Reverse	60	5´-GGAAGGGTTCAAAGGCATC-3´	
Glyma15g00570 transcripts	Forward	61.69	5´-GATTGTGCATTTGCTAATCATGC-3´	105
	Reverse	59.93	5´- GCTATAGAAACTTCGCCAGAAC-3´	
Glyma13g44730 transcripts	Forward	60.53	5´-CAAATCCTTTTGGTGGGAATC-3´	145
	Reverse	59.30	5´-CTATAGAAATTTCGCAAGAACTTAACC-3´	
Glyma09g 41050 tanscripts	Forward	60	5´-TCTCATCTTCCAATAATTTCCCA-3´	135
	Reverse	60	5´-CATGATGCCTTGGTGAGCTA-3´	
Glyma08g23380 transcripts	Forward	60.06	5´-CACCCATCTGCCTCATCAC-3´	234
	Reverse	59.17	5´-GGAGGCCGAGTCTGTACAAT-3´	
Glyma08g02580 transcripts	Forward	60	5´-TTGCAAAGTTCAGAAGTATCTTGTC-3´	264
	Reverse	60	5´-GTGACCTGTTGTAGATCCCATC-3´	
Glyma07g02630 transcripts	Forward	59.72	5´-GGAAATAAAGTTCCACTAAGGATGAC-3´	174
	Reverse	60.57	5´ - CCGAGAATGTGTGCTACAACC-3´	
Glyma05g36970 transcripts	Reverse	60	5´-CAATGCATCATCAACTTCCG-3´	213
	Forward	60	5´-CAAGACCACTTTCACAGCTCAC-3´	
Metalloprotease transcripts	Forward	60.5	5´-ATGAATGACGGTTCCCATGTA-3´	114
	Reverse	60.17	5´-GGCATTAAGGCAGCTCACTCT-3´	
FBox transcripts	Forward	60.25	5´-AGATAGGGAAATGTTGCAGGT-3´	93
	Reverse	59.84	5´-CTAATGGCAATTGCAGCTCTC-3´	

*Calculated Tm under PCR condition.

Table 2. Primer set designed to gene isolation and transgene detection.

Target	Orientation	Tm (ºC)	Primer Sequence	PCR product size (pb)
35S	Forward	52	5´-GGACCCCCACCCACGAGGAG-3´	139*
Glyma15g00570 (overexpression)	Forward	58	5´- CACCATGGATTATTCATCATGGATTAACA-3´	921
	Reverse		5´- TTAATTATTATTGTGCAACATTTTTC-3´	
WRKY (RNAi)	Forward	58	5´- CACCCTTCCTTGGATCTCAACATTAATCT -3´	176
	Reverse		5´- TAACTTCTTGTTTTCTGCACTCACC -3´	
Intron	Forward	60	5´- TGCCTCTTCTTACGGCTTTCTGTG -3´	400
	Reverse		5´ - TGCCGTCTGTGATGGCTTCCA -3´	
Hpt	Forward	60	5´-GCGATTGCTGATCCCCATGTGTGTAT-3´	512
	Reverse		5´-GGTTTCCACTATCGGCGAGTACTT-3´	

* Fragment length was considered from primer until the end of the promoter sequence.

Table 3. Annotation of *Glycine max* WRKY transcription factors

Chr	Gene ID[1] (Phytozome)	Name according to Zhou *et al*. (2008)	Alternative transcripts	CDS (pb)	Protein (aa)	Groups[2]	Expression confirmed[3]	Soybase EST ID	Domain modifications
1	Glyma01g05050			1392	464	IIb	+	-	
1	Glyma01g06550	*GmWRKY9*		1368	456	I	+	EU019557.1	
1	Glyma01g06870	*GmWRKY28*	4	894	298	IIc	+	CA938308.1	
1	Glyma01g31920	*GmWRKY5*		1350	450	I	+	EU019554.1	WRKYGQK → WRKYGEK (N-terminal)
1	Glyma01g39600		2	966	322	IId	+	BG651351.1	
1	Glyma01g43130			720	240	IIe	+	-	$CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}HXD$
1	Glyma01g43420	*GmWRKY12*		969	323	III	+	EU019558.1	
2	Glyma02g01030*			780	260	IIb	-	-	
2	Glyma02g01420			963	321	IIc	+	BT096212.1	
2	Glyma02g02430*			1443	481	IIb	-	-	
2	Glyma02g12490			1368	456	I	+	FK022538.1	
2	Glyma02g12830	*GmWRKY32*		882	294	IIc	+	BM527576.1	
2	Glyma02g15920	*GmWRKY22*	3	1068	356	IId	+	AK244154.1	
2	Glyma02g36510			1518	506	I	+	FG988660.1	
2	Glyma02g39870	*GmWRKY39*		1743	581	I	+	BM188894.1	
2	Glyma02g45530			945	315	IIc	+	BE020472.1	
2	Glyma02g46280*			1086	362	IIb	-	-	
2	Glyma02g46690		2	1767	589	I	+	BG789786.1	
2	Glyma02g47650			1524	508	I	+	CO984087.1	
3	Glyma03g00460			747	249	III	+	BT095645.1	
3	Glyma03g05220			1104	368	I	+	EV272592.1	WRKYGQK → WRKYGEK (N-terminal)
3	Glyma03g25770			717	239	IIc	+	EV274902.1	
3	Glyma03g31630	*GmWRKY15*		1026	342	IId	+	CD397604.1	
3	Glyma03g33380	*GmWRKY29*		1263	421	I	+	EU019569.1	
3	Glyma03g37870	*GmWRKY41*		762	254	IIe	+	EU019577.1	
3	Glyma03g37940	*GmWRKY51*		864	288	IIc	+	BT098285.1	
3	Glyma03g38360			1626	542	IIb	+	DB956313.1	
3	Glyma03g41750	*GmWRKY43*		1089	363	III	+	EU019579.1	
4	Glyma04g05700			486	162	IIc	+	FK004547.1	WRKYGQK → WRKYGKK
4	Glyma04g06470*			750	250	IIa	+	-	
4	Glyma04g06480			735	245	IIa	+	EV275620.1	$CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}$
4	Glyma04g08060	*GmWRKY50*		840	280	IId	+	EU019586.1	
4	Glyma04g12830			2286	762	I	+	BI471108.1	
4	Glyma04g34220*			1377	459	IIb	-	-	
4	Glyma04g39620	*GmWRKY45*		369	123	IIc	+	EU019581.1	
4	Glyma04g39650	*GmWRKY21*		621	207	IIc	+	DQ322691.1	WRKYGQK → WRKYGKK
4	Glyma04g40120			501	167	III	-	-	
4	Glyma04g40130	*GmWRKY58*		954	318	III	+	EU375354.1	
4	Glyma04g41700*			792	264	III	+	BG653111.1	
5	Glyma05g01280			1572	524	IIb	+	GR858756.1	
5	Glyma05g20710	*GmWRKY11*		1005	335	IId	+	EU375356.1	
5	Glyma05g25270			1056	352	IIb	+	EV280519.1	$CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}HXT$
5	Glyma05g25330			897	299	IIe	-	-	
5	Glyma05g25770			1077	359	IIc	+	BW658787.1	
5	Glyma05g29310			768	256	IIe	+	GR846019.1	
5	Glyma05g31800		2	567	189	IIc	+	BT091158.1	WRKYGQK → WRKYGKK
5	Glyma05g31910*			381	127	IIc	-	-	
5	Glyma05g36970	*GmWRKY46*		1092	364	III	+	EH258436.1	
5	Glyma05g37390			798	266	IIe	-	-	
6	Glyma06g05720*			534	178	IIc	-	-	WRKYGQK → WRKYGKK; $CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}WX_{(N)}HXH$
6	Glyma06g06530	*GmWRKY17*		885	295	IIa	+	BT095976.1	
6	Glyma06g08120	*GmWRKY37*		903	301	IId	+	EU375346.1	
6	Glyma06g13090			1095	365	III	+	FK007605.1	
6	Glyma06g14720			960	320	III	+	AK244967.1	
6	Glyma06g14730*			615	205	III	-	-	
6	Glyma06g15220	*GmWRKY61*		591	197	IIc	+	EH220254.1	WRKYGQK → WRKYGKK
6	Glyma06g15260			711	237	IIc	+		
6	Glyma06g17690*			483	161	IIc	-	-	WRKYGQK → WRKYGKK
6	Glyma06g20300			1821	607	IIb	+	DB968378.1	
6	Glyma06g23990*			525	175	IIa	-	-	WRKYGQK → WKKYGQK
6	Glyma06g27440		2	1257	419	I	+	BT093246.1	
6	Glyma06g37100*			516	172	I	-	-	
6	Glyma06g46420			1743	581	IIb	+	CO979705.1	
6	Glyma06g47880	*GmWRKY59*	2	2061	687	I	+	CA801226.1	
7	Glyma07g02630			936	312	IIa	+	AK245986.1	
7	Glyma07g06320	*GmWRKY55*		1110	370	III	+	BT093956.1	
7	Glyma07g16040*			954	318	IIc	-	-	
7	Glyma07g35380*			1023	341	I	+	-	
7	Glyma07g36640			1128	376	IIc	+	DB967901.1	
7	Glyma07g39250	*GmWRKY34*		1554	518	IIb	+	EU019573.1	
8	Glyma08g01430	*GmWRKY25*		444	148	IIc	+	EU019567.1	WRKYGQK → WRKYGEK
8	Glyma08g02160			840	280	IIe	+	CA938468.1	
8	Glyma08g02580	*GmWRKY20*		1080	360	III	+	BT095747.1	
8	Glyma08g08340			1290	430	IIe	-	-	
8	Glyma08g08720			942	314	IIc	-		
8	Glyma08g12460	*GmWRKY48*		786	262	IIe	+	GR844807.1	
8	Glyma08g15050	*GmWRKY6*		555	185	IIc	+	EH260054.1	WRKYGQK →WRKYGKK
8	Glyma08g15210	*GmWRKY40*	3	708	236	IIc	+	DQ322692.1	

Table 3. (Continued from previous page)

Chr	Gene ID[1] (Phytozome)	Name according to Zhou et al. (2008)	Alternative Transcripts	CDS (pb)	Protein (aa)	Groups[2]	Expression confirmed[3]	Soybase EST ID	Domain modifications
8	Glyma08g23380	GmWRKY56	4	942	314	IIa	+	EU375348.1	
8	Glyma08g26230	GmWRKY4		1572	524	I	+	EU375355.1	
8	Glyma08g43260*		2	1437	479	IIb	+	-	
8	Glyma08g43770	GmWRKY35/18		1791	597	I	+	BU080760.1	
9	Glyma09g00820	GmWRKY23		1626	542	IIb	+	AK245933.1	
9	Glyma09g03450			1353	451	IIe		-	
9	Glyma09g03900	GmWRKY26		996	332	IIc	+	GR833156.1	
9	Glyma09g06980	GmWRKY47		891	297	IId	+	EU019583.1	
9	Glyma09g09400			1041	347	IIb	+	CF808085.1	
9	Glyma09g23270*			924	308	IIb	-	-	$CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}$**KXP**
9	Glyma09g24080			867	289	IIe	-	-	
9	Glyma09g37470*			1626	542	IIb	-	-	
9	Glyma09g37930			687	229	IIc	+	BT091680.1	
9	Glyma09g38580*			1554	518	I	+	-	
9	Glyma09g39000			579	193	IIc	+	AW307474.1	
9	Glyma09g39040			1047	349	IIe	+	BW658775.1	
9	Glyma09g41050			903	301	III	+	BT098696.1	
9	Glyma09g41670*			1632	544	I	-	-	WRKYGQK →W**I**KYGQK (N-terminal)
10	Glyma10g01450	GmWRKY54		972	324	IIc	+	DQ322698.1	
10	Glyma10g03820			1179	393	IId	+	DB971123.1	
10	Glyma10g13720			363	121	IIa	+	CO980573.1	WRKYGQK → WRKYG**KK**; $CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}$ (C-terminal)
10	Glyma10g14610			798	266	IIb	-	-	WRKYGQK → **C**RKYGQK; $CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}HX$**N**
10	Glyma10g27860*	GmWRKY1		1449	483	IIb	+	BI426286.1	
10	Glyma10g31410			660	220	indeterminat	-	-	WRKYGQK → **WHQ**YG**L**K ; $CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}$
10	Glyma10g31420*			1011	337	IIc	-	-	
10	Glyma10g37460	GmWRKY2		837	279	IIe	+	CO980938.1	
11	Glyma11g02360			807	269	IIe	-	-	$CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}HX$**Q**
11	Glyma11g05650	GmWRKY14	2	966	322	IId	+	EU019559.1	
11	Glyma11g29720	GmWRKY19		1647	549	I	+	AK245549.1	
12	Glyma12g10350			1686	562	IIb	+	BG839187.1	
12	Glyma12g23950	GmWRKY44		1404	468	I	+	EV282360.1	
12	Glyma12g33990	GmWRKY16		792	264	IIe	+	EU375351.1	
13	Glyma13g00380	GmWRKY13		975	325	IId	+	DQ322694.1	
13	Glyma13g17800			1227	409	IIb	+	CF807620.1	
13	Glyma13g34240*			885	295	III	-	-	
13	Glyma13g34260*			903	301	III	-	-	
13	Glyma13g34280*			813	271	III	-	-	
13	Glyma13g36540	GmWRKY52		798	266	IIe	+	CF807263.1	
13	Glyma13g38630	GmWRKY36		1845	615	IIb	+	EU019575.1	
13	Glyma13g44730			930	310	IIa	+	AK244287.1	
14	Glyma14g01010		2	1560	520	I	+	BM523517.1	
14	Glyma14g01980	GmWRKY3/7		1758	586	I	+	EH257685	
14	Glyma14g03280			1017	339	IIc	+	FK018954.1	
14	Glyma14g11440			450	150	IIc	-	-	WRKYGQK → WRKYG**KK**
14	Glyma14g11920			837	279	IIa	+	CD410097.1	
14	Glyma14g11960			858	286	IIa	+	BF009368.1	
14	Glyma14g17730	GmWRKY31		951	317	IId	+	GR845636.1	
14	Glyma14g36430			696	232	III	+	EV266531.1	
14	Glyma14g36440*			930	310	III	+	AI966709.1	
14	Glyma14g37960			999	333	IIc	+	FG986745.1	WRKYGQK → WRKY**ED**K (C-terminal)
14	Glyma14g38010*	GmWRKY49		1728	576	I	+	EU019585.1	
15	Glyma15g00570	GmWRKY27		921	307	IIa	+	DQ322695.1	
15	Glyma15g11680		2	1674	558	IIb	+	GR856238.1	
15	Glyma15g14370		2	933	311	IIe	-	-	
15	Glyma15g14860			1068	356	IIc	+	BW658350.1	
15	Glyma15g18250	GmWRKY42		882	294	IId	+	EU019578.1	
15	Glyma15g20990			1356	452	IIb	+	BW662875.1	
15	Glyma15g37120*			570	190	I	-	-	N terminal domain lacking; $CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}$**EXL** (C-terminal)
16	Glyma16g02960	GmWRKY60		1122	374	III	+	BT095906.1	
16	Glyma16g03480			528	176	IIc	+	BG650157.1	
16	Glyma16g03570			1008	336	IIe	+	FG989867.1	
16	Glyma16g05880			588	196	IIc	+	GR835181.1	
16	Glyma16g29500*			651	217	IIe	-	-	
16	Glyma16g29560*			903	301	IIe	+	EH260684.1	
16	Glyma16g34590*			798	266	III	+	-	
17	Glyma17g01490			1470	490	IIb	+	BE057555.1	
17	Glyma17g03950		2	1197	399	IIc	+	GR855044.1	
17	Glyma17g04710			1209	403	IIb	+	BG726970.1	
17	Glyma17g06450	GmWRKY33		963	321	IId	+	DQ322696.1	
17	Glyma17g08170	GmWRKY24		1518	506	I	+	AK245832.1	
17	Glyma17g10630*		2	1725	575	IIb	+	-	
17	Glyma17g18480			999	333	IId	+	BE473968.1	
17	Glyma17g25140			366	122	III	-	-	WRKYGQK →WRKYG**KK**; $CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}$**Q**$X_{(N)}$
17	Glyma17g25150*			486	162	I	-	-	WRKYGQK → WRKY**GE**K (N-terminal); C-terminal domain lacking
17	Glyma17g29190			951	317	IId	+	CK768919.1	
17	Glyma17g33890	GmWRKY30		555	185	IIa	+	EU019570.1	$CX_{(N)}CX_{(N)}HXH/C \rightarrow CX_{(N)}CX_{(N)}$**YXT**
17	Glyma17g33920	GmWRKY63		837	279	IIa	+	BT095938.1	
17	Glyma17g34210			570	190	IIc	+	-	WRKYGQK →WRKYG**KK**
17	Glyma17g35750			921	307	IId	-	-	$CX_{(N)}CX_{(N)}HXH/C \rightarrow $ _$X_{(N)}$_$X_{(N)}HXH$
18	Glyma18g06360*	GmWRKY62		1629	543	I	+	AK245515.1	

Table 3. (Continued from previous page)

Chr	Gene ID[1] (Phytozome)	Name according to Zhou et al. (2008)	Alternative Transcripts	CDS (pb)	Protein (aa)	Groups[2]	Expression confirmed[3]	Soybase EST ID	Domain modifications
18	Glyma18g09040*			1788	596	I	+	GD757522.1	
18	Glyma18g10330**			1353	451	IIb	-	-	
18	Glyma18g16170			1248	416	IIb	-	-	
18	Glyma18g39970			864	288	IIc	-	-	
18	Glyma18g44030		2	1626	542	I	+	BU764562.1	
18	Glyma18g44560	GmWRKY57		900	300	III	+	EU375353.1	
18	Glyma18g47300	GmWRKY10		1056	352	IIe	+	EU375344.1	
18	Glyma18g47350	GmWRKY64		579	193	IIc	+	EU019592.1	
18	Glyma18g47740*			2235	745	I	-	-	
18	Glyma18g49140			1416	472	IIb	+	BU547639.1	
18	Glyma18g49830			1563	521	I	+	BQ742680.1	
19	Glyma19g02440*			1488	496	IIb	+	BE020267.1	
19	Glyma19g26400	GmWRKY53		567	189	IIc	+	FK012118.1	
19	Glyma19g36100			1416	472	I	+	FK302159.1	
19	Glyma19g40470	GmWRKY8		795	265	IIe	+	EU019556.1	
19	Glyma19g40560			873	291	IIc	+	BI893911.1	
19	Glyma19g40950		2	1593	531	IIb	+	GR836108.1	
19	Glyma19g44380			1089	363	III	+	AW311275.1	
20	Glyma20g03410			1320	440	I	+	GR851585.1	
20	Glyma20g30290			969	323	IIe	+	-	

[1]Reannotated genes which original sequence presenting wrong start\stop codons are marked with (*). Reannotated genes with original sequence encoding a truncated protein are marked with (**).

[2]Classification according Eugelm et al. (2000).

[3]Expression confirmation by Soybase ESTs (in silico analysis) or RNA-Seq of ASR lesion microdisseccion (experimental analysis).

Table 4. Expression pattern of WRKY encoding-genes under *P. pachyrhizi* infection[1].

Group	Gene ID	SuperSage - LGE Incompatible reaction (PI561356-*Rpp2*) Inoculated X Mock 12, 24, 48h	RNA-Seq of lesion LCM[2] PI561356 X BRS231 Inoculated 10 days	Mortel et al. (2007)[3] Incompatible (PI230970-*Rpp2*) Inoc X Mock 12h	120h	Compatible (Embrapa48) Inoc X Mock 12h	120h	Schneider et al. (2011) Compatible (PI462312-*Rpp3* X Taiwan 80-2) Inoc X Mock 12h	144h	Incompatible (PI462312-*Rpp3* X Hawaii 94-1) Inoc X Mock 12h	144h
I	Glyma03g05220			x	x	x	x				
I	Glyma01g31920			x	x	x	x				
I	Glyma18g44030			x		x	x				
I	Glyma09g41670			x		x	x				
I	Glyma18g06360	x		x	x	x	x				
I	Glyma11g29720			x	x	x	x				
I	Glyma14g38010			x	x	x	x				
I	Glyma02g39870			x	x	x	x				
I	Glyma09g38580	x									
I	Glyma04g12830			x	x	x	x				
I	Glyma06g47880			x	x	x	x				
I	Glyma08g43770			x	x	x	x				
I	Glyma18g09040			x	x	x	x				
I	Glyma07g35380	x									
I	Glyma18g49830			x		x					
I	Glyma08g26230			x		x			x		
IIa	Glyma04g06470	x									
IIa	Glyma17g33920			x	x	x	x				x
IIa	Glyma14g11920			x	x	x	x	x	x	x	
IIa	**Glyma15g00570**	x		x	x	x	x				x
IIa	**Glyma13g44730**			x	x	x	x				
IIa	**Glyma08g23380**			x	x	x	x		x		x
IIa	**Glyma07g02630**			x	x	x	x				x
IIa	Glyma17g33890			x	x	x	x				
IIa	Glyma14g11960	x	x	x		x	x				
IIb	Glyma17g10630		x								
IIb	Glyma01g05050		x								
IIb	Glyma17g04710		x								
IIb	Glyma09g09400		x								
IIb	Glyma15g20990								x		
IIb	Glyma13g38630							x	x	x	x
IIb	Glyma09g00820	x		x	x	x	x				
IIb	Glyma15g11680			x	x	x	x	x	x	x	x
IIb	Glyma07g39250							x		x	x
IIb	Glyma08g43260		x								
IIc	Glyma01g06870									x	x
IIc	Glyma17g03950		x								
IIc	Glyma15g14860		x								
IIc	Glyma08g15050			x			x				
IIc	Glyma06g15220	x	x	x	x	x	x				
IIc	Glyma04g39650		x	x	x	x	x				
IIc	Glyma17g34210		x								
IIc	Glyma06g15260		x								
IIc	Glyma03g25770		x								
IIc	Glyma09g37930		x								
IIc	Glyma08g01430			x	x	x	x				
IIc	Glyma19g26400			x	x	x	x				
IId	Glyma06g08120							x	x		
IId	Glyma04g08060		x								
IId	Glyma17g29190							x			x
IId	Glyma13g00380							x		x	x
IId	Glyma17g06450	x									
IId	Glyma15g18250			x		x					
IId	Glyma09g06980		x								
IId	Glyma05g20710	x									
IIe	Glyma20g30290		x								
IIe	Glyma01g43130		x								
IIe	Glyma11g02360		x								
IIe	Glyma16g03570									x	
IIe	Glyma03g37870	x									
IIe	Glyma13g36540							x	x		
IIe	Glyma05g29310	x									
III	Glyma19g44380				x	x	x				
III	Glyma03g41750				x						
III	Glyma04g41700		x								
III	**Glyma08g02580**			x	x	x	x		x		x
III	**Glyma05g36970**			x		x	x				
III	Glyma01g43420			x		x	x				
III	Glyma16g34590		x								
III	**Glyma09g41050**	x		x	x	x	x		x		
III	**Glyma18g44560**			x	x	x	x				
III	Glyma14g36430		x								
III	Glyma06g14720	x		x		x	x				
III	Glyma04g40130	x		x		x	x				

[1] The expression data were obtained from four global expression experiments: SuperSAGE available at www.lge.ibi.unicamp.br/soja/, RNA-Seq of microdissected lesions and two different microarrays available in the current literature. (x) indicate significant differences (p<0.05). Genes in bold were used in further analyses. Genes were ordered according to the clustering analysis.

[2] LCM: laser capture microdissection.

[3] Some probes hybridize to more than one gene.

Table 5. Identity percentage (%) among the sequences of the four soybean and three Arabidopsis WRKY

	Glyma13g44730	Glyma08g23380	Glyma07g02630	AtWRKY40	AtWRKY18	AtWRKY60
Glyma15g00570	91,3	90,1	74,3	48,04	45,16	39,86
Glyma13g44730		75,72	76,8	53,4	46,77	39,16
Glyma08g23380			94,6	49,52	45,05	39
Glyma07g02630				48,9	46,94	37,94

a- pH7WG2D,1-Glyma15g00570
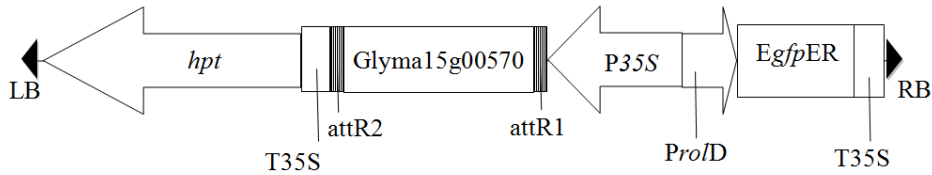
b- pH7GWIWG2D (II),0-*GmWRKY*
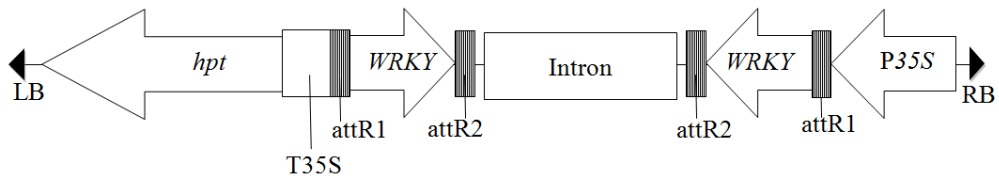
Fig. 1. T-DNA region of binary vectors used for soybean trasformation. **(a)** Overexpression construct - pH7WG2D,1-Glyma15g00570. The full lenght ORF of Glyma15g00570 was cloned in the vector. **(b)** RNAi suppression construct - pH7GWIWG2(II),0-*GmWRKY*. Inverted repeats of a 176 pb WRKY fragment was cloned in the vector. RB – T-DNA right border, LB – left border, *hpt* – hygromycin phosphotransferase gene, P35S – Cauliflower mosaic virus (CaMV) 35S promoter, T35S – CaMV 35S terminator, EgfpER – enhanced green fluorescent protein, ProlD – root loci D promoter, *WRKY* – soybean 176 pb WRKY fragment, attB1 and attB2 – LR reaction site
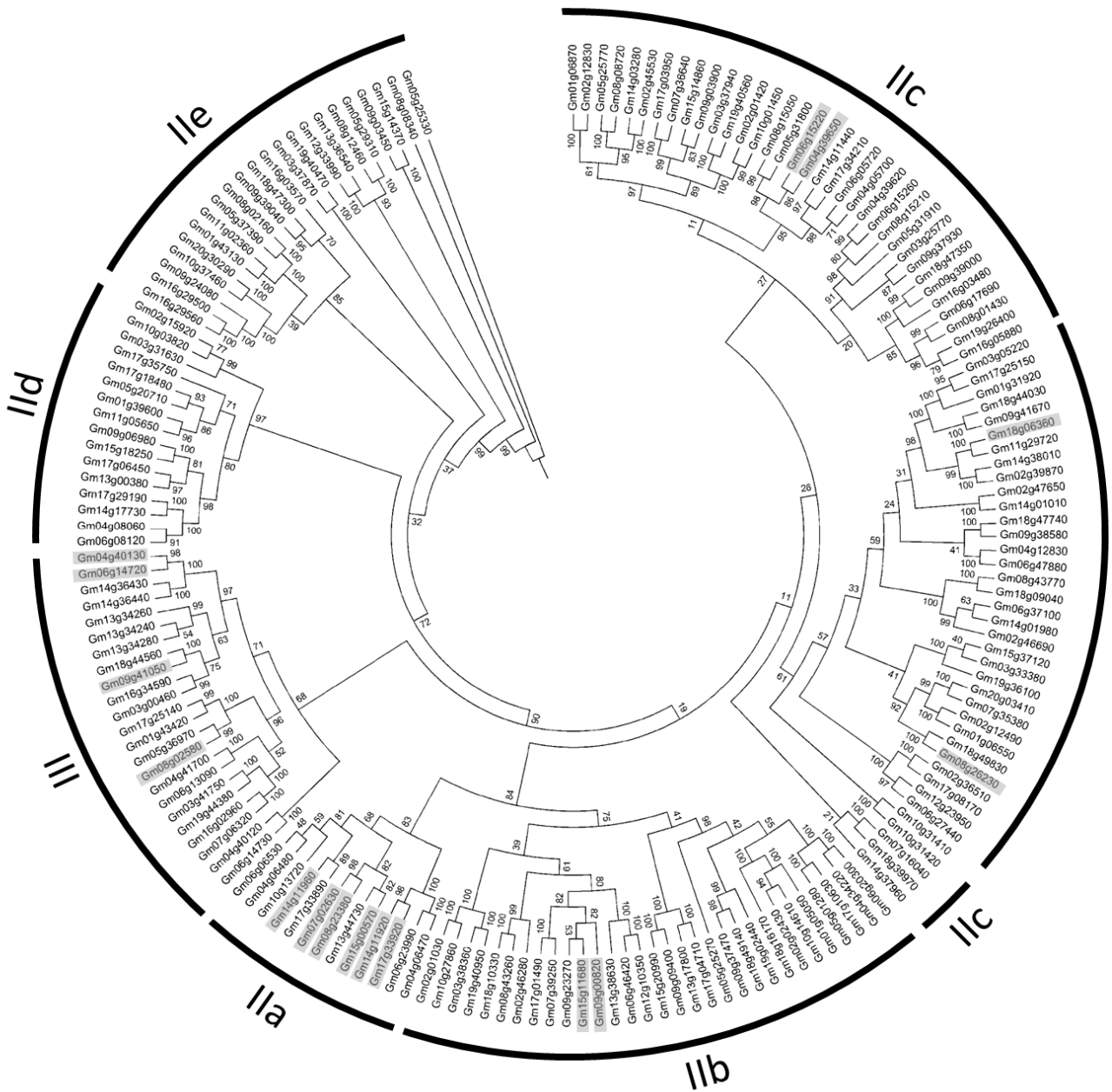
Fig. 2. Cladogram representing relationships among soybean WRKY proteins. The 178 amino acid sequences were aligned with Clustal X tool v2.1. The JTT model was determined using ProTest. Clustering was performed using PhyML3.0. Numbers below branches denote bootstrap values after 100 replications. Differential expressed genes in response to *P. pachyrhizi* infection are highlighted in gray. The cladogram was edited using Fig Tree v1.3.1.
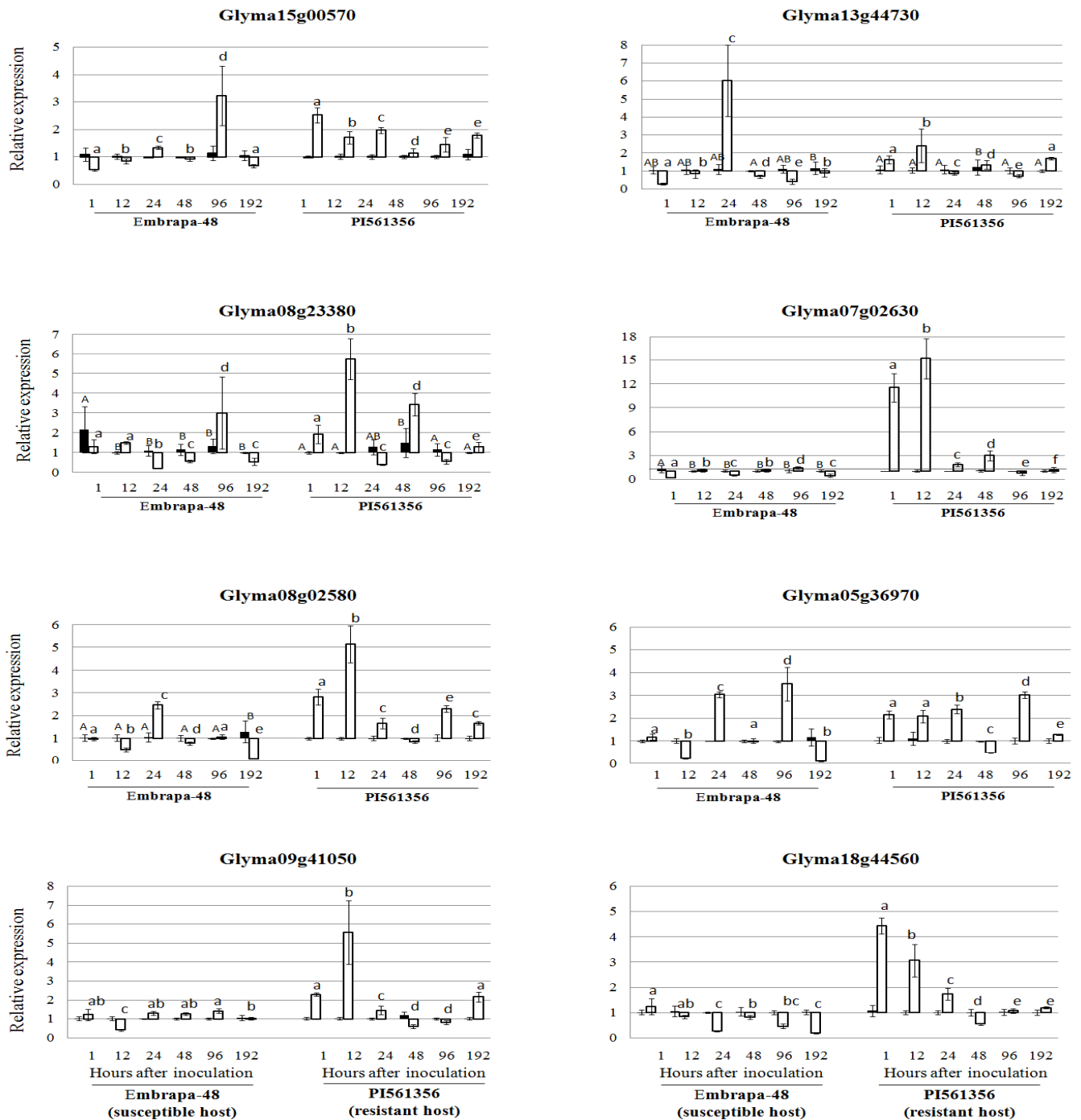
Fig. 3. Expression pattern of eight *WRKY* genes in leaves of three week-old soybean plants infected with *P. pachyrizi.* Gene response in susceptible (Embrapa-48) and resistant (PI 561356) genotypes during infection course of *P. pachyrizi* (inoculated) was evaluated by RT-qPCR. Mock inoculated plants were used as control. Values (mean$\pm$SD) were calculated based on three biological replicates and four technical replicates. Multifactorial analysis of three factors (genotype, treatment and time) was highly significant: Glyma18g44560, Glyma15g00570, Glyma09g41050, Glyma08g02580 and Glyma05g36970 p=0.0001; Glyma13g44730 p=0.0265; Glyma08g23380 p=0.0003; Means followed by equal letters in the same cultivar and treatment do not differ significantly (Tukey multiple comparison test, p<0.05). Low caption letters were used to differentiate inoculated plants and capital letters were used to identified differences among mock inoculated plants. F-Box protein and Metalloprotease reference genes were used as internal controls to normalize the amount of mRNA present in each sample. Transcript levels of *WRKY* genes present in mock inoculated plants was used to calibrate the transcript accumulation in inoculated plants.

```
Glyma08g23380    MDCSSWIN-TSLDLSINPRRVHEEAVPKVVESKLFSLGMPKFN--VEEESTSDLEEELKR
Glyma07g02630    MDCSSWIN-TSLDLNINPRRVHEEVP-KEVESELFSLGMTKFN--VEEESTSDLEEELKR
Glyma15g00570    MDYSSWIN-TSLDLNINLHRVHEELPKKQVENNFFSLDLEVKKSSVKQESAGALAEELKR
Glyma13g44730    MDYSSWMINTSLDLNINPHRLHEELPKKEVENNFLSLNLEVKKSSVKQESAGALAEELKR
                 ** ***:  *****.** :*:***   * **.::**.:   :  *::**:. * *****

Glyma08g23380    VSAENKKLAEMLSVVCENYNTLRSHLMEYMRKNGEKEVSPTSKKRKSESSNNNNSNLMGT
Glyma07g02630    VTAENKKLAEMLSVVCENYNTLRNHLMECMRKNGEKEVSPTSKKRKSESSNNN-SNLMGT
Glyma15g00570    VSAENKKLTEMLTEMCENYNTLRSNLMEYMRKNPDKELS-SSRKRKSASSNNNSTIPMGV
Glyma13g44730    VSAENKKLTEMLTEMCENYNTLRGNLMEYMRKNPDKEHS-SSKKRKSES--NNNSIPMGV
                 *:*****:***: :********.:*** **** :** * :*:**** * ** : **.

Glyma08g23380    NNGNSESSSTDEESCKKPREETIKAKISRVYVRTESSDTSLIVKDGYQWRKYGQKVTRDN
Glyma07g02630    NNGNSESSSTDEESCKKPREEIIKAKISRVYVRTEASDTSLIVKDGYQWRKYGQKVTRDN
Glyma15g00570    N-GTSESSSTDEESCKNPKE-DMKTKISRVYMRTEASDTSLIVKDGYQWRKYGQKVTRDN
Glyma13g44730    N-GTSESSSTDEESCKKQKE-DIKTKISRVYMRTEASDKSLIVKDGYQWRKYGQKVTRDN
                 * *.************: :*   :*:*****:***:**.*****************

Glyma08g23380    PMPRAYFKCSFAPSCPVKKKVLRSVDDHSVLLATYEGEHNHPQASSQMEATSGSGRSVTL
Glyma07g02630    PLPRAYFKCSFAPSCPVKKKVQRSVDDQSVLVATYEGEHNHPQFSSQMEATSGSGRSVTL
Glyma15g00570    PHPRAYFKCSFAPSCPVKKKVQRSVDDQSVLVATYEGEHNHTHP-SQMEVTTGSN-----
Glyma13g44730    PHPRAYFKCSFAPSCPVKKKVQRSVDDQSVLVATYEGEHNHPHP-SQMEVTTGSNRCMTL
                 * ********************:***:*********.:   ****.*:**.

Glyma08g23380    GSVPCSASLSTSTPTLVTLDLTKSKGSNDSKSTKPKGDSPKVPQVLVEQMATSLTTDPNF
Glyma07g02630    GSVPCTASLSTSTPTLVTLDLTKSQGSNDSKSTKPKGDSPKVPQVLVEQMATSLTTDPNF
Glyma15g00570    RSVSCSASLSSSAP-TVTLDWTKSKSSSESKNVNPKTESPEVPQVLVEQMATSLTKDPNF
Glyma13g44730    GSVPCSASLSSSPP-TATLDWTKSKSSSESKNTSPKTESPEVPQVLVEQMATSLTKDPNF
                  **.*:****:*.*  .*** ***:.*.:**...** :**:*************.****

Glyma08g23380    RAALVAAISGRLLHNN-
Glyma07g02630    RAALVAAISGRLLHNN-
Glyma15g00570    RAALVAAISGKMLHNNN
Glyma13g44730    RAALVAAISGKMLHNN-
                 **********::****
```

Fig. 4a. Amino acid alignment and identification of conserved residues. The conserved WRKY amino acid signature and the amino acid forming the zinc finger motif are highlighted in black and gray, respectively. Other conserved amino acids are boxed in black. Multiple sequence alignment was performed using CLUSTAL W 2.1. Highly conserved residues are indicated by (*), strongly similar by (:) and weakly similar by (.).
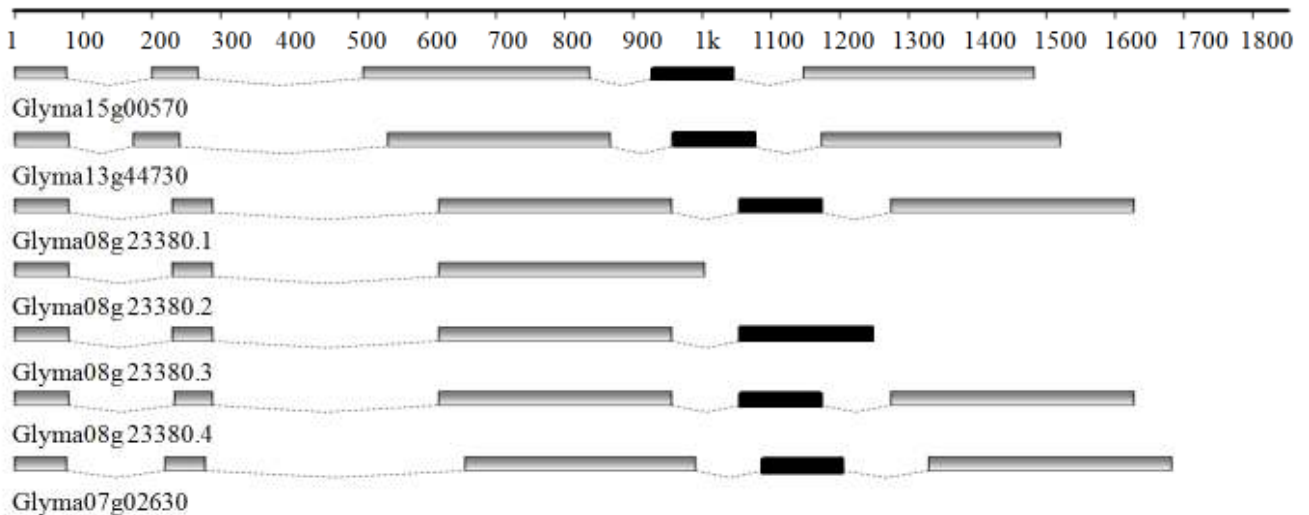
Fig. 4b. Structure of four soybean *WRKY*-encoding genes. Glyma08gg23380.1, Glyma08gg23380.2, Glyma08gg23380.3 and Glyma08gg23380.4 are alternative transcripts of Glyma08gg23380. Gray boxes represent exons, black boxes indicate the exon that contain the WRKY domain and dotted lines represent introns.

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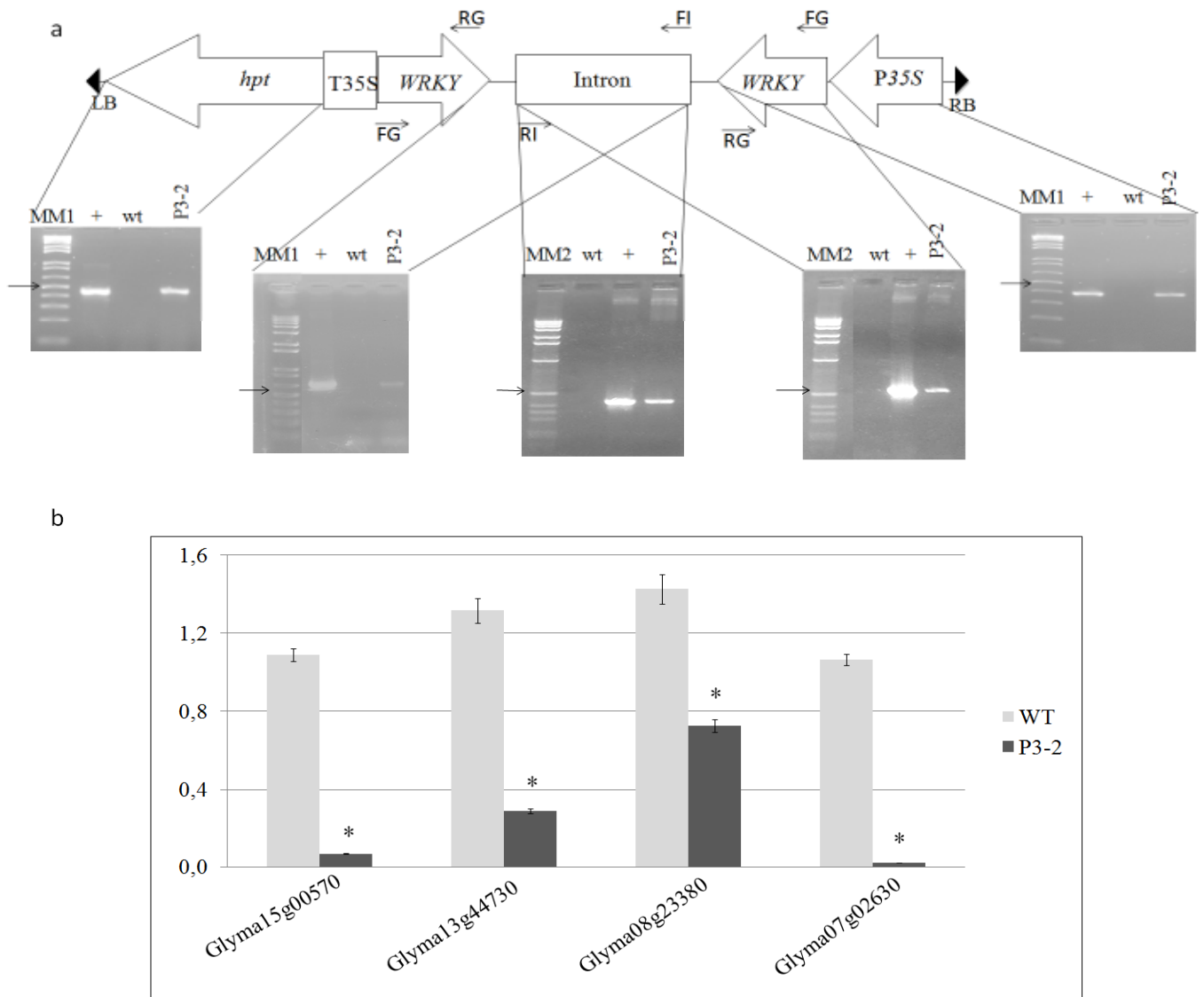
Fig. 5. Characterization of soybean silenced transgenic line for four WRKY genes. **(a)** Detection of the RNAi suppression construct in a transgenic soybean line. PCR products were amplified from: pH7GWIWG2,II-*GmWRKY27* plasmid (positive control); WT (DNA of wild-type plant – untransformed) and P3-2 (DNA of a transgenic soybean plant from line P3-2). MM1: 100 bp Ladder, Ludwig; MM2: 1Kb Plus Ladder, Invitrogen. Arrows indicates 500 bp. 1% agarose gel, stained with ethidium bromide visualized under UV light. FG- forward WRKY RNAi primer, RG- reverse WRKY RNAi primer, FI- forward intron primer, RI- reverse intron primer. **(b)** Expression levels (RT-qPCR) of the four *WRKY* genes in a wild-type (wt) soybean plants and in a transgenic soybean line P3-2. F-Box protein and Metalloprotease reference genes were used as internal controls to normalize the amount of mRNA present in each sample. Transcript levels of *WRKY* genes present in wt was used to calibrate transcript amount in P3-2. *Means are statistically different in wt and P3-2 plants (Student's *t* - test, $p < 0.05$).
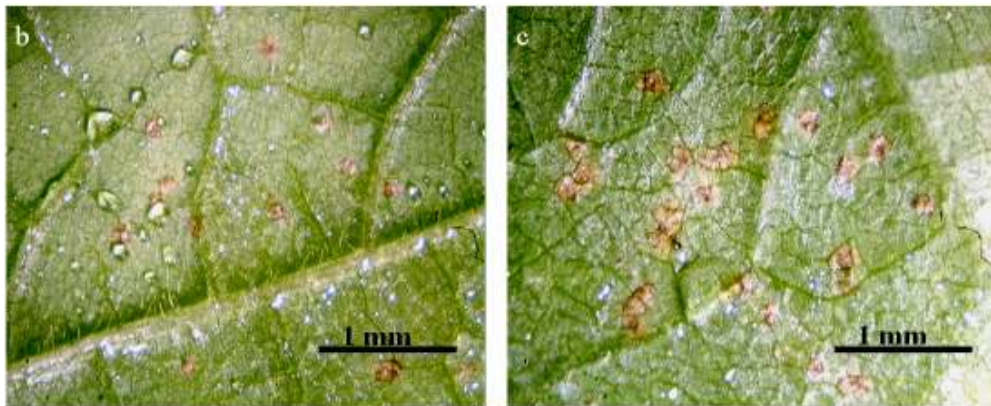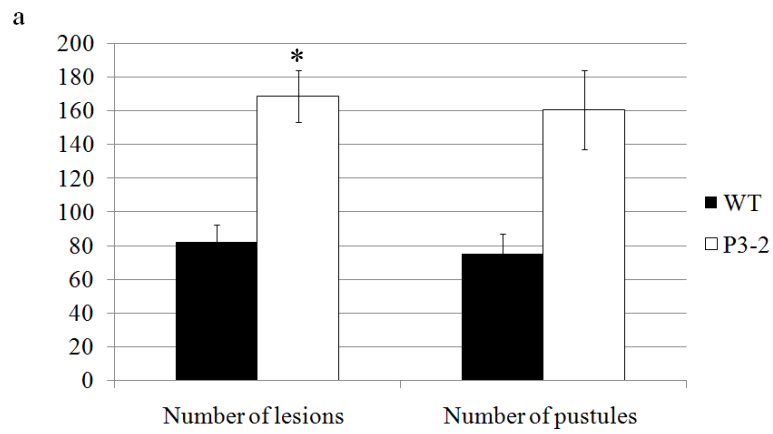
Fig. 6. *P. pachyrhizi* development on detached leaves 12 days after inoculation. Detached leaves were inoculated with 10^5/mL spore suspension and incubated at 20°C. **(a)** Two infection parameters were evaluated: number of lesions and number of pustules. *Means are statistically different in leaves of wild-type (wt) and transgenic soybean line P3-2. (Student's *t* -test, p<0.05). **(b)** Low number of tan-colored lesions and pustules under stereomicroscope in a leaf of wild-type (wt) plant. **(c)** High number of tan-colored lesions and pustules under stereomicroscope in a leaf of transgenic soybean line P3-2 with suppression of four WRKY.

Supplementary **Fig 1**. 178 WRKYs CDS

>Glyma01g05050.1
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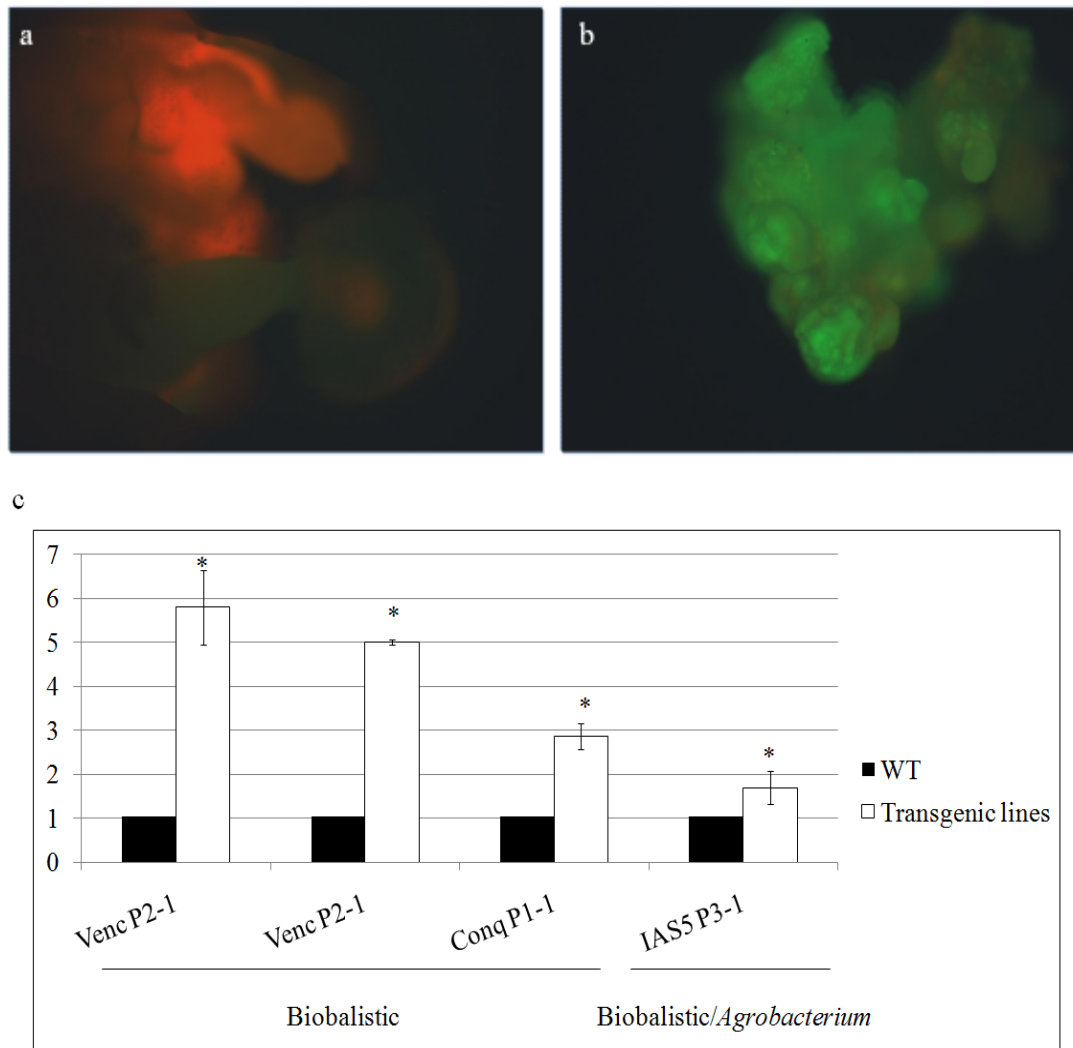
Supplementary Fig. 2. Characterization of soybean transgenic lines overexpressing Glyma15g00570. GFP expression analyses in wild-type **(a)** and hygromycin-resistant embryogenic tissues **(b)**. GFP expression was detected under blue light using a fluorescence stereomicroscope Olympus®, equipped with a BP filter set containing a 488 ηm excitation filter and a 505-530 ηm emission filter. **(c)** Expression levels (RT-qPCR) of the Glyma15g00570 in wild-type (WT) soybean plants and in histodifferentiated embryos of different transgenic soybean lines. Venc (BRSMG68 Vencedora) P2-1, IAS-5 P1-1, Conq (MGBR-46 Conquista) P1-1 lines were obtained from Biobilistic and IAS-5 P3-1 line from Biobalistic/*Agrobacterium* transformation experiments. *F-Box protein* and *Metalloprotease* reference genes were used as internal controls to normalize the amount of mRNA present in each sample. Transcript levels of WRKY gene present in wt was used to calibrate transcript amount in transgenic embryos. *Means are statistically different in wt and transgenic lines (Student's *t* -test, p<0.05).

CONCLUSÕES E PERSPECTIVAS

4. CONCLUSÕES E PERSPECTIVAS

No presente estudo, foram anotados 178 membros da família WRKY no genoma da soja. A presença de transcritos para a maioria (140) dos genes foi detectada. Estudos em condições específicas serão necessários para a detecção de transcritos dos demais genes. Entretanto, não se pode descartar a possibilidade de que alguns sejam pseudogenes.

A nomenclatura que tem sido utilizada para membros da família WRKY em soja não tem um consenso na literatura. No banco de dados Phytozome, os genes estão nomeados de acordo com os ortólogos de Arabidopsis, enquanto Zhou *et al.* (2008) numeraram aleatoriamente os 64 membros identificados pelo seu grupo de pesquisa, os quais foram depositados no NCBI. Além disso, em estudos de genes individuais (Zhang *et al.*, 2008; Kang *et al.*, 2009) os WRKYs foram nomeados de forma diferente do proposto por Zhou *et al.* (2008). Com o objetivo de unificar a terminologia, estamos propondo uma nomenclatura baseada no gene ID do Phytozome.

Análises de agrupamento de sequências do domínio WRKY de arroz (Zhang & Wang, 2005) e tabaco (Rushton *et al.*, 2008) dividiram a família em grupos I, IIa+IIb, IIc, IId+IIe and III. No presente estudo, o cladograma dos genes *WRKY* de soja foi construído com base nas sequências completas das proteínas. O cladograma obtido para os *WRKY* de soja resultou na separação que reproduz os mesmos grupos descritos para arroz e tabaco. Este resultado comprova a importância do domínio WRKY para a caracterização dos genes desta família

As análises do cladograma sugerem, também, que a maior parte dos genes *WRKY* de soja estão presentes como cópias duplas ou quádruplas. Esse padrão é esperado já que dois eventos de duplicação ocorreram no genoma da soja (Schmutz *et al.*, 2010).

Em soja a assinatura WRKYGQK é altamente conservada nas proteínas da família WRKY. Mas, no presente estudo, foram identificadas variantes em 20 genes. Nossos resultados fornecem forte indicação de que as proteínas com variações tanto na assinatura WRKYGQK quanto no "dedo-de-zinco" devem ser funcionais, porque transcritos de alguns dos genes que as apresentam foram detectados (Tabela 4). No entanto, a habilidade de ligação ao W-box pode ter sido abolida ou diminuída (Maeo *et al.*, 2001; Ciolkowski *et al.*, 2008). Este é um aspecto que merece ser investigado. Há sugestões, na literatura, que além de alteração na habilidade de ligação ao W-box, genes

sem os motivos conservados podem ter diferentes sítios de ligação ao DNA (Ciolkowski *et al*., 2008; van Verk *et al*., 2008,), genes-alvo diferentes e, possivelmente, papéis divergentes (Yang *et al*., 2009).

Estudos de expressão gênica global têm demonstrado a importância dos genes *WRKY* na reprogramação transcricional durante a infecção de soja pelo fungo *P. pachyrhizi*, causador da Ferrugem Asiática da Soja (Mortel *et al*., 2007; Choi *et al*., 2008; Panthee *et al*., 2007; Panthee *et al*., 2009; Tremblay *et al*., 2010; Schneider *et al*., 2011). Para identificar os genes *WRKY* envolvidos na defesa contra esse fungo, realizamos a análise de dados de microarranjos disponíveis na literatura (Mortel *et al*., 2007; Schneider *et al*., 2010) e resultados obtidos em dois outros experimentos: SuperSAGE e RNA-Seq de lesão LCM. Setenta e quatro genes, distribuídos entre os três grupos de classificação, mostraram expressão diferencial em pelo menos um experimento e 16 deles em mais de um experimento. Desses últimos, oito tiveram a modulação dos níveis de transcritos validados por RT-qPCR. Esses resultados comparados com os da clusterização mostraram que alguns genes agrupados tem padrões de expressão similares em resposta a *P. pachyrhizi*. Isso sugere genes com função similar na resistência a doença. A redundância funcional de genes *WRKY* pode ser benéfica na proteção da célula ou organismo sob condições estressantes e em elicitar múltiplas rotas, que levam a um conjunto amplo de respostas fisiológicas, que ocorrem em conseqüência da infecção por patógenos (Ryu *et al*., 2006).

Mortel *et al*. (2007) and Schneider *et al*. (2011) registraram que *P. pachyrhizi* induz uma expressão global bifásica, com um pico de expressão às 12 h após inoculação do fungo (hai) e outro que começa às 72 hai. Isso não foi observado em nosso estudo. Os autores sugerem que o primeiro pico corresponde à resposta de defesa não específica, similar a PTI. A segunda fase de expressão gênica é coincidente com a ativação dos genes mediadores de resistência *RPP2* e *RPP3*. Foi demonstrado que a expressão gênica é mais rápida e de maior magnitude na interação incompatível (Mortel *et al*., 2007, Panthee *et al*., 2007; Schneider *et al*., 2011).

Dados de expressão gênica global têm sugerido que o tempo e o nível de indução de uma rota de defesa são determinantes para induzir a defesa de resistência contra *P. pachyrhizi* (Mortel *et al*., 2007; Choi *et al*., 2008; Goellner *et al*., 2010; Schneider *et al*., 2011). Em nosso estudo, a indução da expressão dos oito genes (Glyma18g44560, Glyma15g00570, Glyma13g44730, Glyma09g41050 Glyma08g23380,

Glyma08g02680, Glyma07g02630 e Glyma05g36970) em resposta a *P. pachyrhizi* foi mais precoce e intensa no genótipo resistente. Além disso, como os genes mostraram o pico de expressão nas primeiras 24 h após a infecção, assumimos que tais genes devem estar envolvidos em uma resposta de defesa não específica.

Os genes homólogos Glyma15g00570, Glyma13g44730, Glyma08g23380 e Glyma07g02630 são possíveis ortólogos dos genes *AtWRKY40, AtWRKY18* e *AtWRKY60* de Arabidopsis. Em ambas as espécies os genes foram classificados no grupo IIa.

A participação de quatro genes homólogos (Glyma15g00570, Glyma13g44730, Glyma08g23380 e Glyma07g02630) em resposta a *P. pachyrhizi* foi demonstrada através da técnica de RNA de interferência. A linhagem RNAi transgênica obtida de experimentos de transformação de soja apresentou significante redução nos níveis de transcritos dos quatro genes-alvo. Quando infectada por *P. pachyrhizi*, a linhagem transgênica mostrou maior suscetibilidade ao fungo. Esses resultados, em conjunto com os dados de expressão, sugerem que pelo menos um dos quatro genes deve estar envolvido no fenótipo de resistência da soja. Apesar de ser desejável a obtenção de novas linhagens transgênicas para reforçar os resultados, o presente estudo é o primeiro a identificar e caracterizar genes *WRKY* que respondem à infecção pelo fungo causador da Ferrugem Asiática.

Nos experimentos visando a superexpressão, linhagens de embriões histodiferenciados expressando o gene Glyma15g00570 foram obtidas, no entanto, nenhuma planta foi regenerada. A explicação mais provável é que a expressão constitutiva desse gene deve estar afetando processos iniciais de desenvolvimento das plantas. O possível efeito deletério da produção excessiva desses WRKYs no crescimento da planta sugere que a expressão destes genes deve requerer regulação apropriada durante a ativação de respostas de defesa. Por outro lado, em plantas saudáveis a expressão desses genes deve ser regulada negativamente, como demonstrado por Chen & Chen (2002) para *AtWRKY18*.

Os problemas de letalidade observados no presente estudo poderiam ser parcialmente superados pelo uso de promotores tecido-específicos ou promotores induzíveis. No entanto, promotores folha-específicos de soja, que seriam os ideais, já que a Ferrugem Asiática se desenvolve principalmente nesse órgão, ainda não estão

disponíveis. Seria muito importante a identificação de promotores tecido-específicos ou responsivos a estresse-específicos para a continuidade do estudo. Em curto prazo, contamos com a perspectiva de realizar trabalhos de transformação, com o objetivo de superexpressar o Glyma15g00570, com a utilização de promotores induzíveis disponíveis.

Em um trabalho anterior, o Glyma15g00570 (nomeado como *GmWRKY27*) foi identificado como diferencialmente expresso em resposta a estresses bióticos (Zhou *et al.*, 2008). Através da técnica de RT-PCR, foi demonstrado que os transcritos desse gene foram altamente induzidos em resposta a seca e sal. Esse resultado, em conjunto com os dados de expressão apresentados no nosso estudo, sugerem que o gene deve estar envolvido em resposta a estresses de uma forma geral, possivelmente atuando mais *upstream* nas rotas de defesa.

Um outro aspecto importante a ser investigado é o relacionado à identificação dos genes alvo e possíveis interações proteína-proteína. Segundo Zhou *et al.* (1999), modificações e dimerização entre fatores de transcrição WRKY, assim como a sua interação com outros fatores de transcrição, podem produzir uma função regulatória distinta. Um exemplo já registrado envolve o pequeno clado (*At*WRKY18, *At*WRKY40 e *At*WRKY60) de Arabidopsis, composto pelos três possíveis ortólogos dos genes de soja silenciados em nosso trabalho. As três proteínas formam homocomplexos e heterocomplexos e a atividade de ligação ao DNA é mudada dependendo de qual das proteínas está presente no complexo (Xu et al., 2006). Assim, para um melhor entendimento da função biológica dos quatro WRKYs de soja silenciados, devem ser realizados experimentos de interação proteína-proteína e identificação de genes-alvo afetados pela presença do transgene. A análise da expressão diferencial de genes em resposta ao silenciamento nas linhagens transgênicas permitirá a avaliação de processos moleculares nos quais os genes podem estar envolvidos.

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