TETSU SAKAMOTO

THE TOMATO RLK SUPERFAMILY: PHYLOGENY AND FUNCTIONAL PREDICTIONS ABOUT THE ROLE OF THE LRRII-RLK SUBFAMILY IN ANTIVIRAL DEFENSE

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Genética e Melhoramento, para obtenção do título de *Magister Scientiae*.

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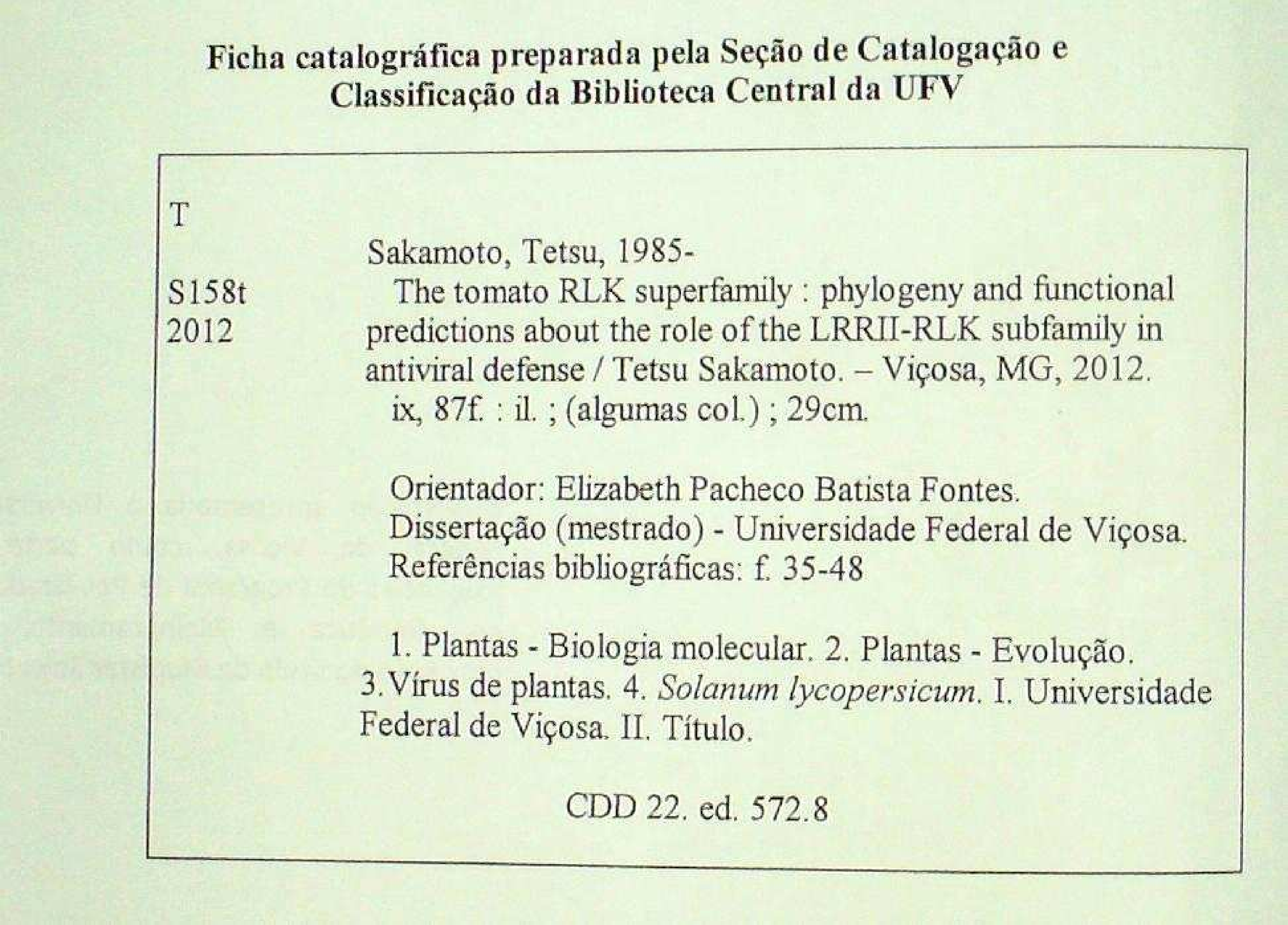

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APROVADA: 03 de agosto de 2012.

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Aos meus pais...
que dedicaram as suas vidas
para eu chegar até aqui...

AGRADECIMENTOS

À Deus pela oportunidade de estar aqui e de conviver com todas essas pessoas, às quais agradeço;

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"A ciência nunca resolve um problema sem criar pelo menos outros dez."

(George Bernard Shaw)

RESUMO

SAKAMOTO, Tetsu, M.Sc., Universidade Federal de Viçosa, agosto de 2012. **A superfamília RLK de tomate: filogenia e predição funcional do papel da subfamília LRRII-RLK na defesa antiviral**. Orientadora: Elizabeth Pacheco Batista Fontes. Coorientadoras: Karla Suemy Clemente Yotoko e Poliane Alfenas Zerbini.

Receptores cinases (RLKs) compõem uma grande famíla de proteínas transmembrânicas que possuem funções importantes na propagação e percepção de sinais celulares nas plantas. Em *Arabidopsis thaliana*, a superfamília de RLK é composta de mais de 600 membros e vários destes, principalmente aqueles que possuem repetições ricas em leucina (LRR), são considerados excelentes alvos para manipulação molecular em cultivares superiores no intuito de aumentar a produtividade e a resistência contra estresses bióticos e abióticos. A subfamília LRRII é particularmente relevante neste aspecto uma vez que seus membros apresentam funções duplas tanto no desenvolvimento quanto na resposta de defesa da planta. Apesar da relevância desta superfamília e da recente finalização do sequenciamento do genoma de tomateiro, a superfamília de RLK de tomate ainda não se encontra caracterizada e são poucos os trabalhos que analisaram a função biológica de seus membros. Neste trabalho, foi construído um inventário completo dos membros da superfamília de RLK de tomate. Para identificar os membros da superfamília RLK em tomate, foi realizado uma análise filogenética utilizando a superfamília de RLK de Arabidopsis como modelo. Um total de 647 RLKs foram recuperados do genoma de tomate e estes encontravam-se organizados no mesmo clado das subfamílias de RLKs de Arabidopsis. Apenas oito das 58 subfamílias exibiram expansão/redução específica no número de menbros comparado com Arabidopsis e apenas seis RLKs foram específicos em tomate, indicando que os RLKs de tomate compartilham aspectos funcionais e estruturais com os RLKs de Arabidopsis. Também foi caracterizado a subfamília LRRII através de análises filogenéticos, genômico, expressão gênica e interação com o fator de virulência de begomovírus, o “*nuclear shuttle protein*” (NSP). Os membros da subfamília LRRII de tomate e Arabidopsis demonstraram-se altamente conservados tanto em sequência quanto em estrutura. No entanto, a maioria dos pares ortólogos não mostraram conservados em relação à expressão gênica, indicando que estes ortólogos tenham se divergido na função após a especiação do ancestral comum entre o tomate e Arabidopsis. Baseado no fato de que membros de RLKs de Arabidopsis (NIK1, NIK2, NIK3 e NsAK) interagem com o NSP de begomovirus, foi verificado se ortólogos de *NIK*s, *BAK1* e *NsAK* interagem com o NSP de *Tomato Yellow Spot Virus* (ToYSV). Os ortólogos dos genes que interagem com o NSP em tomate, SlNIKs e SlNsAK, interagiram especificamente com NSP na levedura e demonstraram um padrão de expressão consistente com o padrão de infecção de geminivírus. Além de sugerir uma analogia funcional entre estes ortólogos, estes resultados confirmam a observação anterior de que as interações NSP-NIK não são específicos para um vírus ou para um hospedeiro. Portanto, a sinalização antiviral mediado por NIK provavelmente ocorre em tomate, sugerindo que NIKs de tomate sejam alvos potenciais para manipular a resistência contra begomovírus que infectam esta planta.

ABSTRACT

SAKAMOTO, Tetsu, M.Sc., Universidade Federal de Viçosa, August, 2012. **The tomato RLK superfamily: phylogeny and functional predictions about the role of the LRRII-RLK subfamily in antiviral defense**. Adviser: Elizabeth Pacheco Batista Fontes. Co-adivisers: Karla Suemy Clemente Yotoko and Poliane Alfenas Zerbini.

Receptor-like kinases (RLKs) represent a large family of transmembrane proteins that play important roles in cellular signaling perception and propagation in plants. In *Arabidopsis thaliana*, the RLK superfamily is made-up of over 600 proteins and many of these RLKs, mainly those bearing leucine-rich repeats (LRR), have been considered as excellent targets for engineering superior crops with enhancement of yield and resistance to biotic and abiotic stresses. The LRRII-RLK subfamily is particularly relevant due to the dual function of its members in both development and defense. In spite of the relevance of the RLK family and the completion of the tomato genome sequencing, the tomato RLK family has not been characterized and a framework for functional predictions of the members of the family is lacking. In this investigation we disclosed a complete inventory of the members of the tomato RLK family. To generate a complete list of all members of the tomato RLK superfamily, we performed a phylogenetic analysis using the Arabidopsis RLKs as a template. A total of 647 RLKs were identified in the tomato genome, which were organized into the same RLK subfamily clades as Arabidopsis. Only eight of 58 RLK subfamilies exhibited specific expansion/reduction compared to their Arabidopsis counterparts and only six proteins were lineage-specific in tomato, indicating that the tomato RLKs share functional and structural conservation with Arabidopsis. We also characterized the LRRII-RLK family by phylogeny, genomic analysis, expression profile and interaction with the virulence factor from begomoviruses, the nuclear shuttle protein (NSP). The LRRII subfamily members from tomato and Arabidopsis were highly conserved in both sequence and structure. Nevertheless, the majority of the orthologous pairs did not display similar conservation in the gene expression profile, indicating that these orthologs may have diverged in function after speciation of tomato and Arabidopsis common ancestor. Based on the fact that members of the Arabidopsis RLK superfamily (NIK1, NIK2, NIK3 and NsAK) interact with the begomovirus nuclear shuttle protein (NSP), we examined whether the tomato orthologs of *NIK*, *BAK*1 and *NsAK* genes interacted with NSP of

Tomato Yellow Spot Virus (ToYSV). The tomato orthologs of NSP interactors, SlNIKs and SlNsAK, interacted specifically with NSP in yeast and displayed an expression pattern consistent with the pattern of geminivirus infection. In addition to suggesting a functional analogy between these phylogenetically classified orthologs, these results expand our previous observation that NSP-NIK interactions are neither virus-specific nor host-specific. Therefore, NIK-mediated antiviral signalling is also likely to operate in tomato, suggesting that tomato NIKs may be good targets for engineering resistance against tomato-infecting begomoviruses.

SUMÁRIO

Title

The tomato RLK superfamily: phylogeny and functional predictions about the role of the LRRII-RLK subfamily in antiviral defense.

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Abstract

Background

Receptor-like kinases (RLKs) play key roles in the transduction of extracellular signals and plant-specific adaptations. They are among the largest plant gene families, comprising over 50 subfamilies. The leucine-rich repeat (LRR) II-RLK subfamily is particularly important due to the dual function of its members in both development and defense. Despite the relevance of the RLK family and the completion of the tomato genome sequencing, the tomato RLK family has not yet been characterized, and a framework for functional predictions of the members of the family is lacking.

Results

To generate a complete list of all the members of the tomato RLK family, we performed a phylogenetic analysis using the Arabidopsis family as a template. A total of 647 RLKs were identified in the tomato genome, which were organized into the same subfamily clades as Arabidopsis RLKs. Only eight of 58 RLK subfamilies exhibited specific expansion/reduction compared to their Arabidopsis counterparts. We also characterized the LRRII-RLK family by phylogeny, genomic analysis, expression profile and interaction with the virulence factor from begomoviruses, the nuclear shuttle protein (NSP). The LRRII subfamily members from tomato and Arabidopsis were highly conserved in both sequence and structure. Nevertheless, the majority of the orthologous pairs did not display similar conservation in the gene expression profile, indicating that these orthologs may have diverged in function after speciation. Based on the fact that members of the Arabidopsis LRRII subfamily (AtNIK1, AtNIK2 and AtNIK3) interact with the begomovirus nuclear shuttle protein (NSP), we examined whether the tomato orthologs of *NIK*, *BAK*1 and *NsAK* genes interact with NSP of

Tomato Yellow Spot Virus (ToYSV). The tomato orthologs of NSP interactors, SlNIKs and SlNsAK, interacted specifically with NSP in yeast and displayed an expression pattern consistent with the pattern of geminivirus infection. In addition to suggesting a functional analogy between these phylogenetically classified orthologs, these results expand our previous observation that NSP-NIK interactions are neither virus-specific nor host-specific.

Conclusions

The tomato RLK superfamily is made-up of 647 proteins that form a monophyletic tree with the Arabidopsis RLKs and is divided into 58 subfamilies. Few subfamilies have undergone expansion/reduction compared to Arabidopsis, and only six proteins were lineage-specific. Therefore, the tomato RLK family shares functional and structural conservation with Arabidopsis. For the LRRII-RLK members *NIK1*, *NIK3* and *BAK1*, we observed functions analogous to those of their Arabidopsis counterparts with respect to protein-protein interactions and similar expression profiles, which were associated with tissues that support high efficiency of begomovirus infection. Therefore, NIK-mediated antiviral signalling is also likely to operate in tomato, suggesting that tomato NIKs may be good targets for engineering resistance against tomato-infecting begomoviruses.

Keywords: Receptor-like kinase, NIK, NSP, BAK1, virus infection, protein-protein interaction, functional divergence, plant signaling, *Solanum lycopersicum*.

Background

Plant cells constantly react to multiple signals that come from the local environment, neighbouring cells, or even from other organisms. Depending on the stimuli, plant cells may expand, divide, synthesize compounds, prepare against pathogen infection, or induce necrosis [1]. To perceive and receive these signals, plant cells possess complex systems of transmembrane receptor proteins that facilitate communication between the intracellular environment and the outside world.

One of the largest groups of these receptors is the receptor-like kinase (RLK) superfamily, which contains over 600 members in Arabidopsis [2–4]. RLKs are structurally organized into a highly divergent extracellular domain, followed by a transmembrane segment and a conserved intracellular serine/threonine kinase domain. Most RLKs are localized in the plasma membrane, although there are exceptions, such as THYLAKOID-ASSOCIATED KINASE 1 (TAK1) [5], which is localized in the thylakoid membrane. There are also RLK members that are found in the cytoplasm. In this case, RLKs do not possess either an extracellular region or a transmembrane domain and are called receptor-like cytoplasmic kinases (RLCKs). Analyses of Arabidopsis RLKs by structural comparison of their extracellular region and phylogenetic analysis of their kinase domain revealed that they can be divided into over 50 subfamilies [6].

Several distinct RLKs have been studied in the past decade, and a common theme that has emerged is that binding of a specific signal molecule to their extracellular domain is required to initiate a signal transduction cascade [7]. Generally, ligand-receptor interactions at the extracellular domain of RLKs initiate the propagation of the signal through the membrane by inducing a conformational change in the receptor kinase domain, which allows interactions with other RLKs resulting in homo- or heterodimers. Dimerized RLKs are then transphosphorylated by their cytoplasmic kinase domain, leading to both activation of the kinase and establishment of docking sites for phosphorylation of downstream phosphorylation targets. This activation mechanism of RLK-mediated signal transduction enables plant cells to activate or inactivate specific biochemical pathways in response to extracellular signals [8]. This activation model of plant RLKs is similar to that of signal transduction mediated by receptor tyrosine kinases in animal cells, which share a common origin with plant serine/threonine kinases [3].

Functional analysis of RLKs indicates that the majority of them are associated with plant development or defense response, but there are also RLKs involved in cell wall attachment (extensin, proline-rich extensin and lectin RLKs), plant-bacterial symbiotic interactions (LysM RLKs) and self-incompatibility (S-domain containing RLKs). Among all RLKs, those bearing a leucine-rich repeat (LRR) domains are overrepresented in the RLK superfamily, comprising over 38% of Arabidopsis RLKs. LRR-RLKs are distributed into 15 subgroups (LRR I to LRR XV). These receptors vary in number (from one to 25) and in the distribution pattern of the LRRs along the extracellular region. They are known to interact with a wide range of substrates, including proteins, nucleic acids, lipids and small molecule hormones, and mediate a variety of important biological process in plants. Examples of well-known LRR-RLKs include CLAVATA1, which controls the size of stem cells in the apical meristem by forming a heterodimer with CLAVATA2 and then interacting with CLAVATA3 through the extracellular domain [9], and BRASSINOSTEROID INSENSITIVE-1 (BRI1) [10], which perceives brassinosteroids and interacts with it receptor partner, BAK1 (BRI1-ASSOCIATED KINASE-1), reviewed in [11] and [12]. Other functions associated with LRR-RLKs include morphogenesis [13–20], embryogenesis [21, 22], pollen self-incompatibility [23] and responses to environmental signals [24]. In addition, some LRR-RLKs are known to function as regulators of defense response to bacterial pathogen [25–27], necrotrophic fungus [28] and viral infection [29, 30].

Many of these RLK-mediated biological processes, mainly those mediated by LRR-RLKs, are of great interest due to their potential as targets to increase crop yield and plant resistance to biotic and abiotic stresses. Although most of the characterized RLKs are from model plants such as Arabidopsis and *Medicago truncatula*, significant efforts have been made to expand these studies to relevant field crops. Bioinformatic analyses using whole-genome sequencing and gene expression data have enabled the identification and characterization of RLKs from other crops. Arabidopsis RLKs were used for large-scale comparative analyses with rice [6, 31, 32] and soybean [33] RLKs. These studies identified over 1000 kinase proteins in rice and 600 in soybean belonging to the RLK superfamily, and almost all members were grouped into previously determined Arabidopsis RLK subfamilies. The RLK subfamilies with developmental function have conserved numbers of members, whereas those involved in defense response have expanded their members, mainly by tandem duplication [6].

Although tomato (*Solanum lycopersicum*) is one of the most consumed and cultivated field crops in the world, a large-scale phylogenetic analysis of tomato RLKs has not yet been performed, and few members of the tomato RLK/Pelle family (RLKs + RLCKs) have been studied and characterized. These members include Pto [34], Pti1 (Pto-INTERACTING 1) [35], and Bti9 (AvrPtoB-TOMATO INTERACTING PROTEIN 9) [36], which interact with *Pseudomonas syringae* elicitors; TARK1 (TOMATO ATYPICAL RECEPTOR KINASE-1) [37], which interacts with the *Xanthomonas campestris* elicitor; TPK1b (TOMATO PROTEIN KINASE 1) [38], whose expression is induced by mechanical wounding and oxidative stress; and SR160 (SYSTEMIN RECEPTOR) [39], which is the AtBRI1 ortholog and binds to systemin to respond to wounding or herbivore attack, although there is some debate about the function of this receptor [40]. Another well-studied RLK in tomato is NIK (NSP-INTERACTING KINASE) [41], which interacts with nuclear shuttle protein (NSP) of geminivirus during infection [41]. Three homologs of NIK in Arabidopsis (AtNIK1, AtNIK2 and AtNIK3) have also been shown to interact with NSP through their kinase domain [29]. This interaction causes inhibition of the kinase activity of NIKs and hence prevents the activation of the signal transduction cascade that evokes a plant defense response [30]. These RLKs are members of the LRRII subfamily that also contains the SOMATIC EMBRYOGENESIS RECEPTOR KINASES (SERKs) [42].

With the completion of the tomato genome sequencing along with the annotation of the encoded proteins [43], it has become possible to study the RLK superfamily in this species using a large-scale phylogenetic approach. According to genomic analyses, the tomato genome was predicted to have approximately 900 megabases of DNA and encode 34,727 proteins. In this investigation, we identified and classified all putative tomato RLKs by comparison with previously described Arabidopsis RLKs [6]. We also showed that the tomato RLK members of LRRII subfamily, which comprises *NIK*s and *SERK*s genes, share similar biochemical activity (capacity to interact with the geminivirus NSP), genomic structure and partial overlapping expression profiles with the Arabidopsis orthologs. Our results provide a framework for understanding RLK function in tomato and reveal that some tomato and Arabidopsis LRRII-RLK orthologs may play similar roles in antiviral defense.

Results

The tomato RLK superfamily

The identification of the RLK superfamily members in tomato was initially performed by a batch BLAST search against a tomato protein database (ITAGv2.3, available in solgenomics.net) using the kinase sequences of representative Arabidopsis RLKs as queries. This analysis retrieved 955 tomato proteins that seemed to be RLKs. All of these retrieved tomato proteins were submitted for annotation of their domain structure using SMART [44] (smart.embl-heidelberg.de) and Pfam [45] (pfam.sanger.ac.uk) databases. Four proteins that did not bear a kinase domain were not considered for further analysis. The remaining 951 proteins were used for phylogenetic analysis based on their kinase domain sequences. For this analysis, we included all Arabidopsis RLKs to compare with tomato RLKs and used representative proteins of other kinase families of Arabidopsis and human as outgroups (Additional file 1). All Arabidopsis RLKs were placed in a major cluster together with 647 tomato proteins that were identified as members of the RLK superfamily (Figure 1). The other 304 proteins were clustered with outgroups; consequently, they were not considered to be members of RLK superfamily (Additional file 2).

The size of the tomato RLK superfamily (647 RLKs) did not differ greatly from that of the Arabidopsis RLK superfamily (623 RLKs). Furthermore, almost all tomato RLKs (631 RLKs) were clustered with at least one Arabidopsis RLK. Therefore, the tomato RLK superfamily was divided into the same 58 subfamilies as described previously for Arabidopsis [6]. As in Arabidopsis, in which 236 out of all 623 RLKs belong to leucine-rich repeat (LRR) subfamilies, tomato LRR subfamilies were the most abundant and contained 257 proteins. Another large RLK subfamily was RLCK, which included 128 members in tomato, almost the same number as in Arabidopsis (150). Among the 16 tomato RLKs that were not clustered in the same branches as Arabidopsis RLKs, ten proteins were quite small and lacked a typical RLK structure, but the other six proteins had a clear RLK structure and as such were considered to be tomato-specific RLKs. Among those six tomato-specific RLKs, Solyc03g080060 contained a legume lectin domain similar to members of the lectin subfamily, and Solyc02g083410 harboured an amino oxidase domain (flavin containing amine oxidoreductase activity), which is not found in any Arabidopsis RLKs. The remaining four proteins did not have any predicted protein domains in their extracellular region.

Although the RLK superfamilies of Arabidopsis and tomato share common features, a close inspection reveals some interesting differences between them. A comparison of the number of members of each subfamily showed that at least eight subfamilies from these plant species differ in size (Figure 2). The tomato LysM, SD and WAK/LRK10L1 subfamilies display twice as many RLK members as the Arabidopsis subfamilies. Conversely, members of the DUF26, L-lectin and RLCKXII/XIII subfamilies are considerably more abundant in Arabidopsis than in tomato. A more remarkable difference in size was observed for the LRRIa and LRRXII subfamilies. The Arabidopsis LRRIa subfamily has 43 members, whereas the tomato counterpart possesses only two members. By contrast, the tomato LRRXII subfamily is made-up of 48 RLKs, whereas only eight RLKs are found in Arabidopsis. Furthermore, the Arabidopsis and tomato RLK members of the LRK10L2 subfamily did not share a common domain structure in their extracellular region. Whereas the Arabidopsis members of this subfamily harbor diverse structures in their extracellular region, such as thaumatin, glycerophosphoryldiester phosphodiesterase family (GDPD) or malectin domains, the tomato RLKs of this same subfamily do not contain any predicted domain structures in their N-terminal region.

Motif prediction, genomic structure and phylogenetic analysis of the LRRII subfamily

Compelling evidence in the literature has revealed a fundamental role for members of the Arabidopsis LRRII-RLK subfamily as co-receptors for transducing developmental and defense signals [46–48]. The potential of the members of this subfamily as co-receptors involved in the activation of RLK-mediated signal transduction prompted us to perform a comprehensive analysis of the tomato LRRII-RLK subfamily to uncover related functions in tomatoes. Based on the phylogenetic tree of all members of RLK superfamily, the tomato LRRII-RLK subfamily encompassed 13 proteins. The members of this group from both plant species have over 600 amino acids on average. Phylogenetic analysis of this group using full-length protein sequences resulted in a tree with three well-resolved clusters; the tomato and Arabidopsis proteins were well distributed among those clusters, although they had distinct sizes (Figure 3A). These clades were termed NIK, SERK and LRRIIc based on annotation of the Arabidopsis members in each cluster. The tomato NIK clade was overrepresented with seven members, whereas the tomato SERK clade was reduced in size (three members) compared with the five well-characterized SERKs in Arabidopsis. The LRRIIc clade consisted of three tomato proteins and three Arabidopsis proteins whose functions are unknown. Motif prediction analysis on these proteins revealed that tomato and Arabidopsis LRRII-RLK members display similar protein domains organized in the same fashion (Figure 4). The consensus structural organization of the conserved domains between both species included a N-terminal signal peptide followed by a leucine zipper, five LRRs at the extracellular side and a transmembrane domain separating the N-terminal portion from the cytoplasmic C-terminal kinase domain. Among the *SERK* genes of both species, there was also a proline-rich domain (SPP) localized between the last LRR and the transmembrane domain (Figure 4). Sequence alignment of the LRRII RLKs showed several conserved amino acid positions among members of both plant species. Exon/intron boundaries were also well conserved. Variation at the sequence level was observed within the SPP and signal peptide recognition domains. Among the LRRII clades, the proteins comprising the SERK clade were more conserved with a larger number of conserved positions compared with the predicted proteins of the LRRIIc and NIK clades (Figure 4). Genomic structure analysis revealed that in general LRRII genes are organized into 11 exons (Figure 5). Genes that varied in this number displayed fused exons, including *AtNIK1*, At5g10290.1 and *SlNIK3*, or had deleted exons, such as At5g63710.1, Solyc02g072310.2.1 and Solyc05g005140.2.1. Intronic regions were larger in tomato members than in Arabidopsis members and in *SERK* genes compared with genes from other clades.

Expression analysis of LRRII subfamily genes in different tissues

We examined the expression profiles of LRRII-RLK genes in different tomato tissues, including leaf, stem, root, flower, cotyledon and hypocotyl, by real-time PCR. The results are presented in Figure 6 and summarized in Figure 3B. Almost all analyzed genes exhibited significant expression in at least one organ, except for Solyc05g005140 and Solyc02g072310 in the NIK clade, which had very low expression in all tissues tested. The tomato genes in the SERK clade were expressed more highly in leaf and cotyledon tissue than in stem or flower tissue. The NIK clade genes were highly expressed in diverse organs, such as in leaves, flowers and roots. The LRRIIc group encompassed genes with a higher level of expression in cotyledon, flower and leaf tissues and with lower expression in stem tissue.

The expression data for LRRII subfamily members from Arabidopsis (Figure 3C) were extracted from AtGenExpress [49] to examine whether the expression profiles between orthologous pairs of tomato and Arabidopsis genes were correlated. A comparison of the expression analysis from both plants revealed that the majority of the orthologous genes displayed partially but not entirely overlapping expression profiles, although a few of them showed a more strict correlation (Figure 3D). The orthologous groups that presented similar expression profile were *AtSERK1*/*AtSERK2* and Solyc04g072570, which had high expression levels in leaves, *AtNIK1* and *SlNIK1*, which were lowly expressed in stem and cotyledon tissues, and *AtNIK3* and *SlNIK3*, which were most highly expressed in the leaf. The remaining orthologs did not share similar expression profiles at the quantitative level.

Interactions between representatives of the LRRII subfamily and NSP of ToYSV

We have previously shown that NSP from begomovirus interacts with members of the LRRII-RLK subfamily, such as AtNIK1, AtNIK2 and AtNIK3, to suppress host defense, and it interacts with a member of the PERK-like RLK subfamily, NSP-ASSOCIATED KINASE (NsAK), to potentiate virus infection [29, 50]. Because begomovirus negatively impacts tomato cultivation worldwide, we selected representatives of tomato RLKs from the LRRII subfamily and examined their capability to interact with NSP of *Tomato Yellow Spot Virus* (ToYSV) similar to the interaction observed with Arabidopsis *NIK* genes [29]. Yeast two-hybrid experiments were performed using the ToYSV-NSP (accession number: YP_459917.1) as prey (TYNSP-AD) and kinase domains of SlNIK1 (Solyc02g089550), SlNIK2 (Solyc04g005910), SlNIK3 (Solyc04g039730) and SlBAK1 (Solyc10g047140) as bait. We also analyzed a PERK representative (Solyc12g007110, SlNsAK) that is similar to the NSP-interactor PERK-like gene of Arabidopsis (At5g24550, AtNsAK). A tomato gene (Solyc03g019980, SlEFR) from the LRRXII subfamily, a homolog of the Arabidopsis EF-Tu receptor (AtEFR), was used as a negative control. Interactions between the viral NSP and host proteins were detected after co-transforming the yeast cells with both bait and prey plasmids and monitoring for histidine prototrophy. NSP was found to interact with the kinase domains of SlNIK1, SlNIK2, SlNIK3 and SlBAK1 or with the kinase domain of the PERK representative SlNsAK (Figure 7, upper panel). The NSP interactions were specific to the tomato LRRII-RLK orthologs and to PERK-like SlNsAK because the *HIS* marker gene was not activated in yeast cells co-transformed with TYNSP-AD and with either the empty vector expressing the GAL4-binding domain alone (empty-BD) or with the kinase domain of SlEFR fused to GAL4-binding domain (SlEFR-BD). Furthermore, co-transformation of yeast with the NSP interactors fused to the GAL4-binding domain and the empty vector expressing the GAL4-activating domain alone also failed to activate the *HIS* marker gene (Figure 7, lower panel). These results expanded our previous observation that NSP-NIK complex formation was neither virus-specific nor host-specific [29, 41]. They also suggest that

SlNsAK is a NSP target during begomovirus infection in tomato. Certainly, the *in vivo* demonstration of these interactions will further support these interpretations.

Discussion

The structure of the tomato RLK superfamily and the proposed evolution of RLK superfamily in plants

To date, the phylogenetic and structural characterization of the RLK superfamily has been limited to the following plant species: moss, rice, poplar, soybean and Arabidopsis [6, 32, 33]. The size of these families ranges from 300 to 1200 proteins (Figure 8), and their extracellular regions bear a great variety of protein domain structures. In the present investigation, we characterized and generated a complete list of the tomato RLK superfamily members (Additional file 2 and 3), identifying 647 RLKs, which falls in the size range of the Arabidopsis (623 RLKs) and soybean (605 RLKs) superfamilies.

Evolutionary analyses of the RLK superfamily has suggested that the RLK structure was established prior to the divergence of land plants from algae because proteins with RLK configurations were discovered in the unicellular algae *Clamydomonas reinhardtii* [32]. Comparative analysis of RLKs among moss, rice, poplar and Arabidopsis revealed that the RLK superfamily underwent expansion in the beginning of the land plant lineage, after the divergence of angiosperm and bryophyte and independently during diversification of each angiosperm lineage. The most dramatic expansion was observed in the rice and poplar lineages, which have almost twice as many as RLK members as Arabidopsis [32]. This evolutionary scenario has not been changed by inclusion of data regarding the soybean [33] and tomato (this work) RLK family expansion (Figure 8).

The phylogenetic tree of the members of the RLK superfamilies in tomato and Arabidopsis revealed that most of the RLK subfamilies have maintained approximately the same number of RLK members between these species. Exceptions were observed for the DUF26, L-lectin, LysM, SD1, SD2b, LRRIa, LRRXII, RLCKXII/XIII and WAK/LRK10L1 subfamilies, in which specific extensive expansion or reduction was observed in one of the two plant species. Functional annotations of some Arabidopsis RLKs that compose those subfamilies indicated a predominance of defense-related RLKs (Table 1) that had been shown previously to be overrepresented in microarray analysis of Arabidopsis under different stress conditions [32]. Taken together, these results are consistent with the previous assumption that specific expansions and reductions of RLK genes have occurred more frequently for those RLKs associated with defense response.

The overrepresentation of tomato RLKs compared to Arabidopsis occurred in the LRRXII, LRRXIIb, SD-1, SD-2b, LysM and WAK/LRK10L1 subfamilies. Interestingly, all of those RLK subfamilies were also overrepresented in rice when compared with Arabidopsis [6]. The LRRXII subfamily comprises the EF-Tu RECEPTOR (EFR) and FLAGELLIN-SENSITIVE 2 (FLS2) in Arabidopsis, and Xa21 in rice, all of which are associated with defense responses. The expansion of the LRRXII subfamily in cultivated plants such as tomato and rice has previously been suggested to be associated with the accumulation of resistance genes by intense breeding programs [6]. Likewise, the LysM subfamily includes RLKs known to interact with bacterial elicitors. In Arabidopsis and rice, RLK members of this subfamily recognize those elicitors, such as chitin, and trigger the activation of defense responses in the plant [51, 52]. In other plants, such as *M. truncatula*, *Lotus japonicus* and *Glycine max*, recognition of these elicitors by LysM RLKs mediates symbiotic interactions with other bacteria, such as rhizobia [53, 54]. The SD subfamily also has representatives involved in defense response, but this subfamily is also strongly associated with the self-incompatibility process [55]. Arabidopsis is known to be self-compatible, while rice, tomato and the close relative of *A. thaliana*, *A. lyrata*, are self-incompatible. Thus, the deletion of some representatives in *A. thaliana* could have contributed to the generation of the self-compatible mode in this species. By contrast, some RLK subfamilies were overrepresented in Arabidopsis. Those include DUF26, L-Lectin, LRRIa and RLCKXII/XIII. These subfamilies were also overrepresented in rice compared to tomato, with the exception of the RLCKXII/XIII subfamily that has no RLK member in rice. In spite of a reduction in size of these subfamilies in tomato, they all contain RLKs that are involved in defense response, such as FLS2-INDUCED RECEPTOR-KINASE 1 (FRK1), IMPAIRED OOMYCETE SUSCEPTIBILITY 1 (IOS1), LECTIN RECEPTOR KINASE 1.9 (LecRK-1.9) and CYSTEINE-RICH RLK 5 (CRK5). This apparently contradicts the assumption that defense response genes would be amplified through artificial selection. Nevertheless, those RLK subfamilies also have receptor members associated with others biological process, such as development, programmed cell death and hormone response. Some tomato orthologs of these Arabidopsis genes could have had negative impacts on tomato cultivation and hence were not selected for during the breeding program.

Another relevant distinction between tomato and Arabidopsis RLK subfamilies derives from the diversification of the extracellular domain patterns of the LRK10L2 subfamily representatives. Arabidopsis members of the LRK10L2 subfamily have unique domain structures, such as GDPD, thaumatin and malectin domains, while the tomato members do not possess any characterized domain structure in their extracellular region. Likewise, these domain structures have not been found in rice, poplar or moss RLKs, indicating that within the RLK superfamily they are specific to Arabidopsis. We also identified a tomato-specific RLK that possesses an amino oxidase domain in its extracellular region. These RLKs may respond to molecular signals not perceived by other plants. Although gaining a novel protein structure could increase the repertoire of signals perceived by plants, the small number of lineage-specific RLKs in tomato, as was also reported in rice and poplar, further substantiates the hypothesis that the expansion of existing RLK subfamilies is the major mechanism of evolution of these proteins.

The members of the RLK superfamily are involved in diverse biological processes at all steps of plant development. Thus, the gain or loss of a RLK gene could have serious repercussions on plant phenotype. The specific profiles of the RLK superfamily found in tomato and Arabidopsis are certainly responsible for several differences between these plants, such as morphology, reproduction and, importantly, responsiveness to different stress conditions. Among tomato and Arabidopsis, few RLK subfamilies have undergone specific expansion or reduction after their speciation. This scarcity may indicate that variation in RLK superfamily profiles in both plants appeared recently. The domestication process that tomatoes underwent could have been a significant factor contributing to this variation because the majority of RLKs has been directly linked to relevant agronomic traits, such as disease resistance and growth. However, to further examine the influence of artificial selection on the repertoire of plant RLKs, new genetic resources for closely related wild plants are necessary.

Functional expression analysis of the LRRII subfamily members in tomato and Arabidopsis

The LRRII subfamily contains RLKs with dual functions in development and defense response [46–48]. Characterized members of this subfamily include (i) *SERK* genes, which are associated with diverse processes, such as brassinosteroid signaling, flagellin, cell death, light and pathogen-associated molecular pattern (PAMP) responses [47], and (ii) *NIK* genes, which interact directly with geminivirus NSP during viral infection [29, 30]. Phylogenetic and protein structure analyses on LRRII subfamily members of tomato and Arabidopsis demonstrated that this group is highly conserved between these species. In rice, in which the RLK superfamily has undergone a large expansion, the LRRII subfamily members are also conserved in number and sequence, indicating that biochemical pathways regulated by LRRII-RLKs have essential and conserved roles in angiosperm species.

Although LRRII members have well-conserved amino acid sequences among various species [56], expression analysis of the members of the tomato and Arabidopsis LRRII subfamilies demonstrated that only a few of the orthologous pairs exhibited correlated expression profiles. By analogy with some evidence in the literature from other plant species, one may envision that these orthologous genes could have functionally diverged after the speciation event separating tomato and Arabidopsis. Functional divergence in orthologous genes is not an uncommon event in both plants [57–59] and animals [60, 61]. For example, the CRABS CLAW transcription factor in Arabidopsis is expressed in the carpel primordial abaxial region and in floral nectarines and regulates carpel morphology and nectar development, whereas its orthologous in rice, DROOPING LEAF (DL), is expressed in the whole carpel primordium and in central undifferentiated cells of leaves, where it regulates carpel identity and midrib development [59]. The expression of orthologous genes has also been shown to vary differently in response to a stress condition. In barley, which is tolerant to salinity, the expression of genes involved in root development, such as CONSTAN-LIKE 3 (COL3), is suppressed by high salinity, whereas the expression of the rice orthologous is unchanged under the same stress condition [58]. Likewise, a large fraction of orthologous pairs of rice and Arabidopsis genes with receptor activity do not display conserved co-expression [62]. Therefore, the lack of correlation between the expression patterns of orthologous genes in the LRRII subfamilies from tomato and Arabidopsis may be a result of functional divergence that occurred between these genes. Functional divergence in receptor proteins with a developmental function may lead to a dramatic change in the plant phenotype because plant development is heavily guided by external signals. For example, a tissue that displays high expression of certain RLKs is likely to be more sensitive to perception of RLK-specific sensing signals, leading to a rapid and effective response. In contrast, reduced expression of an orthologous gene from a different species in the same tissue would decrease the effectiveness and delay the signal perception and response. This difference in the cell responsiveness to a specific signal could represent the differential timing of biochemical reactions that are regulated by this signal. In developmental process, small differences in reaction time may be sufficient to generate a distinct phenotype in the plant. By contrast, the orthologous pairs SERK1/SERK2/Solyc04g072570.2.1, which display correlated quantitative expression profiles (Figure 3), also contain the most conserved extracellular and intracellular domains (approximately 80% and 93% of sequence identity, respectively, additional file 4). The other two orthologous pairs, NIK1/SlNIK1 and NIK3/SlNIK3, which also displayed a high degree of correlation in their expression profiles, also had highly conserved extracellular and intracellular regions. In both orthologous pairs, sequence identity was approximately 65% in the extracellular regions and approximately 80% in the intracellular regions (additional file 4). This finding may indicate a tight conservation of function between these members of the Arabidopsis and tomato LRRII-RLK subfamilies.

Conservation of geminivirus interactions with members of the RLK family in tomato

Although most of LRRII subfamily orthologous pairs exhibited functional divergence, we showed that the tomato orthologs of the LRRII-RLKs members NIK1, NIK2 and NIK3 retain the capacity to interact with geminivirus NSP in yeast (Figure 7)

[29]. At least for the NIK1 and NIK3 ortholog pairs, the functional conservation associated with specific protein-protein interactions may be linked to the high conservation of their NSP-interacting kinase domain (approximately 80% sequence identity, additional file 4) and quantitative correlation of their expression profiles (Figure 3). The current model of NIK-mediated defense response posits that the immune receptor protects plant against geminiviruses by phosphorylating the ribosomal protein L10 (rpL10) [30]. Phosphorylation of rpL10 by NIK redirects the ribosomal protein to the nucleus, where it may mount a defense mechanism to prevent viral proliferation. During geminivirus infection, NSP interacts with the kinase domain of NIKs to inhibit their kinase activity, preventing activation of the defense response. Despite the high similarity between *NIK* genes and *SERK* genes, AtBAK1/SERK3 and AtSERK1 do not functionally replace the AtNIK1 role in transducing an antiviral signalling response and do not interact with the viral NSP [29, 30]. In contrast, we found that the *AtBAK1*ortholog from tomato interacts with NSP in yeast. Although the functional relevance of this interaction *in planta* remains to be determined, it is worth noting that the expression profiles of the *BAK1* orthologs do not correlate quantitatively, as would be expected for functionally divergent orthologs. Although both orthologs are ubiquitously expressed in the cognate plant species, they are expressed to different extents in distinct organs. Whereas AtBAK1 expression is quantitatively similar and relatively low in all organs analyzed, its ortholog from tomato displays a higher level of expression in the cotyledon, hypocotyl and leaves, where geminivirus infection largely takes place. Therefore, the expression profiles of the NSP interactors (SlNIKs and SlBAK1) seemed to correlate nicely with the onset of geminivirus infection. Due to the high expression of the AtBAK1 tomato orthologous in leaves, one may envision the existence of evolving selective pressures to diverge the corresponding NSP-interacting

domains of the BAK1 orthologs towards functional fitness with regard to geminivirus infection.

In contrast to NIK receptors, which are inhibited by NSP interaction, AtNsAK, a member of PERK subfamily, interacts with NSP and phosphorylates the viral protein *in vitro* [50]. Loss of *nsak* function enhances tolerance to geminivirus infection, indicating that AtNsAK is a positive contributor to geminivirus infection in Arabidopsis. Here, we showed that the NsAK tomato orthologous retains its capacity to interact with viral NSP. This demonstrates that specific members of the RLK family have conserved defense functions (such as NIKs) or compatibility functions (such as NsAK) in response to viral infection. Due to the emergence of new species of tomato-infecting begomoviruses that rapidly evolve through recombination or pseudo-recombination to produce divergent genome sequences that gives the virus an advantage over its host's recognition system, a survey of the interactions between NSPs from distinct tomato-infecting geminiviruses and SlNIKs and SlNsAK may add insights into the co-evolution of the viral protein and host defense/compatibility functions.

Conclusions

The RLK superfamily is a large and diverse group of transmembrane receptors that enables plants to perceive a diverse array of signals at the cell surface, creating an efficient mechanism for cell-environment communication. In this investigation, we generated a complete list of the members of the tomato RLK superfamily, which is made-up of 647 proteins. The tomato RLK sequences exhibited a typical receptor-like kinase configuration and almost all of them were phylogenetically clustered with at least one member of the Arabidopsis RLK superfamily. Therefore, the tomato RLK superfamily is similarly organized, with the same number and identity of subfamilies as previously defined for Arabidopsis RLKs. Among the 58 RLK subfamilies, eight showed specific and extensive expansion or reduction in the number of their RLK members, which may be a reflection of lineage-specific responses to various biotic and abiotic stresses. The intense breeding programs tomatoes have been subjected to may also have contributed to the establishment of the current RLK superfamily profile in this species. This comprehensive analysis comparing the complete repertory of Arabidopsis and tomato RLKs may provide a framework to rationalize future functional studies of the members of this family.

Phylogenetic and structural analyses of LRRII subfamily members from both tomato and Arabidopsis reveal a well-conserved group both in terms of sequence and protein domain organization. As a consequence, the tomato LRRII-RLK subfamily is organized into the same three phylogenetically supported clades, SERK, NIK and LRRIIc clusters. Nevertheless, a comparison of the quantitative expression profiles between orthologous genes of this subfamily demonstrated that the majority of the orthologous pairs did not share a correlated expression profile, indicating that these orthologous LRRII-RLKs may have undergone functional divergence. This finding is supported by the observation that, in contrast to the Arabidopsis AtBAK1, SlBAK1 interacts with the geminivirus NSP and is highly expressed in leaves and the cotyledon. This pattern of SlBAK1 expression is consistent with the pattern of infection by tomato-infecting begomoviruses, which infect leaf tissues and move through the phloem but do not invade roots. A perfect correlation between expression profile and functional biological activity was observed for the orthologous pairs NIK1 and NIK3. As immune receptors, both orthologous pairs displayed the capacity to interact with the begomovirus virulence factor NSP and their pattern of expression parallels the onset of begomovirus infection. Evidence for functional conservation between NIK1 orthologs has been previously provided with the demonstration that NIK1 from Arabidopsis is capable of protecting tomato plants against tomato-infecting begomovirus [63].

Collectively, our results indicate that NIK orthologs retain similar functions as defense receptors to protect plant cells against viral attack. Therefore, NIK-mediated antiviral signalling likely also operates in tomato, suggesting that the tomato NIKs may be good candidate targets for engineering resistance against tomato-infecting begomoviruses.

Methods

Identification and classification of tomato RLKs

Tomato RLK proteins were retrieved through a batch BLAST analysis (blastp, e-value cutoff = 0.01) [64] using an *A. thaliana* representative of each subfamily of the RLK superfamily against a protein database of tomato (iTAGv2.3) available on the Sol Genomics Network website (solgenomics.net) [65]. Through this procedure, 955 predicted proteins were retrieved and annotated using SMART (smart.embl-heidelberg.de) [44] and Pfam (pfam.sanger.ac.uk) [45] databases. Among these proteins, 951 contained a predicted kinase domain and hence were considered to be putative RLKs. The sequences of the kinase domains of Arabidopsis RLKs, previously described in [6], and tomato putative RLKs were submitted to sequence alignment and tree reconstruction using ClustalW (v. 2.0.12) [66] and FastTree (v. 2.1.4) [67], respectively (Figure 1 and additional file 2) using default parameters. The kinase domain of other kinase protein families from *A. thaliana* and human were used as outgroups [3, 68]. The accession numbers for all outgroup members are reported in additional file 1. Those proteins that clustered with outgroup members were not considered to be RLKs and were discarded from further analysis. Additionally, short putative RLKs were deleted manually from the analysis. The identified RLK-related tomato sequences comprised a list of 647 members. Tomato RLKs that clustered with *A. thaliana* RLK subfamily members, as defined previously in [6], were classified as members of the same subfamily. Phylogenetic trees (Figure 1 and additional file 2) and protein schemes (Additional file 2) were generated using iTOL tool (itol.embl.de) [69].

Motif prediction, genomic structure and phylogenetic analysis of the LRRII subfamily

Full-length amino acid sequences of members of the LRRII subfamily from tomato and Arabidopsis were aligned using ClustalW (v. 2.0.12) [66] using the default parameters. A phylogenetic tree was constructed using the maximum likelihood method (JTT model, bootstrap replicates = 1000) implemented in MEGA5 software [70]. Motif, signal peptide and transmembrane prediction were carried out using Pfam [45] and SMART [44] databases. The genomic structure of the LRRII subfamily members of tomato and Arabidopsis was determined by aligning the coding sequence (CDS) of each gene with genomic sequences of the respective organism. The alignment was carried out using the BLAST algorithm (blastn) [64] with high-stringency parameters. Amino acid, CDS and genomic sequences for tomato and Arabidopsis were retrieved from the Sol Genomics Network (solgenomics.net) [65] and TAIR (www.arabidopsis.org) [71] websites, respectively.

Protein-protein interaction assays

The analysis of protein-protein interactions between viral NSP and the kinase domain of tomato RLKs was performed using the Proquest^{TM} Yeast Two-Hybrid System with Gateway Technology (Invitrogen Inc.). The tomato RLKs that presented the highest identity with AtNIK1 (At5g16000), AtNIK2 (At3g25560), AtNIK3 (At1g60800), AtBAK1 (At4g33430) and AtNsAK (At5g24550) were selected for the assay. These tomato proteins are referred to as SlNIK1 (Solyc02g089550), SlNIK2 (Solyc04g005910), SlNIK3 (Solyc04g039730), SlBAK1 (Solyc10g047140) and SlNsAK (Solyc12g007110), respectively. As a negative control, we used the kinase domain of the tomato RLK that displayed the highest identity with AtEFR (At5g20480), referred to as SlEFR (Solyc03g019980).

The NSP coding region was amplified from ToYSV (Tomato Yellow Spot Virus – Geminiviridae, *Begomovirus*) [72] using gene-specific primers with appropriate extensions for cloning via the Gateway system, as described in additional file 5. The amplified fragment was cloned into pDONR201 to generate pUFV1780.1 and then transferred by recombination to pDEST22 yielding pUFV1781, also designated as TYNSP-AD.

For amplification of the C-terminal kinase domain of the tomato RLKs, we prepared cDNA from cotyledons of wild-type tomato plants (var. Santa Clara). Briefly, total RNA from tomato cotyledons was isolated using a RNeasy® Kit (Qiagen Inc.). First-strand cDNA was synthesized from 1 μg of total RNA using the M-MLV Reverse Transcriptase (Invitrogen Inc.) according to the manufacturer’s instructions. Primers used in the amplification step were designed with recombination sites for further cloning procedures using the Gateway System (Invitrogen Inc.). The primers used are listed in additional file 5. PCR assays were performed using Platinum® *Taq* DNA Polymerase High Fidelity (Invitrogen Inc.) according to the manufacturer‘s instructions. The amplified fragments were cloned into the entry vector pDONR201 (Invitrogen Inc.) and sequenced. The resulting vectors were the following: pUFV1756.1, pUFV1596, pUFV1757.1, pUFV1734.2, pUFV1744.1 and pUFV1955.2, corresponding, respectively to the fragment encoding the kinase domain of SlNIK1, SlNIK2, SlNIK3, SlBAK1, SlNsAK and SlEFR. Then, the cloned fragment in pDONR201 was transferred to pDEST32, which contains the DNA-binding domain of the GAL4 promoter (Invitrogen Inc.). This procedure resulted in the following recombinant plasmids: pUFV1768.1, pUFV1760.1, pUFV1779.1, pUFV1769.1, pUFV1770.1 and pUFV1975.1, also designated as SlNIK1-BD, SlNIK2-BD, SlNIK3-BD, SlBAK1-BD, SlNsAK-BD and SlEFR-BD, respectively.

Competent cells of yeast strain AH109 (Clontech Inc., genotype: *MATα*, *trp1-901*, *leu2-3,112*, *ura3-52*, *his3200*, *gal4Δ*, *gal80Δ*, *LYS2::GAL1*$_{UAS}$*-GAL1*$_{TATA}$*-HIS3*, *GAL2*$_{UAS}$*-GAL2*$_{TATA}$*-ADE2*, *URA3::MEL1*$_{UAS}$*-MEL1*$_{TATA}$*-lacZ*) were sequentially co-transformed with TYNSP-AD and with one of the pDEST32 constructs. Co-transformed yeasts were plated onto synthetic dropout medium lacking leucine, tryptophan and histidine, and incubated at 28°C. Yeast growth was monitored for 5 days.

Expression analysis of the LRRII subfamily genes

The expression patterns of genes in the LRRII subfamily were assayed by quantitative Real-Time PCR (qRT-PCR) in various tomato tissues. Wild-type tomato plants (var. Santa Clara) were cultivated in a greenhouse for 45 days after germination. Leafs, stems, roots and flowers from three plants were collected separately. We also cultivated plants in half-strength Murashige and Skoog medium (1/2 MS, Sigma-Aldrich Co.) for 10 days after germination under normal conditions to collect cotyledons and hypocotyls tissue. For these tissues, due to the small amount of material, each sample represented a pool of three young plants. Total RNA from each sample was extracted using TRIzol (Invitrogen Inc.), and the quality and integrity of extracted RNA were monitored by spectrophotometry and electrophoresis. For cDNA synthesis, 3 µg of total RNA from each sample was first treated with RNase-free DNAse I (Promega Inc.) and then reverse-transcribed using M-MLV Reverse Transcriptase (Invitrogen Inc.) and oligo-dT primers. qRT-PCR assays were performed using an ABI7500 *Real Time PCR System* (Applied Biosystems Inc.) and *SYBR® Green PCR Master Mix* (Applied Biosystems Inc.). The amplification reactions were performed using default parameters for thermal cycling (50° for 10 min, 95° for 1 min, followed by 40 cycles of 95° for 15 sec and 60° for 1 min). Primers were designed using PerlPrimer [73], attempting to choose primer pairs in which at least one of them extended across an intron-exon boundary. Expression quantification of each gene was determined according to the Ct relative quantification method ($2^{-\Delta Ct}$) [74] using *SlAPT1* (adenine phosphoribosyltransferase, Solyc04g077970.2.1) as an endogenous control for data normalization. Expression data from Arabidopsis were obtained from the AtGenExpress website (jsp.weigelworld.org/expviz/expviz.jsp) [49].

Authors' contributions

The project was coordinated by EPBF. OJBB and TS performed the bioinformatic and phylogenetic analyses. AAS, MD and TS were involved in the gene expression assays. MD and TS carried out the yeast two-hybrid assays. EPBF, MD and TS prepared the manuscript. All authors read and approved the final manuscript.

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Figures

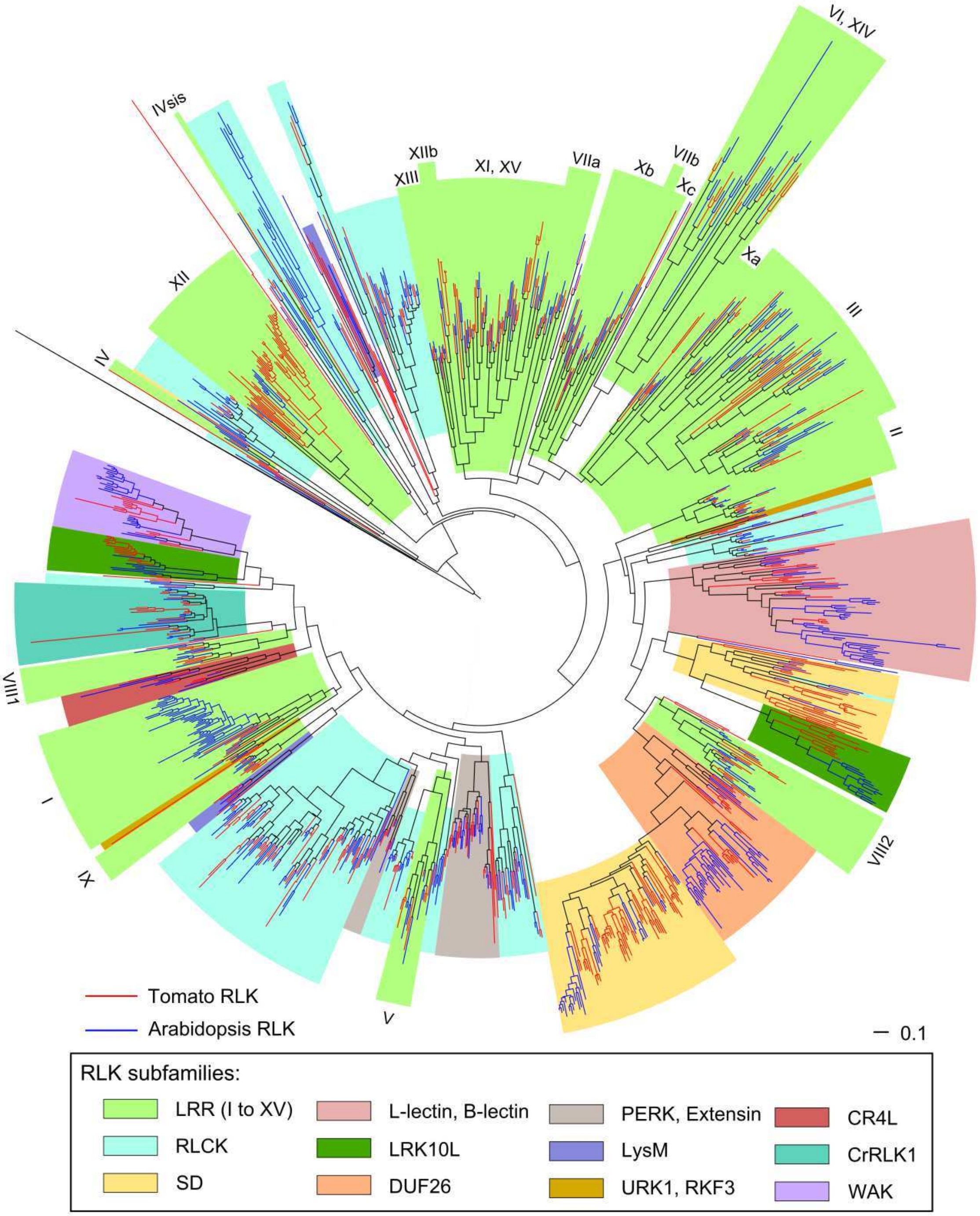


Figure 1 -The tomato RLK superfamily is composed of 647 proteins.

Phylogenetic tree constructed by sequence alignment of kinase domain of Arabidopsis RLKs together with putative tomato RLKs. The alignment was carried out with CLUSTALW, and the phylogenetic tree reconstruction was made using FastTree. Almost all tomato RLKs (red branches) clustered with Arabidopsis RLKs (blue branches). Color ranges delimit the RLK subfamilies. LRR subfamilies (light green) are subdivided in 15 groups, and each group is identified in the tree with Roman numerals (I to XV).

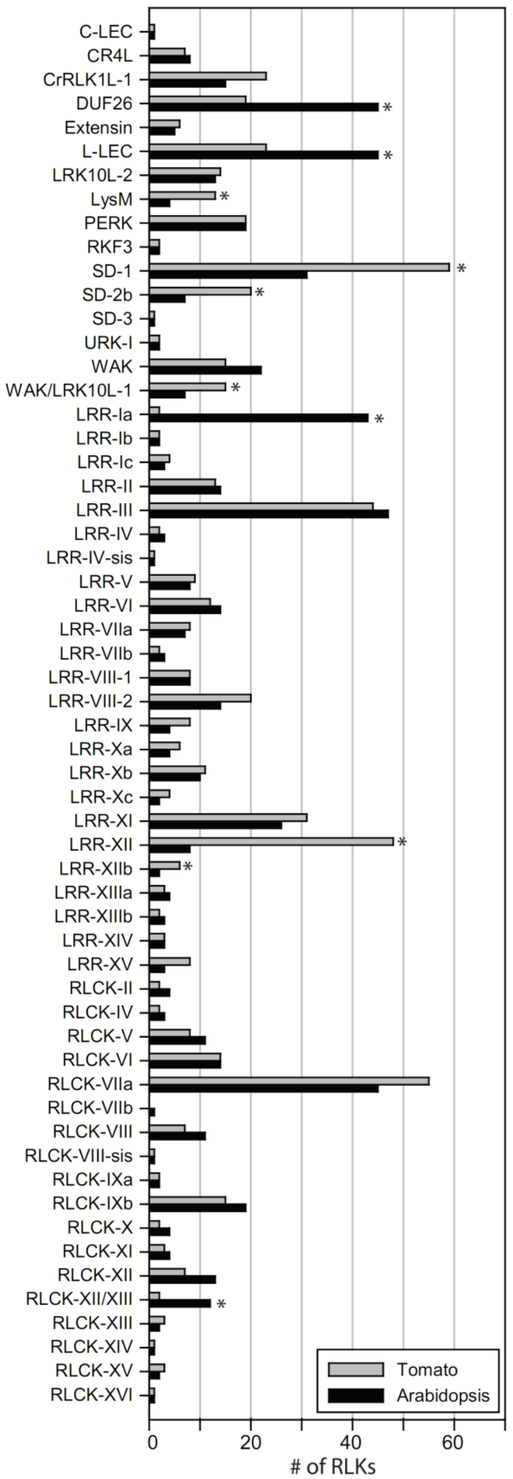


Figure 2 - The number of members varies in some tomato and Arabidopsis RLK subfamilies.

The distribution profile of tomato and Arabidopsis RLKs in subfamilies is presented. Almost all RLK subfamilies described in Arabidopsis have representatives in tomato. RLK subfamilies that have undergone specific and extensive expansion or reduction in one species are indicated with asterisk.

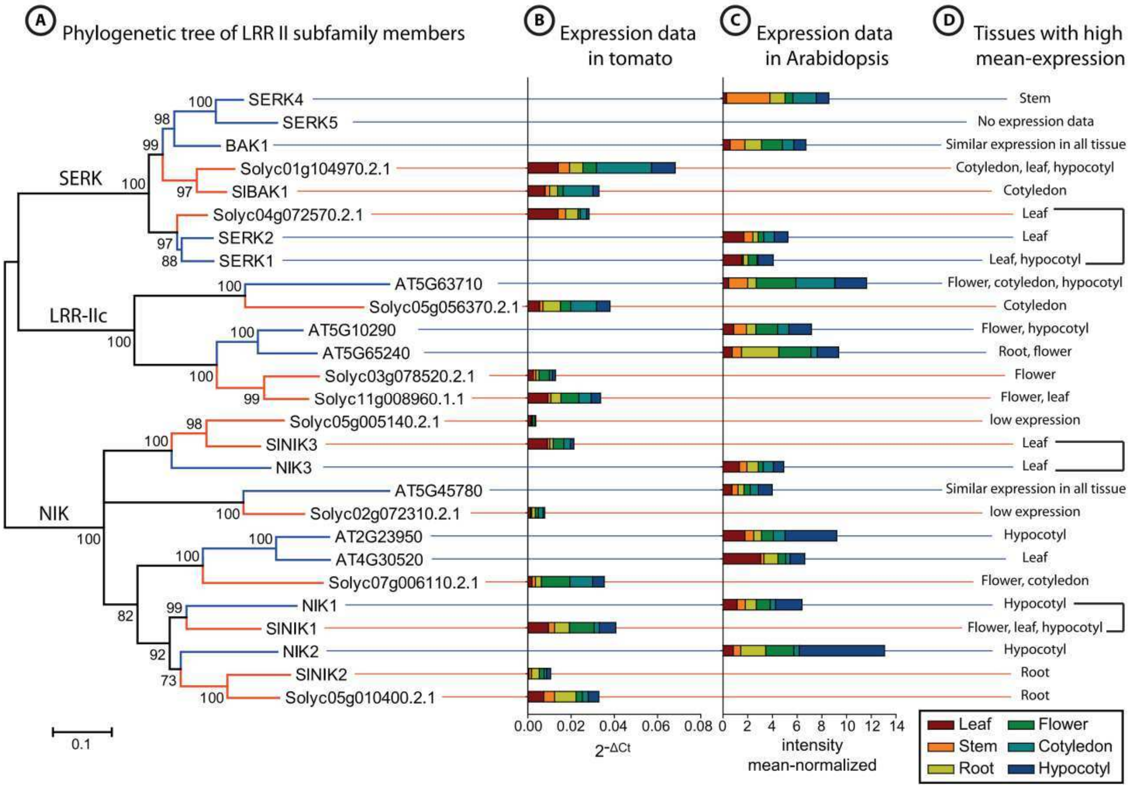


Figure 3 -Phylogenetic and expression analysis of LRRII subfamily members.

(A) Phylogenetic tree reconstructed by the maximum likelihood method (JTT+G+I, bootstrap replicates = 1000) of the LRRII subfamily. Members of this subfamily can be separated in three well-supported clades, referred to here as SERK, NIK and LRRIIc clades. Expression analysis of LRRII subfamily members in (B) tomato and (C) Arabidopsis in different plant tissues. The expression data of tomato and Arabidopsis members were obtained by qRT-PCR and from normalized data from the AtGenExpress database [49], respectively. No expression data were obtained for SERK5 (At2g13800). (D) Tissues with high mean-expression are summarized for each gene. Orthologous genes that had similar expression profiles are delimited by brackets.

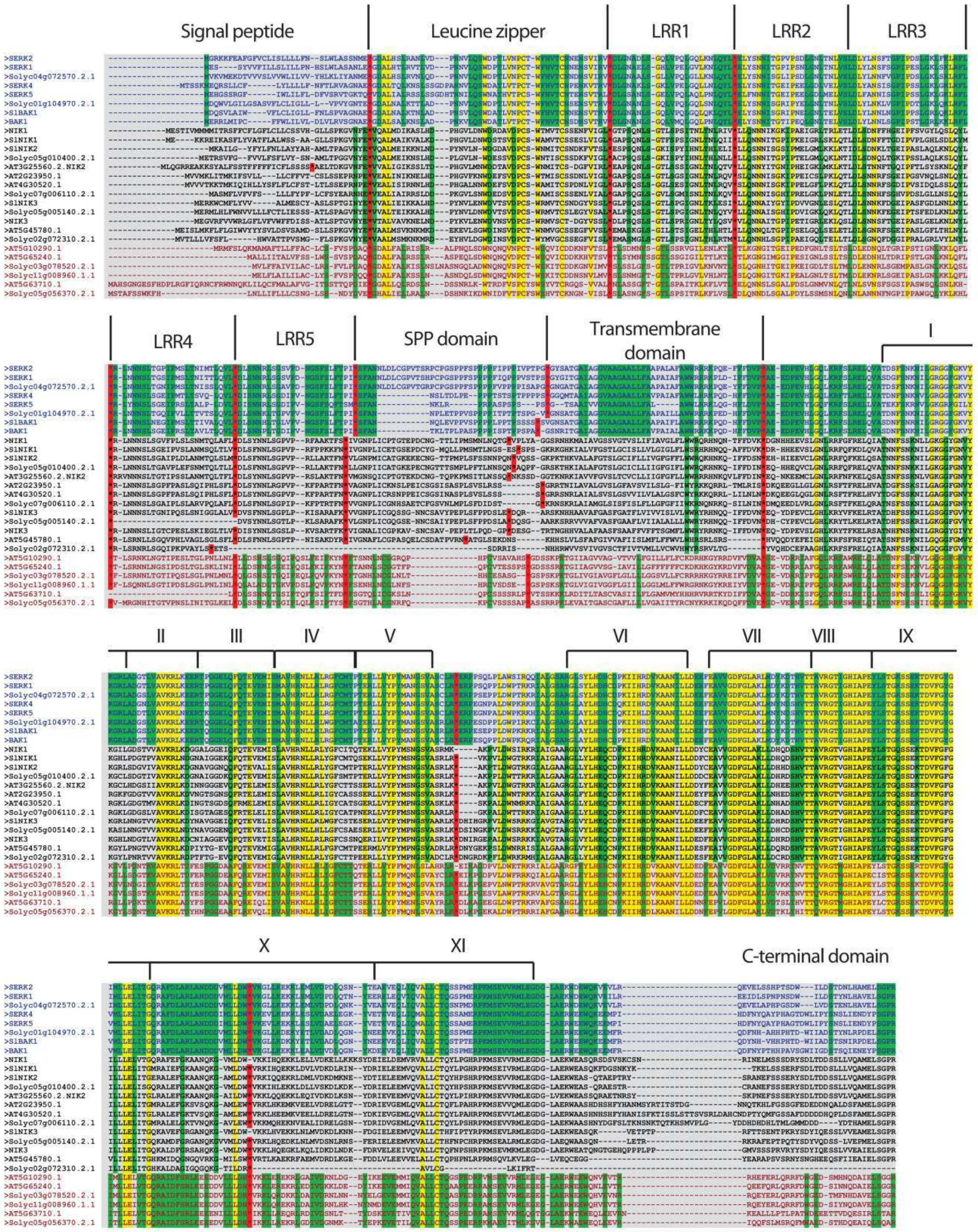


Figure 4 -Full-length sequence alignment of LRRII subfamily members of tomato and Arabidopsis demonstrate sequence and structure conservation.

Sequences of SERK, NIK and LRRIIc clades members are represented with blue, black and red letter colors, respectively.Yellow sites represent conserved sites in all sequences, and green sites represent conserved sites in each clade. Red sites represent the exon-exon junctions. Domain structures are indicated above the alignment. Roman numerals delimit the 11 subdomains of the kinase domain.

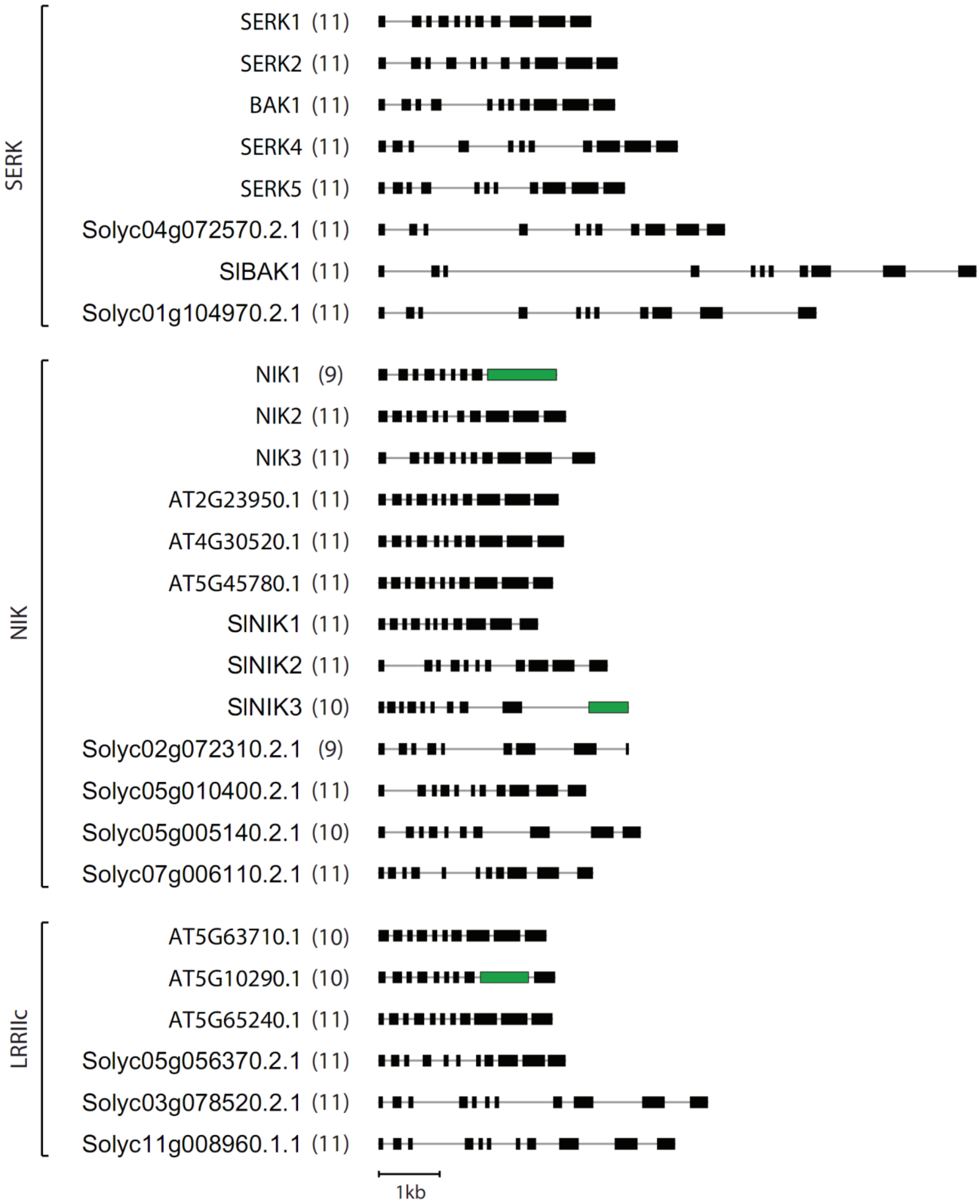


Figure 5 -Genomic structure analysis of members of the LRRII subfamily of tomato and Arabidopsis.

Exons are shown as dark boxes and introns as grey lines. Green box represent fused exons. The number between parentheses represents the number of exons in each gene. Almost all genes contain 11 exons. Note the large length of intronic regions in SERK genes compared with genes from other clades, and in tomato sequences compared with Arabidopsis sequences.

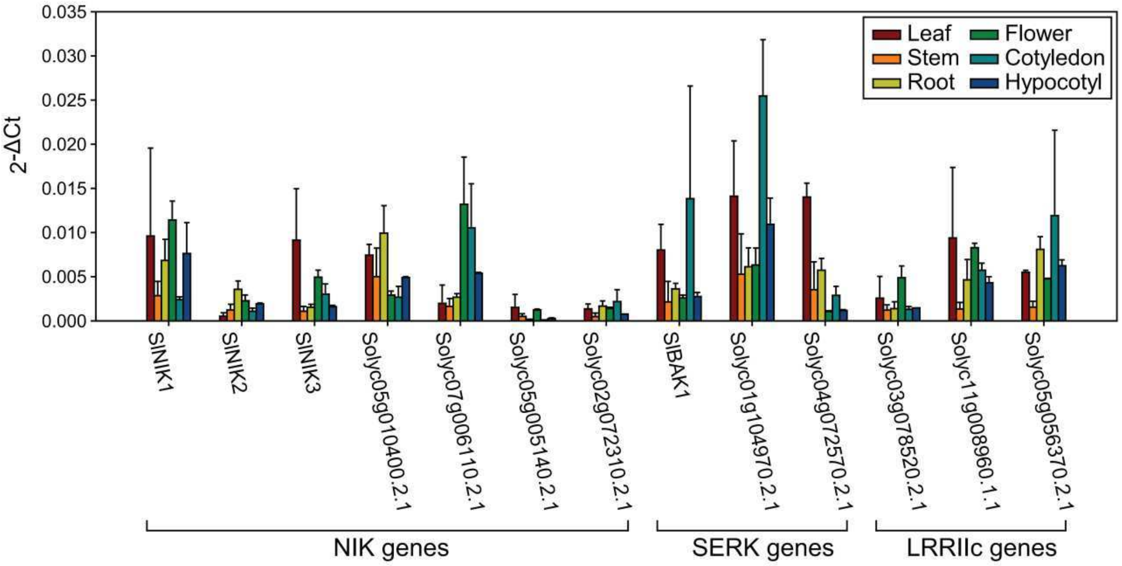


Figure 6 -Expression analysis of tomato members of the LRRII subfamily in various plant organs by qRT-PCR.

Expression of each gene was quantified using *SlAPT1* as an endogenous control. Bars represent the mean expression from three biological samples and two replicates, except for the flower and hypocotyl samples, for which two biological samples and two replicates were used. Error bars represent a confidence interval of 95%.

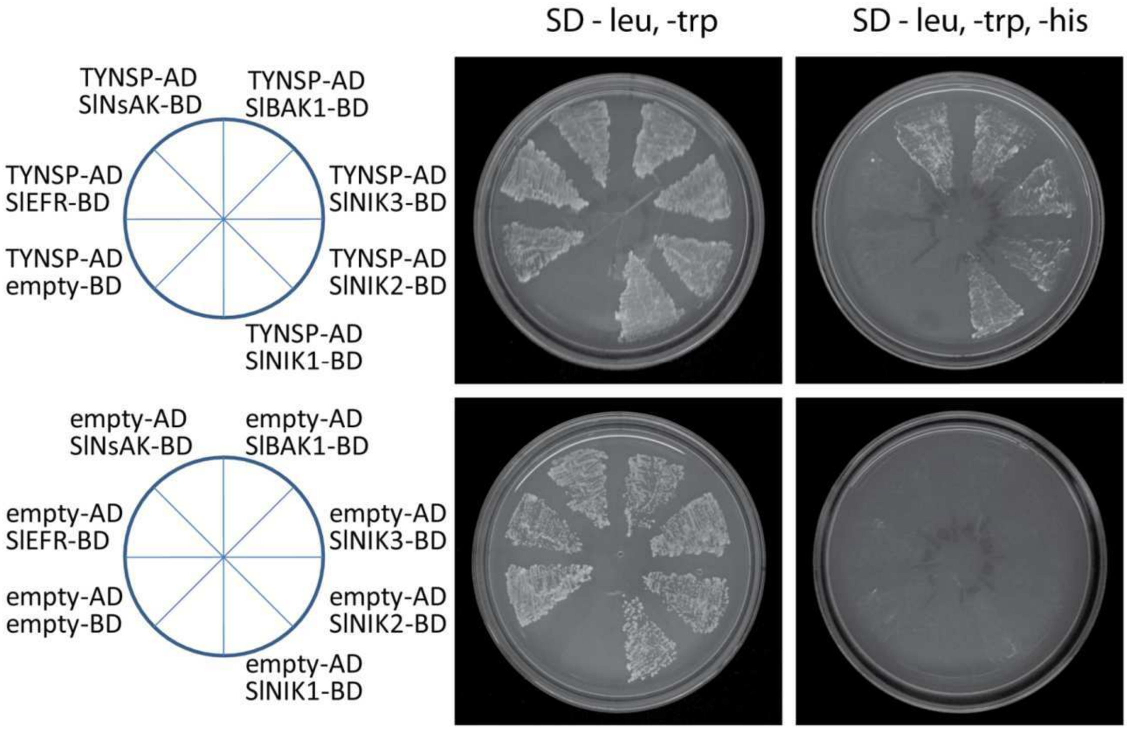


Figure 7 -Tomato members of the LRRII and PERK subfamilies interact with NSP of ToYSV.

Yeast two-hybrid assay using the kinase domain of LRRII and PERK subfamily members of tomato as bait and the NSP of ToYSV as prey (TYNSP-AD). All co-transformed yeast strains were grown on synthetic defined (SD) medium lacking leucine and tryptophan (SD –leu, -trp), indicating the presence of both plasmid constructs in their cells. Yeast growth on SD medium lacking leucine, tryptophan and histidine (SD -leu, -trp, -his) indicates an interaction between the bait and prey constructs. This was observed in the yeast strains co-transformed with TYNSP-AD and SlNIK1-BD, SlNIK2-BD, SlNIK3-BD, SlBAK1-BD and SlNsAK-BD. No interaction between TYNSP-AD and SlEFR-BD was observed. All negative controls using empty vector failed to grow on SD -leu, -trp, -his, indicating the absence of transactivation.

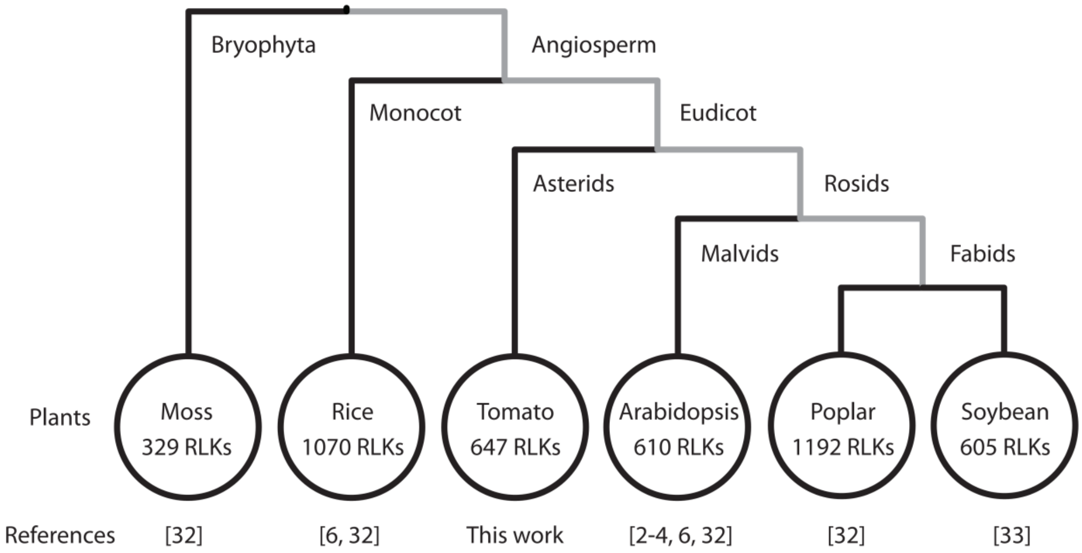


Figure 8 -Cladogram of plants whose RLK superfamily has been characterized.

The RLK superfamily size ranges from 329 (moss) to 1192 (poplar) members. The RLK superfamily expanded after divergence between the Bryophyta and Angiosperm lineages and independently expanded in the plants of the Angiosperm lineage. Dramatic expansions were observed in rice and poplar.

Table

Table 1 -Functional description of representatives of RLK subfamilies with specific expansion or reduction in tomato or Arabidopsis

RLK subfamily	Gene ID	Sp[1]	Synonym	Function	Ref.
LysM	AT3G21630	*At*	CERK1	Defense response	[75]
LysM	BAJ09794	*Os*	CeBIP	Defense response	[76]
LysM	AJ575249	*Lj*	NFR1	Symbiosis	[53, 54]
LysM	AJ575255	*Gm*	NFR5	Symbiosis	[77]
LysM	AY372406	*Mt*	LYK3	Symbiosis	[78, 79]
LysM	ABF50224.1	*Mt*	NFP	Symbiosis	[78, 79]
LysM	ACE81776.1	*Ps*	SYM37	Symbiosis	[80]
LysM	CAE02596.1	*Ps*	SYM10	Symbiosis	[53]
LRRXII	AT5G20480	*At*	EFR	Defense response	[81]
LRRXII	AT5G46330	*At*	FLS2	Defense response	[82]
LRRXII	AAC49123.1	*Os*	Xa21	Defense response	[25]
SD	AT1G65790	*At*	RK1	Development and defense response	[83, 84]
SD	AT1G65800	*At*	RK2	Development	[83]
SD	AT4G21380	*At*	RK3	Development and defense response	[83, 84]
LRRI	AT2G19190	*At*	FRK1	Defense response	[85]
LRRI	AT1G51800	*At*	IOS1	Symbiosis	[86]
LRRI	AT3G46330	*At*	MEE39	Development	[87]
LRRI	AT4G29180	*At*	RHS16	Development	[88]
LRRI	AT1G51880	*At*	RHS6	Development	[88]
DUF26	AT4G23130	*At*	CRK5	Programmed cell death and defense response	[89]
LLEC	AT5G01540	*At*	LECRKA4.1	Development	[90]
LLEC	AT5G01550	*At*	LECRKA4.2	Development	[90]
LLEC	AT5G01560	*At*	LECRKA4.3	Development	[90]
LLEC	AT5G60300	*At*	LecRK-I.9	Defense response	[91]
LRK10L2	AT5G38280	*At*	PR5K	Defense response	[92]

Tomato RLKs were overrepresented in LysM, LRRXII, SD, and WAK/LRK10L1 subfamilies, whereas Arabidopsis RLKs were overrepresented in LRRI, DUF26, L-lectin and RLCK XII/XIII subfamilies. The LRK10L2 subfamilies in tomato and Arabidopsis differ in their patterns of protein domain structure in the extracellular region of members. Note that all RLK subfamilies with specific expansion or reduction in at least one species have members that are associated with defense response. WAK/LRK10L1 and RLCK XII/XIII do not have functionally characterized members yet.

[1] Plant species, *At*: *Arabidopsis thaliana*, *Os*: *Oryza sativum*, *Lj*: *Lotus japonicum*, *Mt*: *Medicago truncatula*, *Ps*: *Pisum sativum*.

Additional files

Additional file 1–List of outgroup proteins

Summary of the names and accession numbers of proteins used as the outgroup in the phylogenetic tree of figure 1 and additional file 1.

Additional file 2 – RLK Phylogenetic tree of tomato and Arabidopsis

This is the same phylogenetic tree as presented in figure 1, but displayed in more detail. It contains additionally the accession numbers and protein schemes evidencing the domain structures of each protein that compose the tree. The local support values beside the nodes were computed by resampling the site likelihoods 1,000 times and performing the Shimodaira Hasegawa test.

Additional file 3 – List of Arabidopsis and tomato RLKs

Summary of all RLK IDs presented in the tree of additional file 1.

Additional file 4 – Sequence identity between members of LRRII-RLK subfamily of tomato and Arabidopsis

Percentage of sequence identity between members of LRRII-RLK subfamily of tomato and Arabidopsis is described. Pairwise comparison was performed using the full-length aminoacid sequences, extracellular and intracellular regions of each LRRII-RLKs.

Additional file 5–List of primers

Summary of all primers used for gene cloning and real-time PCR experiments.

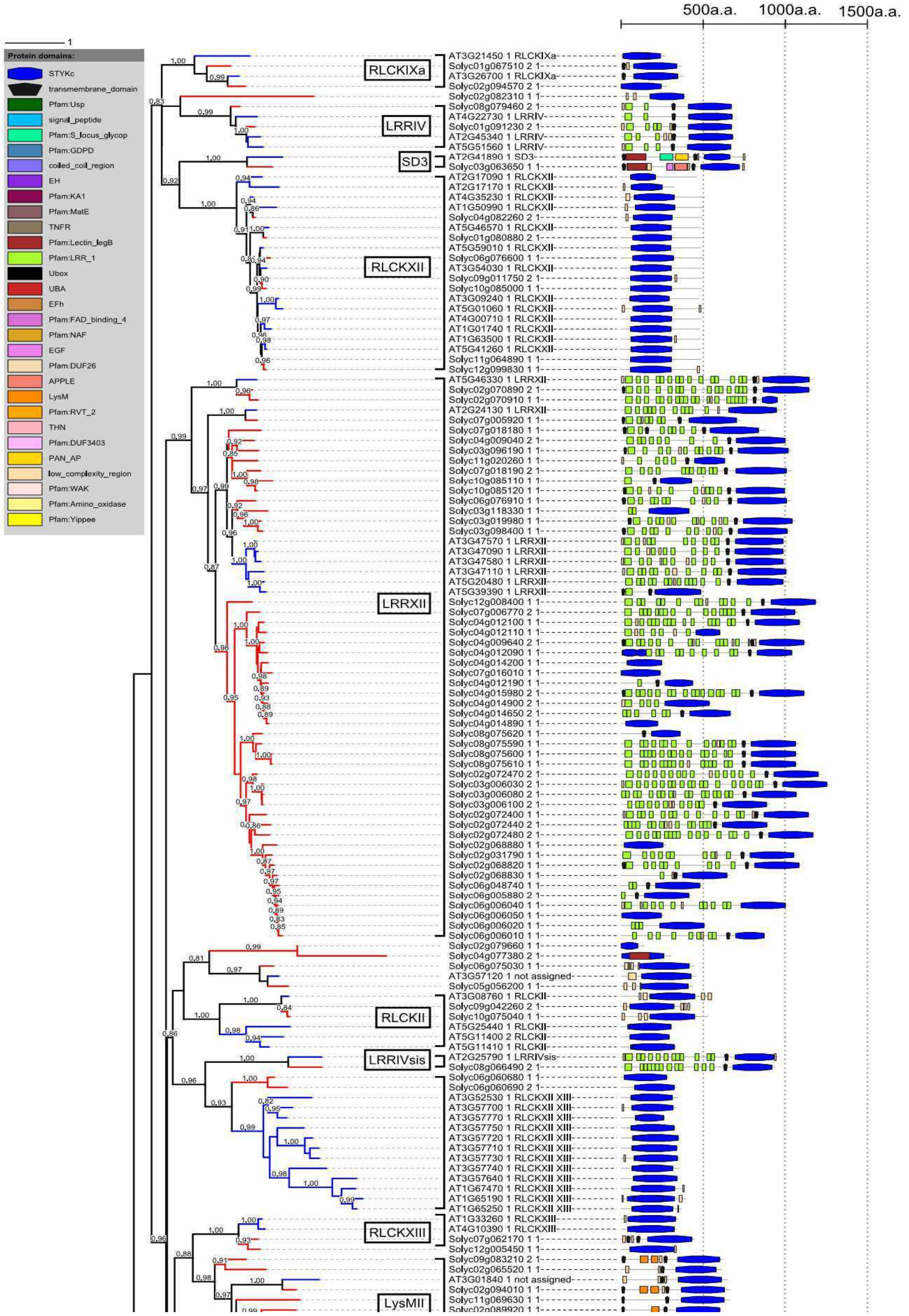
Additional file 1. List of outgroup proteins

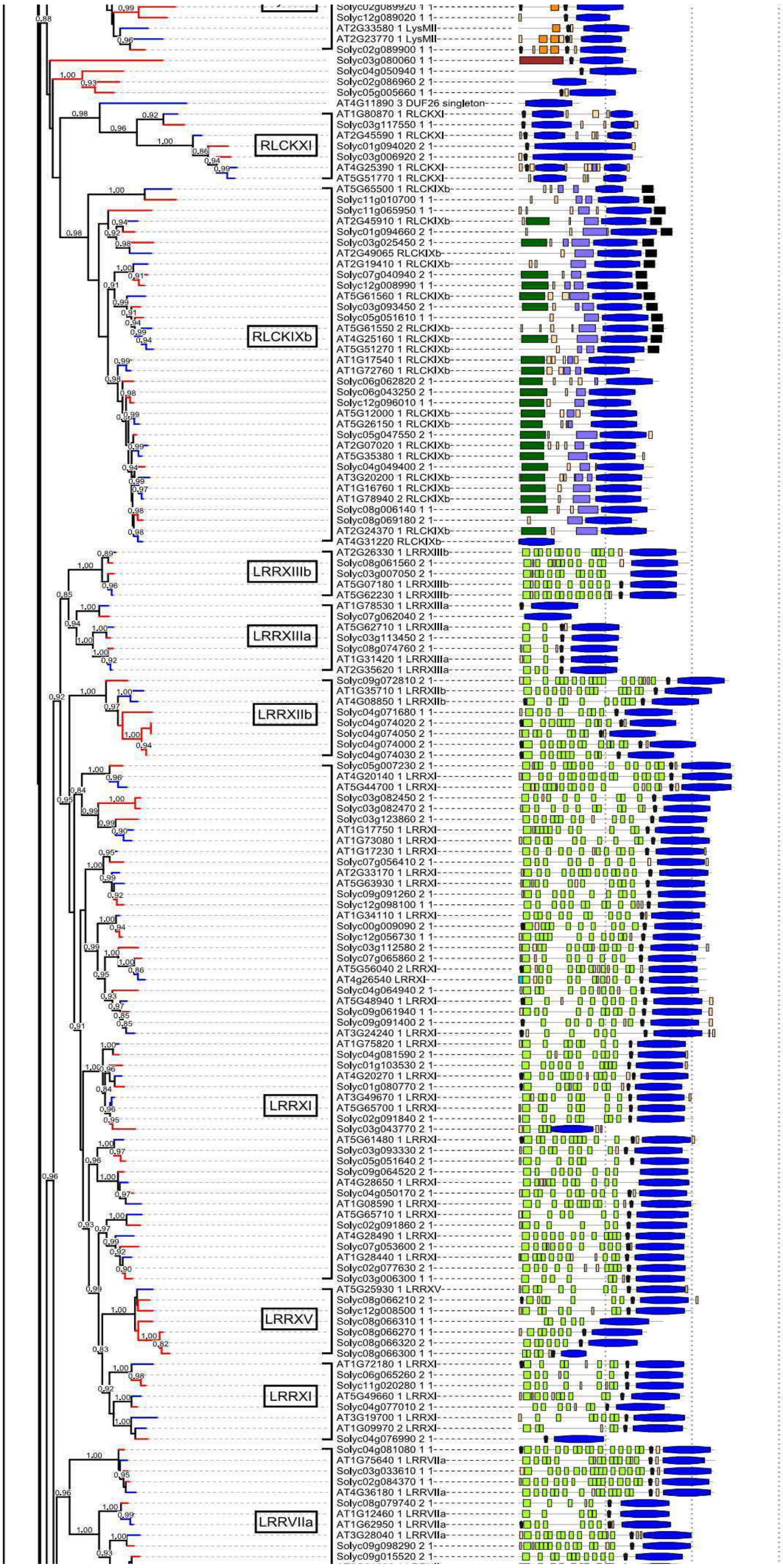
Name and accession number of outgroup proteins used for reconstruction of phylogenetic tree of figure 1 and additional file 2.

Arabidopsis sequences		**Human sequences**	
Gene name	**Accession #**	**Gene name**	**Accession #**
CDC2a	AAB23643	CaMK1	NP003647
CPK7	AAB03247	CDK3	NP001249
CKI1	CAA55395	CK1a1	NP001883
CKA1	BAA01090	CK2a	CAB65624
AME2	BAA08215	GRK6	P43250
MKK3	BAA28829	RK	Q15835
MEKK1	BAA09057	Hunk	NP055401
NAK	AAA18853	CLK1	P49759
NPH1	AAC01753	MAPK10	P53779
PVPK-like PK5	BAA01715	MAPKK1	Q02750
CTR1	AAA32779	MAPKKK1	Q13233
MRK1	BAA22079	cAPK	P17612
S6K-like PK1	AAA21142	Raf1	P04049
GSK3β	CAA64408	c-SRC	P12931
GSK3ι	CAA68027	TLK1	NP036422
SnRK2-like PROKINa	AAA32845	TTK	A42861
Tousled	AAA32874		

Additional file 2. RLK phylogenetic tree of tomato and Arabidopsis

Same phylogenetic tree presented in figure 1 displayed in more details. The kinase domain of tomato and Arabidopsis RLKs were aligned using CLUSTALW and tree were generated using FastTree. Tomato proteins are represented by red branches and Arabidopsis proteins by blue branches. Protein domain schemes were generated using iTols tools. The local support values beside the nodes were computed by resampling the site likelihoods 1000 times and performing Shimodaira-Hasegawa test.




RLCKXI
RLCKIXb
LRRXIIIb
LRRXIIIa
LRRXIIb
LRRXI
LRRXV
LRRXI
LRRVIIa
Solyc02g089920 1 1
Solyc12g089020 1 1
AT2G33580 1 LysMII
AT2G23770 1 LysMII
Solyc02g089900 1 1
Solyc03g080060 1 1
Solyc04g050940 1 1
Solyc02g086960 2 1
Solyc05g005660 1 1
AT4G11890 3 DUF26 singleton
AT1G80870 1 RLCKXI
Solyc03g117550 1 1
AT2G45590 1 RLCKXI
Solyc01g094020 2 1
Solyc03g006920 2 1
AT4G25390 1 RLCKXI
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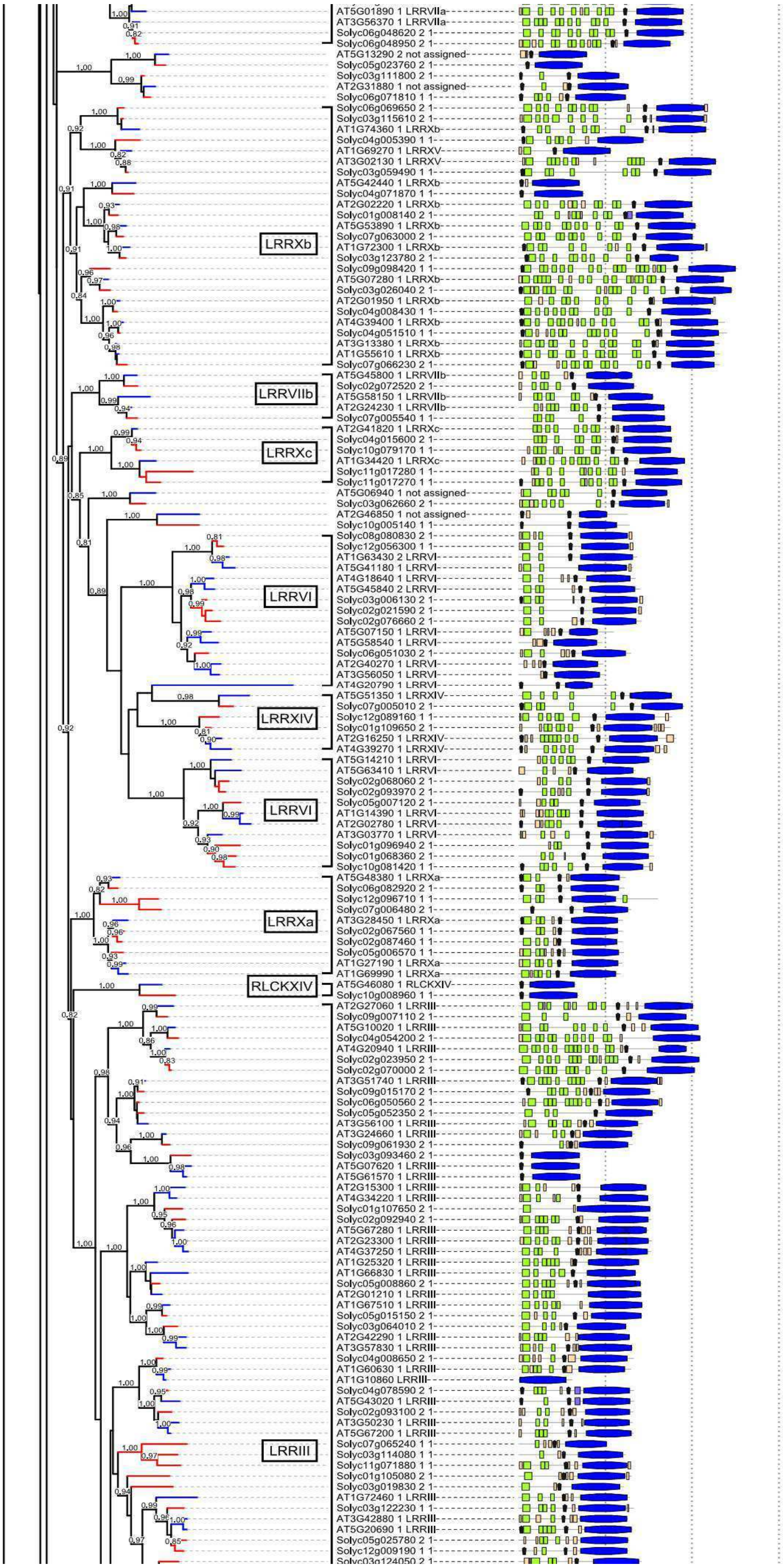
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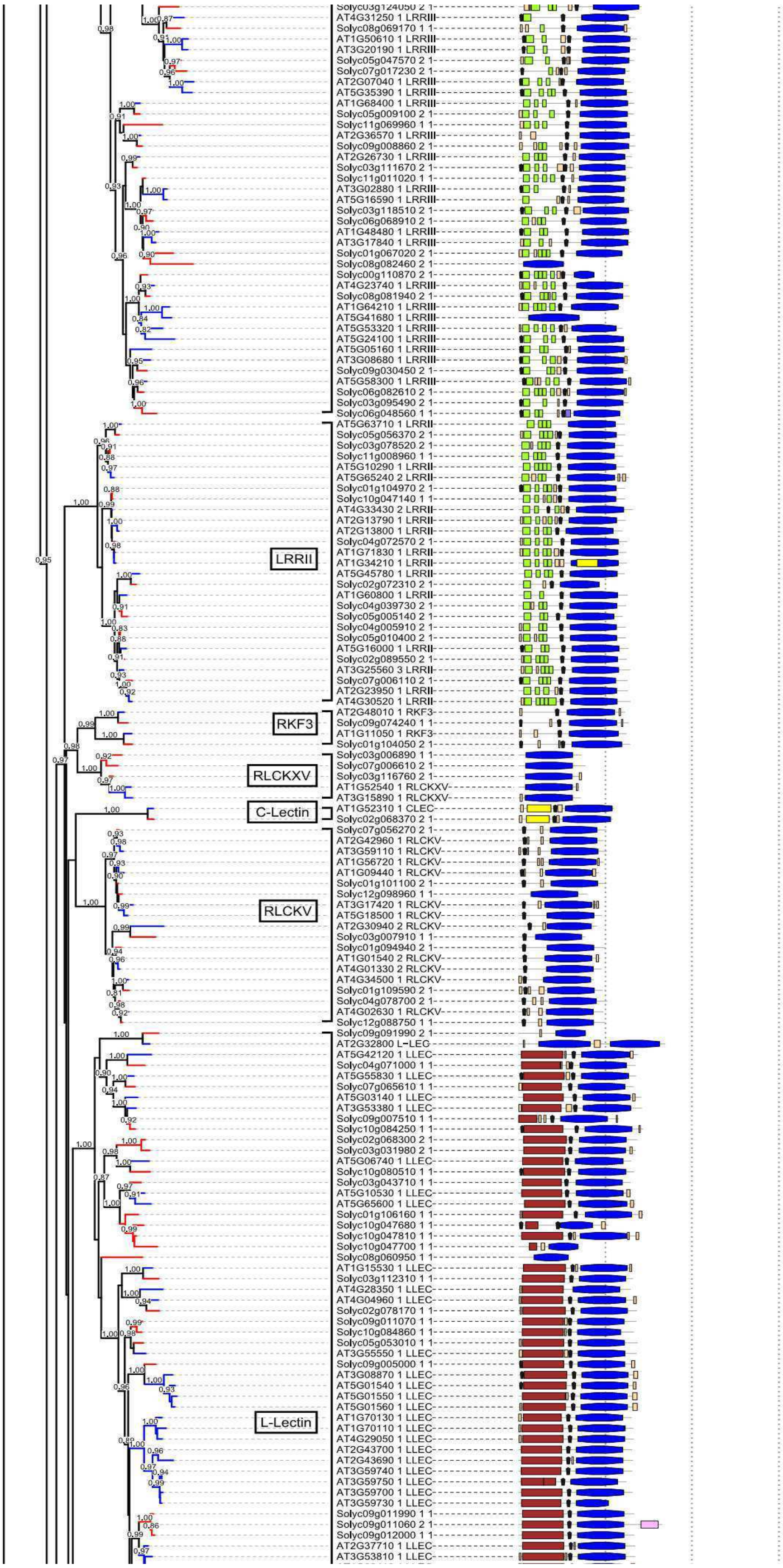
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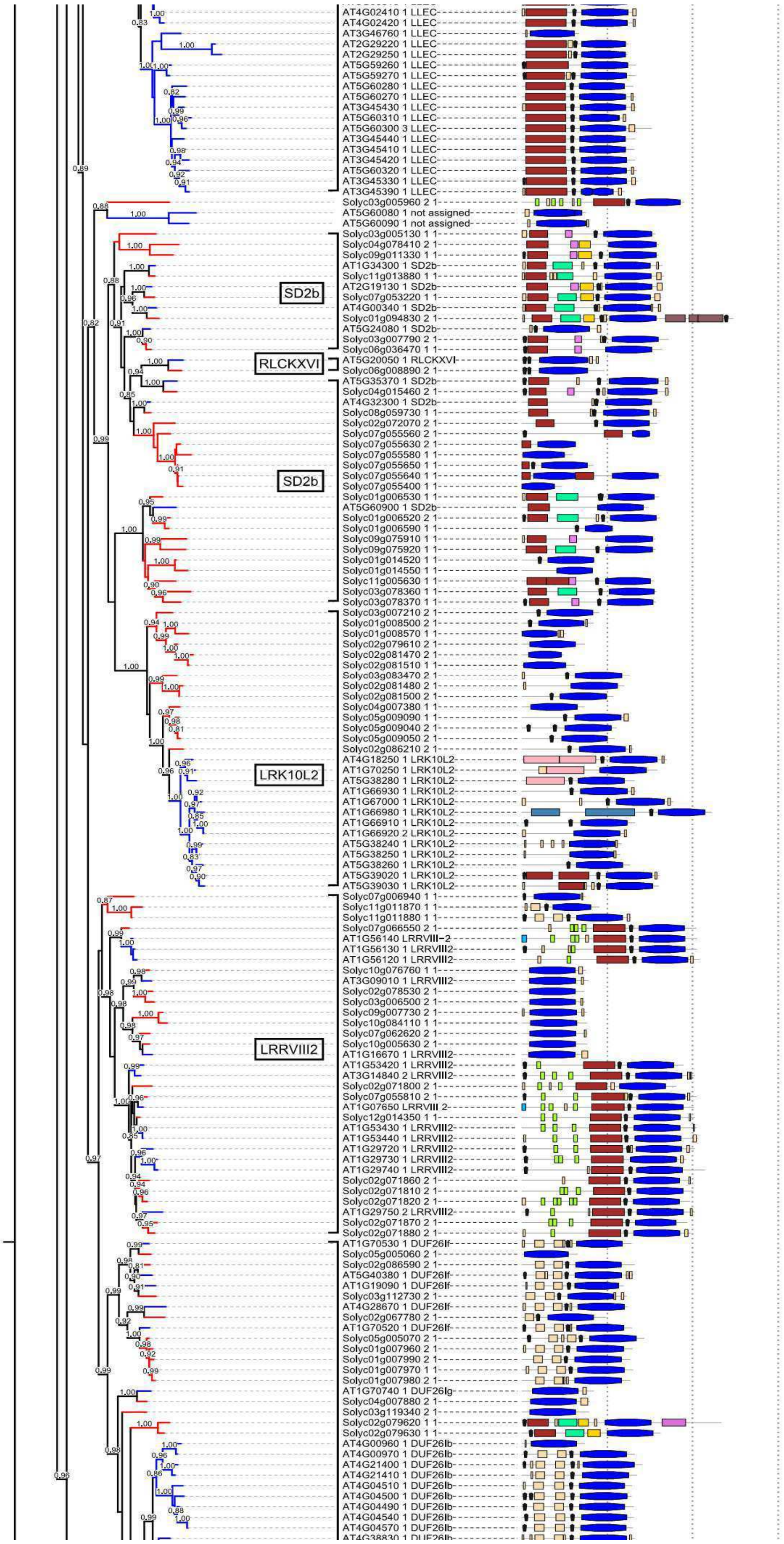
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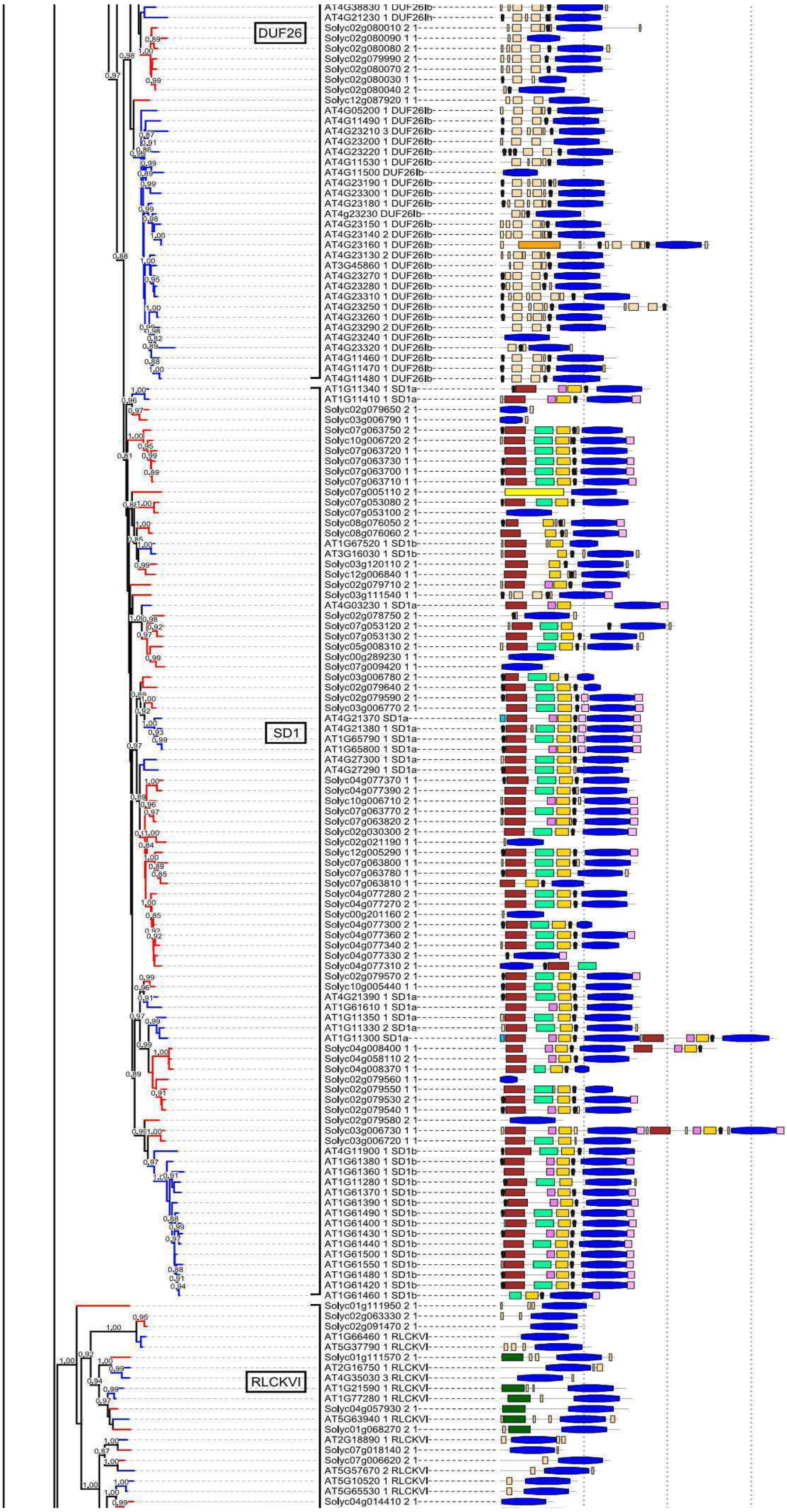
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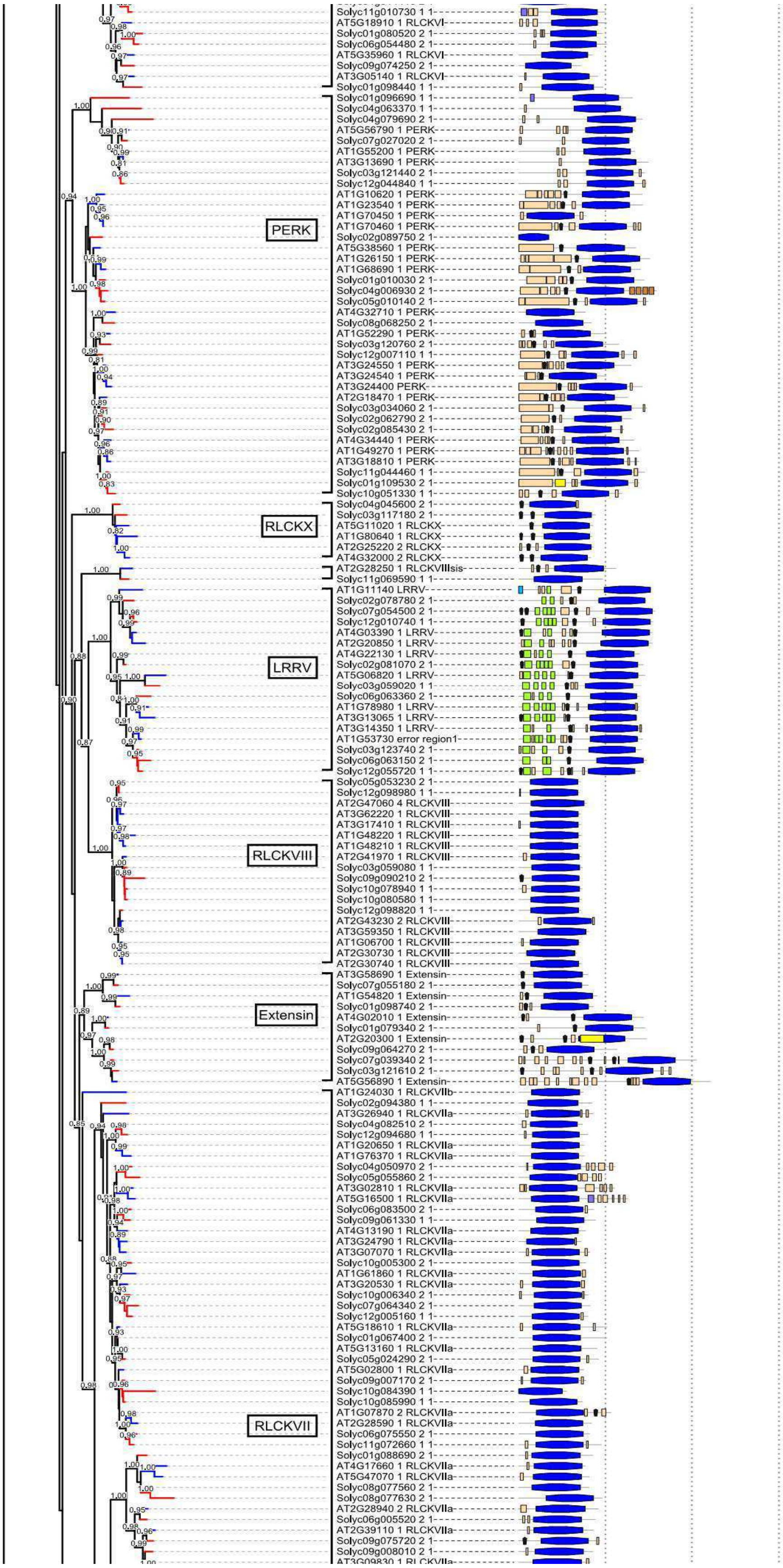
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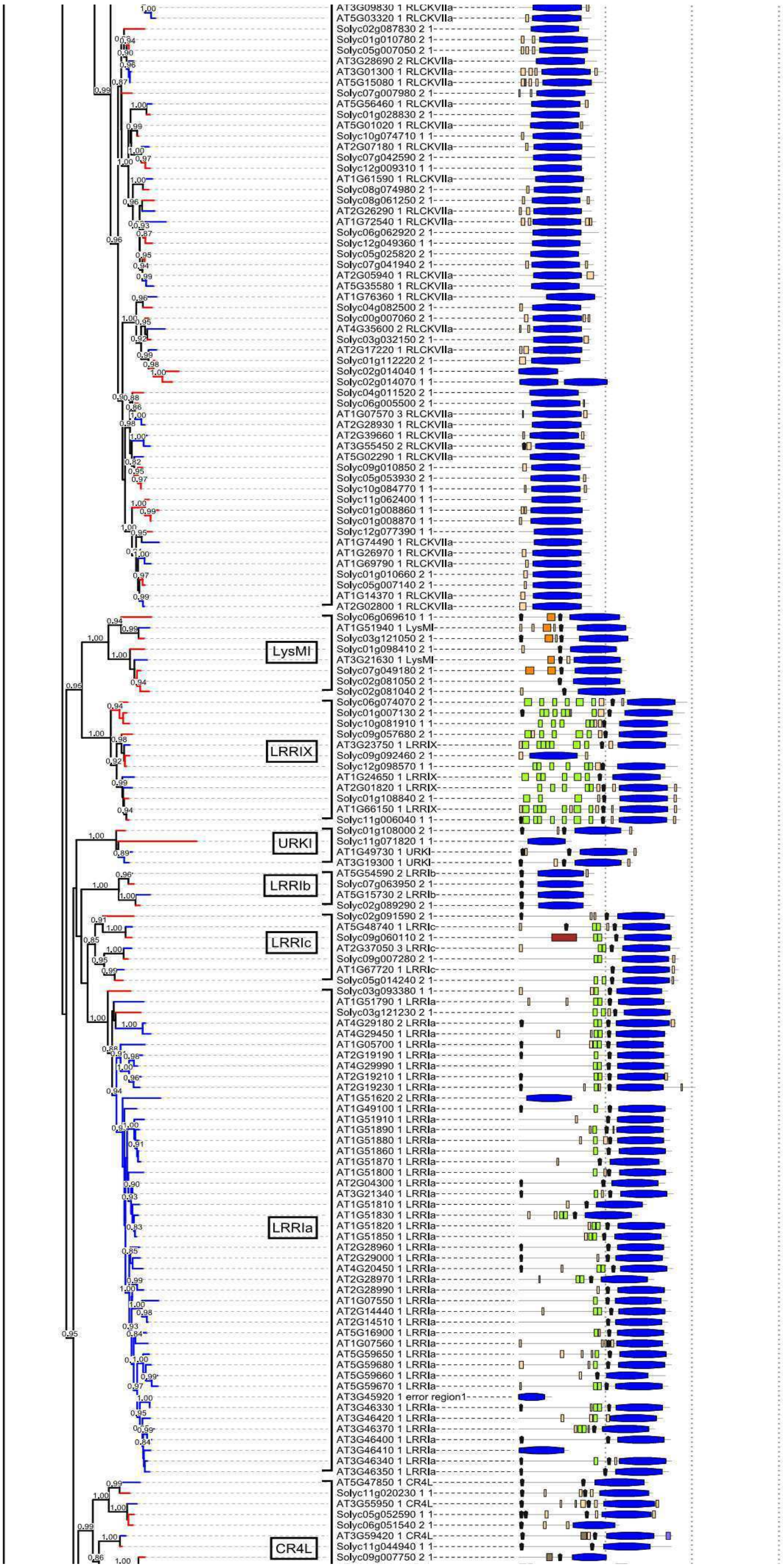
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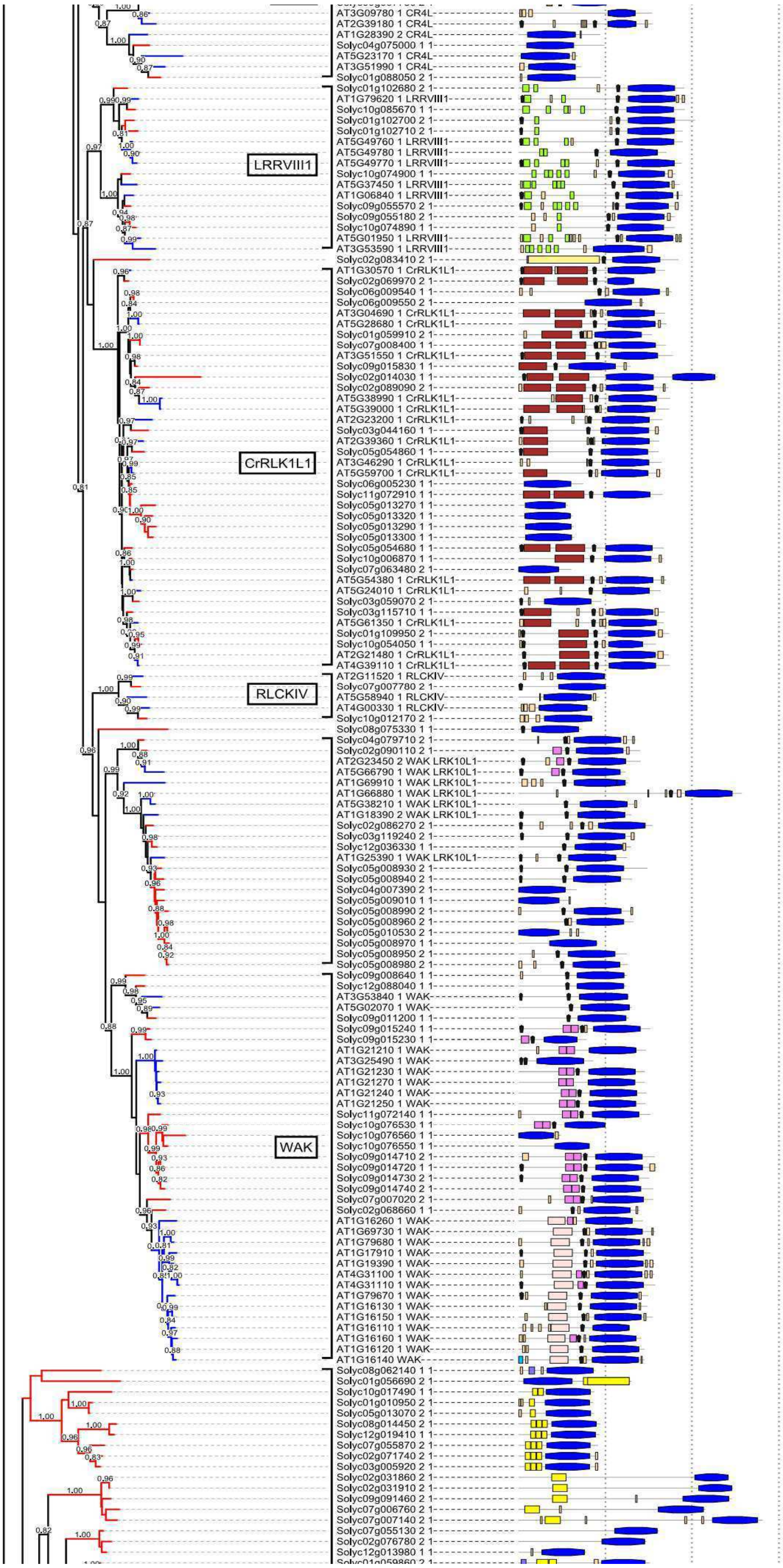
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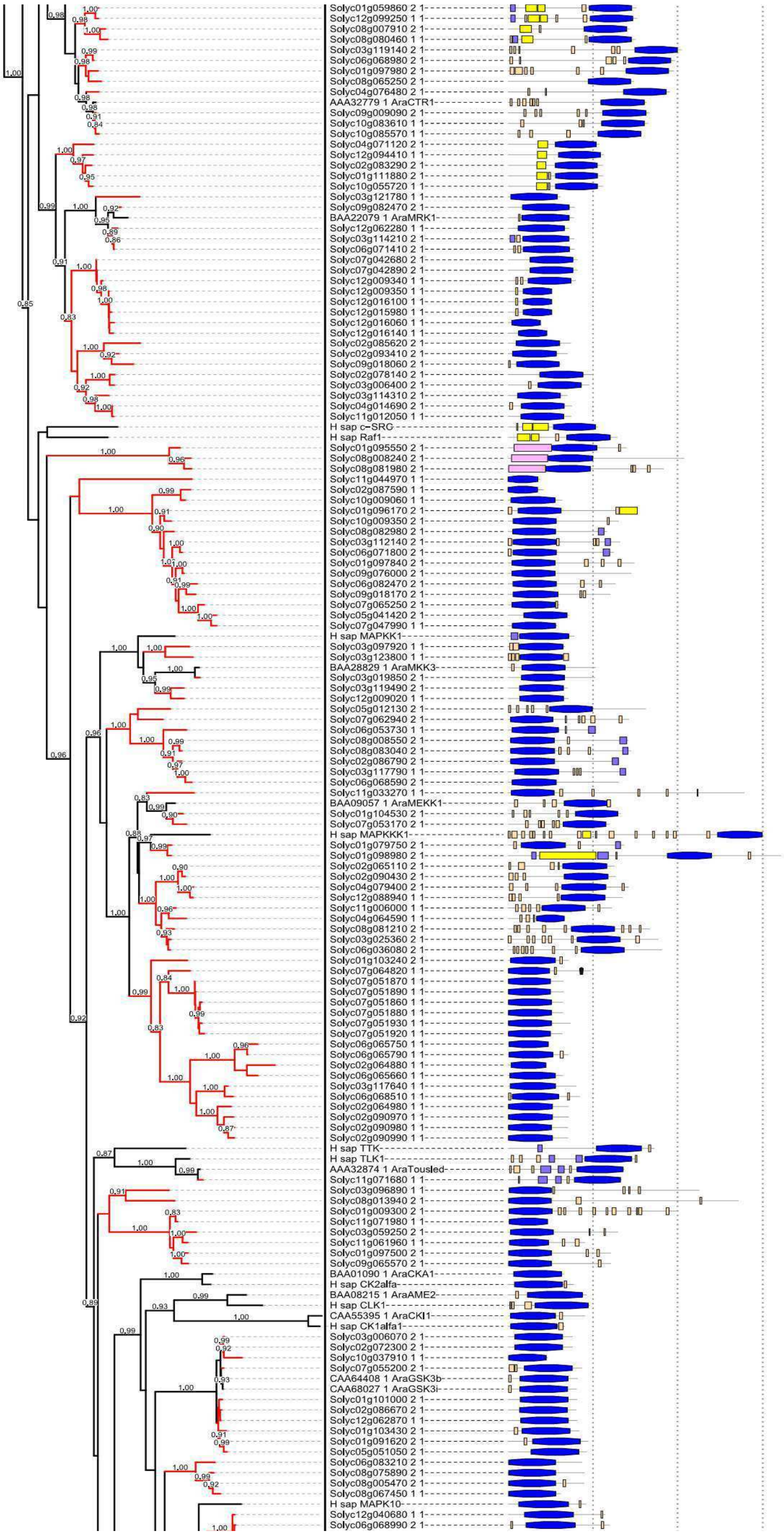
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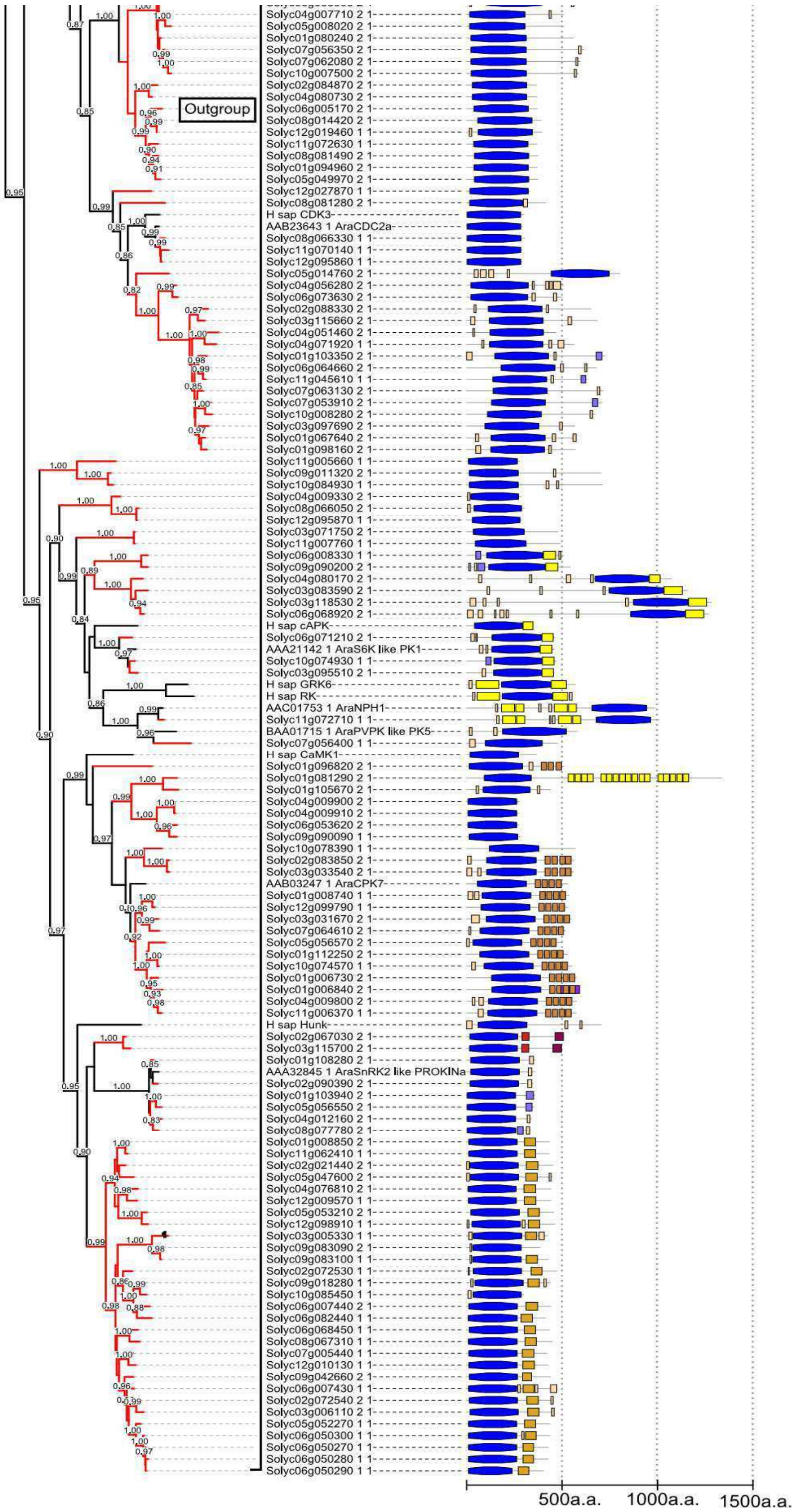
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Solyc12g095860 1 1
Solyc05g014760 2 1
Solyc04g056280 2 1
Solyc06g073630 2 1
Solyc02g088330 2 1
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Solyc04g009330 2 1
Solyc08g066050 2 1
Solyc12g095870 1 1
Solyc03g071750 2 1
Solyc11g007760 1 1
Solyc06g008330 1 1
Solyc09g090200 2 1
Solyc04g080170 2 1
Solyc03g083590 2 1
Solyc03g118530 2 1
Solyc06g068920 2 1
H sap cAPK
Solyc06g071210 2 1
AAA21142 1 AraS6K like PK1
Solyc10g074930 1 1
Solyc03g095510 2 1
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H sap RK
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Solyc11g072710 1 1
BAA01715 1 AraPVPK like PK5
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Solyc05g056550 2 1
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Solyc06g007430 1 1
Solyc02g072540 2 1
Solyc03g006110 2 1
Solyc05g052270 1 1
Solyc06g050300 1 1
Solyc06g050270 1 1
Solyc06g050280 1 1
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500a.a.
1000a.a.
1500a.a.

Additional file 3. List of tomato and Arabidopsis RLKs

Accession #	*RLK subfamily*	*Accession #*	*RLK subfamily*
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AT2G39180.1	CR4L	Solyc02g070890 2 1	LRRXII
AT3G09780.1	CR4L	Solyc02g070910 1 1	LRRXII
AT3G51990.1	CR4L	Solyc02g072400 1 1	LRRXII
AT3G55950.1	CR4L	Solyc02g072440 2 1	LRRXII
AT3G59420.1	CR4L	Solyc02g072470 2 1	LRRXII
AT5G23170.1	CR4L	Solyc02g072480 2 1	LRRXII
AT5G47850.1	CR4L	Solyc03g006030 2 1	LRRXII
Solyc01g088050 2 1	CR4L	Solyc03g006080 2 1	LRRXII
Solyc04g075000 1 1	CR4L	Solyc03g006100 2 1	LRRXII
Solyc05g052590 1 1	CR4L	Solyc03g019980 1 1	LRRXII
Solyc06g051540 2 1	CR4L	Solyc03g096190 1 1	LRRXII
Solyc09g007750 2 1	CR4L	Solyc03g098400 1 1	LRRXII
Solyc11g020230 1 1	CR4L	Solyc03g118330 1 1	LRRXII
Solyc11g044940 1 1	CR4L	Solyc04g009040 2 1	LRRXII
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AT3G04690.1	CrRLKL1	Solyc04g012190 1 1	LRRXII
AT3G46290.1	CrRLKL1	Solyc04g014200 1 1	LRRXII
AT3G51550.1	CrRLKL1	Solyc04g014650 2 1	LRRXII
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AT5G28680.1	CrRLKL1	Solyc04g015980 2 1	LRRXII
AT5G38990.1	CrRLKL1	Solyc06g005880 2 1	LRRXII
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AT1G70530.1	DUF26	AT2G35620.1	LRRXIIIa
AT1G70740.1	DUF26	AT5G62710.1	LRRXIIIa
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AT4G00960.1	DUF26	Solyc07g062040 2 1	LRRXIIIa
AT4G00970.1	DUF26	Solyc08g074760 2 1	LRRXIIIa
AT4G04490.1	DUF26	AT2G26330.1	LRRXIIIb
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AT4G04570.1	DUF26	Solyc08g061560 2 1	LRRXIIIb
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AT4G11480.1	DUF26	Solyc01g109650 2 1	LRRXIV
AT4G11490.1	DUF26	Solyc07g005010 2 1	LRRXIV
AT4G11500	DUF26	Solyc12g089160 1 1	LRRXIV
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AT4G21400.1	DUF26	AT5G25930.1	LRRXV
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AT4G23180.1	DUF26	Solyc08g066310 1 1	LRRXV
AT4G23190.1	DUF26	Solyc08g066320 2 1	LRRXV
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AT4g23230	DUF26	Solyc01g098410 2 1	LysMI
AT4G23240.1	DUF26	Solyc02g081040 2 1	LysMI
AT4G23250.1	DUF26	Solyc02g081050 2 1	LysMI
AT4G23260.1	DUF26	Solyc03g121050 2 1	LysMI
AT4G23270.1	DUF26	Solyc06g069610 1 1	LysMI
AT4G23280.1	DUF26	Solyc07g049180 2 1	LysMI
AT4G23290.2	DUF26	AT2G23770.1	LysMII
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Solyc09g064270 2 1	Extensin	AT1G49270.1	PERK
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AT1G70130.1	L-LEC	AT1G68690.1	PERK
AT2G29220.1	L-LEC	AT1G70450.1	PERK
AT2G29250.1	L-LEC	AT1G70460.1	PERK
AT2G32800	L-LEC	AT2G18470.1	PERK
AT2G37710.1	L-LEC	AT3G13690.1	PERK
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AT3G08870.1	L-LEC	AT3G24540.1	PERK
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AT3G45390.1	L-LEC	AT4G32710.1	PERK
AT3G45410.1	L-LEC	AT4G34440.1	PERK
AT3G45420.1	L-LEC	AT5G38560.1	PERK
AT3G45430.1	L-LEC	AT5G56790.1	PERK
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AT3G46760.1	L-LEC	Solyc01g096690 1 1	PERK

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AT5G06740.1	L-LEC	Solyc12g044840 1 1	PERK
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AT5G42120.1	L-LEC	AT2G48010.1	RKF3
AT5G55830.1	L-LEC	Solyc01g104050 2 1	RKF3
AT5G59260.1	L-LEC	Solyc09g074240 1 1	RKF3
AT5G59270.1	L-LEC	AT3G08760.1	RLCKII
AT5G60270.1	L-LEC	AT5G11400.2	RLCKII
AT5G60280.1	L-LEC	AT5G11410.1	RLCKII
AT5G60300.3	L-LEC	AT5G25440.1	RLCKII
AT5G60310.1	L-LEC	Solyc09g042260 2 1	RLCKII
AT5G60320.1	L-LEC	Solyc10g075040 1 1	RLCKII
AT5G65600.1	L-LEC	AT2G11520.1	RLCKIV
Solyc01g106160 1 1	L-LEC	AT4G00330.1	RLCKIV
Solyc02g068300 2 1	L-LEC	AT5G58940.1	RLCKIV
Solyc02g078170 1 1	L-LEC	Solyc07g007780 2 1	RLCKIV
Solyc03g031980 2 1	L-LEC	Solyc10g012170 2 1	RLCKIV
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Solyc05g053010 1 1	L-LEC	Solyc02g094570 2 1	RLCKIXa
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Solyc08g060950 1 1	L-LEC	AT1G17540.1	RLCKIXb
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AT5G39030.1	LRK10L2	Solyc07g040940 2 1	RLCKIXb
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AT1G07550.1	LRRIa	AT4G34500.1	RLCKV
AT1G07560.1	LRRIa	AT5G18500.1	RLCKV
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AT1G51870.1	LRRIa	AT1G66460.1	RLCKVI
AT1G51880.1	LRRIa	AT1G77280.1	RLCKVI
AT1G51890.1	LRRIa	AT2G16750.1	RLCKVI
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Solyc10g084110 1 1	LRRVIII-2	AT1G61480.1	SD1b
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Solyc11g011880 1 1	LRRVIII-2	AT1G61500.1	SD1b
Solyc12g014350 1 1	LRRVIII-2	AT1G61550.1	SD1b
AT1G27190.1	LRRXa	AT4G11900.1	SD1b
AT1G69990.1	LRRXa	Solyc02g079580 2 1	SD1b
AT3G28450.1	LRRXa	Solyc03g006720 1 1	SD1b
AT5G48380.1	LRRXa	Solyc03g006730 1 1	SD1b
Solyc02g067560 1 1	LRRXa	AT1G34300.1	SD2b
Solyc02g087460 1 1	LRRXa	AT2G19130.1	SD2b
Solyc05g006570 1 1	LRRXa	AT4G00340.1	SD2b
Solyc06g082920 2 1	LRRXa	AT4G32300.1	SD2b
Solyc07g006480 2 1	LRRXa	AT5G24080.1	SD2b
Solyc12g096710 1 1	LRRXa	AT5G35370.1	SD2b
AT1G55610.1	LRRXb	AT5G60900.1	SD2b
AT1G72300.1	LRRXb	Solyc01g006520 2 1	SD2b
AT1G74360.1	LRRXb	Solyc01g006530 1 1	SD2b
AT2G01950.1	LRRXb	Solyc01g006590 1 1	SD2b
AT2G02220.1	LRRXb	Solyc01g014520 1 1	SD2b

AT3G13380.1	LRRXb	Solyc01g014550 1 1	SD2b
AT4G39400.1	LRRXb	Solyc01g094830 2 1	SD2b
AT5G07280.1	LRRXb	Solyc02g072070 2 1	SD2b
AT5G42440.1	LRRXb	Solyc03g005130 1 1	SD2b
AT5G53890.1	LRRXb	Solyc03g007790 2 1	SD2b
Solyc01g008140 2 1	LRRXb	Solyc03g078360 1 1	SD2b
Solyc03g026040 2 1	LRRXb	Solyc03g078370 1 1	SD2b
Solyc03g115610 2 1	LRRXb	Solyc04g015460 2 1	SD2b
Solyc03g123780 2 1	LRRXb	Solyc04g078410 2 1	SD2b
Solyc04g008430 1 1	LRRXb	Solyc06g036470 1 1	SD2b
Solyc04g051510 1 1	LRRXb	Solyc07g053220 1 1	SD2b
Solyc04g071870 1 1	LRRXb	Solyc07g055400 1 1	SD2b
Solyc06g069650 2 1	LRRXb	Solyc07g055560 2 1	SD2b
Solyc07g063000 2 1	LRRXb	Solyc07g055580 1 1	SD2b
Solyc07g066230 2 1	LRRXb	Solyc07g055630 2 1	SD2b
Solyc09g098420 1 1	LRRXb	Solyc07g055640 1 1	SD2b
AT1G34420.1	LRRXc	Solyc07g055650 1 1	SD2b
AT2G41820.1	LRRXc	Solyc08g059730 1 1	SD2b
Solyc04g015600 2 1	LRRXc	Solyc09g011330 1 1	SD2b
Solyc10g079170 1 1	LRRXc	Solyc09g075910 1 1	SD2b
Solyc11g017270 1 1	LRRXc	Solyc09g075920 1 1	SD2b
Solyc11g017280 1 1	LRRXc	Solyc11g005630 1 1	SD2b
AT1G08590.1	LRRXI	Solyc11g013880 1 1	SD2b
AT1G09970.2	LRRXI	AT2G41890.1	SD3
AT1G17230.1	LRRXI	Solyc03g063650 1 1	SD3
AT1G17750.1	LRRXI	AT1G49730.1	URKI
AT1G28440.1	LRRXI	AT3G19300.1	URKI
AT1G34110.1	LRRXI	Solyc01g108000 2 1	URKI
AT1G72180.1	LRRXI	Solyc11g071820 1 1	URKI
AT1G73080.1	LRRXI	AT1G16110.1	WAK
AT1G75820.1	LRRXI	AT1G16120.1	WAK
AT2G33170.1	LRRXI	AT1G16130.1	WAK
AT3G19700.1	LRRXI	AT1G16140	WAK
AT3G24240.1	LRRXI	AT1G16150.1	WAK
AT3G49670.1	LRRXI	AT1G16160.1	WAK
AT4G20140.1	LRRXI	AT1G16260.1	WAK
AT4G20270.1	LRRXI	AT1G17910.1	WAK
AT4g26540	LRRXI	AT1G19390.1	WAK
AT4G28490.1	LRRXI	AT1G21210.1	WAK
AT4G28650.1	LRRXI	AT1G21230.1	WAK
AT5G44700.1	LRRXI	AT1G21240.1	WAK
AT5G48940.1	LRRXI	AT1G21250.1	WAK
AT5G49660.1	LRRXI	AT1G21270.1	WAK
AT5G56040.2	LRRXI	AT1G69730.1	WAK
AT5G61480.1	LRRXI	AT1G79670.1	WAK
AT5G63930.1	LRRXI	AT1G79680.1	WAK
AT5G65700.1	LRRXI	AT3G25490.1	WAK
AT5G65710.1	LRRXI	AT3G53840.1	WAK
Solyc00g009090 2 1	LRRXI	AT4G31100.1	WAK
Solyc01g080770 2 1	LRRXI	AT4G31110.1	WAK

Solyc01g103530 2 1	LRRXI	AT5G02070.1	WAK
Solyc02g077630 2 1	LRRXI	Solyc02g068660 1 1	WAK
Solyc02g091840 2 1	LRRXI	Solyc07g007020 2 1	WAK
Solyc02g091860 2 1	LRRXI	Solyc09g008640 1 1	WAK
Solyc03g006300 1 1	LRRXI	Solyc09g011200 1 1	WAK
Solyc03g043770 2 1	LRRXI	Solyc09g014710 2 1	WAK
Solyc03g082450 2 1	LRRXI	Solyc09g014720 1 1	WAK
Solyc03g082470 2 1	LRRXI	Solyc09g014730 2 1	WAK
Solyc03g093330 2 1	LRRXI	Solyc09g014740 2 1	WAK
Solyc03g112580 2 1	LRRXI	Solyc09g015230 1 1	WAK
Solyc03g123860 2 1	LRRXI	Solyc09g015240 1 1	WAK
Solyc04g050170 2 1	LRRXI	Solyc10g076530 1 1	WAK
Solyc04g064940 2 1	LRRXI	Solyc10g076550 1 1	WAK
Solyc04g076990 2 1	LRRXI	Solyc10g076560 1 1	WAK
Solyc04g077010 2 1	LRRXI	Solyc11g072140 1 1	WAK
Solyc04g081590 2 1	LRRXI	Solyc12g088040 1 1	WAK
Solyc05g007230 2 1	LRRXI	AT1G18390.2	WAK LRK10L1
Solyc05g051640 2 1	LRRXI	AT1G25390.1	WAK LRK10L1
Solyc06g065260 2 1	LRRXI	AT1G66880.1	WAK LRK10L1
Solyc07g053600 2 1	LRRXI	AT1G69910.1	WAK LRK10L1
Solyc07g056410 2 1	LRRXI	AT2G23450.2	WAK LRK10L1
Solyc07g065860 2 1	LRRXI	AT5G38210.1	WAK LRK10L1
Solyc09g061940 1 1	LRRXI	AT5G66790.1	WAK LRK10L1
Solyc09g064520 2 1	LRRXI	Solyc02g086270 2 1	WAK LRK10L1
Solyc09g091260 2 1	LRRXI	Solyc02g090110 2 1	WAK LRK10L1
Solyc09g091400 2 1	LRRXI	Solyc03g119240 2 1	WAK LRK10L1
Solyc11g020280 1 1	LRRXI	Solyc04g007390 2 1	WAK LRK10L1
Solyc12g056730 1 1	LRRXI	Solyc04g079710 2 1	WAK LRK10L1
Solyc12g098100 1 1	LRRXI	Solyc05g008930 2 1	WAK LRK10L1
AT2G24130.1	LRRXII	Solyc05g008940 2 1	WAK LRK10L1
AT3G47090.1	LRRXII	Solyc05g008950 2 1	WAK LRK10L1
AT3G47110.1	LRRXII	Solyc05g008960 2 1	WAK LRK10L1
AT3G47570.1	LRRXII	Solyc05g008970 1 1	WAK LRK10L1
AT3G47580.1	LRRXII	Solyc05g008980 2 1	WAK LRK10L1
AT5G20480.1	LRRXII	Solyc05g008990 2 1	WAK LRK10L1
AT5G39390.1	LRRXII	Solyc05g009010 1 1	WAK LRK10L1
AT5G46330.1	LRRXII	Solyc05g010530 2 1	WAK LRK10L1
Solyc02g031790 1 1	LRRXII	Solyc12g036330 1 1	WAK LRK10L1

Additional file 4. Sequence identity between members of LRRII-RLK subfamily of tomato and Arabidopsis

Full-length sequences (1), intracellular (2), and extracellular (3) regions of LRRII subfamily members were aligned using CLUSTALW. Number in the table corresponds to the sequence identity between two members. Thick lines delimit the sequence comparison between members of the same clade (NIK, SERK and LRRIIc). Blue cells indicate high sequence identity, whereas red cells indicate low sequence identity.

(1) Alignement of full-length sequences

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
AT1G34210_1_SERK2	1																										
AT1G71830_1_SERK1	2	89																									
Solyc04g072570_2_1	3	88	88																								
AT2G13790_1_SERK4	4	74	73	74																							
AT2G13800_1_SERK5	5	69	67	70	85																						
Solyc01g104970_2_1	6	81	80	81	77	72																					
Solyc10g047140_1_1	7	80	79	81	78	73	89																				
AT4G33430_1_BAK1	8	77	77	77	81	78	83	84																			
AT5G16000_1_NIK1	9	53	52	52	49	48	53	51	50																		
Solyc02g089550_2_1	10	52	53	52	47	50	51	50	51	75																	
Solyc04g005910_2_1	11	52	52	52	48	47	51	51	50	70	72																
Solyc05g010400_2_1	12	54	54	53	47	47	51	51	51	72	72	83															
AT3G25560_2_NIK2	13	50	51	51	46	46	49	50	49	69	70	73	72														
AT2G23950_1	14	45	47	46	44	44	45	46	46	61	60	58	59	59													
AT4G30520_1	15	47	47	48	45	46	46	47	47	60	61	58	59	58	82												
Solyc07g006110_2_1	16	49	49	49	46	45	48	49	47	61	63	61	60	58	68	68											
Solyc04g039730_2_1	17	53	54	54	50	49	52	52	51	63	63	65	62	61	57	56	55										
Solyc05g005140_2_1	18	49	50	49	46	46	50	49	48	62	61	62	61	60	56	55	54	79									
AT1G60800_1_NIK3	19	51	52	52	48	48	49	50	50	59	61	61	61	59	56	53	54	73	70								
AT5G45780_1	20	44	44	43	41	43	45	43	44	52	53	53	51	51	49	47	50	55	52	54							
Solyc02g072310_2_1	21	49	49	49	47	48	50	50	49	57	57	55	55	56	53	54	53	58	57	57	70						
AT5G10290_1	22	53	54	54	49	50	52	52	54	47	47	46	46	48	42	43	44	44	43	45	42	47					
AT5G65240_1	23	54	53	53	49	50	51	51	53	47	49	48	47	48	43	43	44	45	43	48	42	48	83				
Solyc03g078520_2_1	24	53	55	54	49	49	50	51	52	48	49	47	47	49	45	45	45	49	46	47	42	47	75	71			
Solyc11g008960_1_1	25	55	56	55	50	49	53	52	52	49	48	47	47	48	44	44	45	47	43	46	43	46	76	74	85		
AT5G63710_1	26	44	46	45	42	41	43	43	43	40	41	40	40	41	40	41	40	43	43	42	38	43	52	52	54	55	
Solyc05g056370_2_1	27	49	49	49	43	42	45	46	46	44	43	43	43	47	43	42	42	45	44	43	39	45	55	55	56	57	65

SERK

NIK

LRRIIc

(2) Alignment of intracellular regions (C-terminal)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
AT1G34210_1_SERK2	1																										
AT1G71830_1_SERK1	2	93																									
Solyc04g072570_2_1	3	93	93																								
AT2G13790_1_SERK4	4	80	80	82																							
AT2G13800_1_SERK5	5	77	77	79	95																						
Solyc01g104970_2_1	6	87	86	88	84	81																					
Solyc10g047140_1_1	7	86	87	88	85	82	94																				
AT4G33430_1_BAK1	8	86	85	85	86	83	90	91																			
AT5G16000_1_NIK1	9	65	65	65	59	58	63	62	60																		
Solyc02g089550_2_1	10	66	66	66	60	59	62	62	63	84																	
Solyc04g005910_2_1	11	65	66	66	62	60	63	63	63	81	83																
Solyc05g010400_2_1	12	67	68	67	61	59	64	65	63	83	85	89															
AT3G25560_2_NIK2	13	64	64	64	58	56	61	62	62	79	80	83	82														
AT2G23950_1	14	57	58	58	56	54	57	56	57	69	71	69	70	70													
AT4G30520_1	15	56	58	58	56	53	56	56	57	68	70	68	69	69	87												
Solyc07g006110_2_1	16	60	60	61	56	53	60	60	57	69	73	70	70	68	75	75											
Solyc04g039730_2_1	17	66	67	66	63	61	64	64	65	73	73	75	74	72	66	65	65										
Solyc05g005140_2_1	18	62	62	62	58	57	61	61	60	70	70	70	71	67	62	60	62	84									
AT1G60800_1_NIK3	19	64	65	66	60	58	59	60	60	70	71	70	72	70	64	60	63	80	76								
AT5G45780_1	20	55	59	55	54	53	57	56	57	61	61	63	61	61	58	57	57	66	62	65							
Solyc02g072310_2_1	21	65	66	66	66	64	64	65	66	68	69	68	69	68	65	65	65	71	68	69	79						
AT5G10290_1	22	66	67	67	61	59	63	63	64	60	61	60	62	60	52	53	53	60	56	58	52	62					
AT5G65240_1	23	67	67	68	61	59	63	63	64	60	60	60	62	60	53	54	53	57	56	58	52	62	90				
Solyc03g078520_2_1	24	66	68	69	61	59	64	64	64	59	60	60	61	60	53	54	54	60	58	58	51	61	86	84			
Solyc11g008960_1_1	25	67	68	68	61	59	66	64	64	60	60	60	62	60	53	53	54	60	56	57	52	61	89	87	93		
AT5G63710_1	26	57	59	59	54	53	55	56	56	51	52	52	52	52	50	49	49	52	52	52	49	57	68	66	68	70	
Solyc05g056370_2_1	27	61	62	62	55	54	57	59	59	54	54	55	55	58	51	51	52	54	54	53	49	59	72	72	71	73	79

SERK

NIK

LRRIIc

(3) Alignment of extracellular regions (N-terminal)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
AT1G34210_1_SERK2	1																										
AT1G71830_1_SERK1	2	84																									
Solyc04g072570_2_1	3	80	81																								
AT2G13790_1_SERK4	4	65	65	61																							
AT2G13800_1_SERK5	5	57	52	57	71																						
Solyc01g104970_2_1	6	70	68	70	64	58																					
Solyc10g047140_1_1	7	69	66	68	66	60	79																				
AT4G33430_1_BAK1	8	66	64	66	72	68	72	73																			
AT5G16000_1_NIK1	9	38	36	34	34	34	40	37	33																		
Solyc02g089550_2_1	10	36	36	33	30	37	36	34	36	65																	
Solyc04g005910_2_1	11	37	36	35	31	30	36	34	32	57	56																
Solyc05g010400_2_1	12	37	37	35	30	32	34	31	33	60	54	73															
AT3G25560_2_NIK2	13	34	37	35	30	33	32	33	33	59	59	59	58														
AT2G23950_1	14	35	36	36	29	30	32	32	34	58	51	47	50	52													
AT4G30520_1	15	38	37	39	33	35	33	34	33	54	53	47	51	52	80												
Solyc07g006110_2_1	16	38	39	38	35	36	34	35	36	58	56	49	52	51	62	63											
Solyc04g039730_2_1	17	36	37	37	33	31	33	34	31	51	53	53	46	49	50	49	48										
Solyc05g005140_2_1	18	32	32	33	26	27	30	28	30	51	50	52	46	52	50	50	46	73									
AT1G60800_1_NIK3	19	35	36	35	31	36	35	38	40	47	48	48	48	49	51	49	47	65	63								
AT5G45780_1	20	33	33	31	31	33	31	33	31	45	46	44	41	41	40	40	43	45	43	44							
Solyc02g072310_2_1	21	34	34	32	28	32	34	34	32	48	50	45	44	45	42	44	44	47	48	47	64						
AT5G10290_1	22	38	37	36	34	41	37	38	38	32	30	27	27	36	30	31	35	29	27	35	31	32					
AT5G65240_1	23	37	37	34	32	37	35	36	39	32	34	34	28	35	31	30	33	33	27	35	34	34	74				
Solyc03g078520_2_1	24	36	38	35	35	35	33	34	36	34	32	30	33	36	37	36	36	33	30	35	35	34	61	53			
Solyc11g008960_1_1	25	40	42	39	36	36	36	38	39	35	31	31	32	30	35	35	33	33	27	34	35	30	61	58	76		
AT5G63710_1	26	28	29	28	23	23	23	23	23	29	27	26	25	28	32	32	32	33	32	31	28	29	31	32	36	35	
Solyc05g056370_2_1	27	33	32	32	25	28	27	28	26	34	30	30	28	35	37	35	34	35	30	34	31	29	36	35	38	38	50

SERK

NIK

LRRIIc

Additional file 5. List of primers

Primers used for genes clonning (for yeast two-hybrid assay)

Accession #	Gene name	Primer	Sequence (5'-->3')	Amplicon size
Solyc02g089550.2.1	SlNIK1	FWD	AAAAAGCAGGCTTCACAATGGATCTCCAAGTTGC	996
		RVS	AGAAAGCTGGGTCTCACCTAGGACCAGACAGCTC	
Solyc04g005910.2.1	SlNIK2	FWD	AAAAAGCAGGCTTCACAATGGAGCTTCAGTCTGC	996
		RVS	AGAAAGCTGGGTCTCATCTTGGACCAGATAGTTC	
Solyc04g039730.2.1	SlNIK3	FWD	AAAAAGCAGGCTTCACAATGGAATTGCGAACTGC	1008
		RVS	AGAAAGCTGGGTCTCATCTAGGTCCTGAAAGCTC	
Solyc10g047140.1.1	SlBAK1	FWD	AAAAAGCAGGCTTCACAATGCGTGAACTACAAGT	1088
		RVS	AGAAAGCTGGGTCTCATCTTGGCCCTGACAACTC	
Solyc12g007110.1.1	SlNsAK	FWD	AAAAAGCAGGCTTCACAATGGTTCGAGCAACTGA	1137
		RVS	AGAAAGCTGGGTCCTAAGAAGTTCCACTGAAGCC	
Solyc03g019980.1.1	SlEFR	FWD	AAAAAGCAGGCTTCACAATGAACAATCAACCAGC	1053
		RVS	AGAAAGCTGGGTCTCACTTATAGCTTGGTGCCTC	
ABC68293.1	ToYSV-NSP	FWD	AAAAAGCAGGCTTCACAATGTATCAAGCCAAGTA	768
		RVS	AGAAAGCTGGGTCAATTGGTTATATTAGTTCTAG	

*In blue, adaptor sequence of recombination site

Primers used for Real-time PCR assay

Accession #	Primer	Position on gene	Sequence (5'-->3')	Amplicon size
Solyc01g104970.2.1	FWD	81	GGTAACACTGAAGGTGATGCGTT	184
	RVS	265	GGAACGAGTTGACCCGACAAA	
Solyc02g072310.2.1	FWD	638	CACAGGATATGTGCAACACGATT	174
	RVS	812	TTTGACAGCCACTACTGTCCTAT	
Solyc02g089550.2.1	FWD	444	GACCTCAAGTACATGAGGCTCAA	140
(SlNIK1)	RVS	584	TTTCTTGGGAGGGAACCTAGGTA	
Solyc03g078520.2.1	FWD	273	AATACACTGTCCTTGCAAGGGAA	204
	RVS	477	GTCCCGAAAGTGACTGAGGGATA	
Solyc04g005910.2.1	FWD	60	ATGCTTACTCCAGCTGGTGTCAA	175
(SlNIK2)	RVS	235	TGGCTAGGACTTTCCAGGCTAGT	
Solyc04g039730.2.1	FWD	500	CCTCGCTCTCGTGGATGTTT	164
(SlNIK3)	RVS	664	AAACTATCTGGCGGGAAGGACA	
Solyc04g072570.2.1	FWD	1394	TACAACTGCTGTGCGTGGTACAA	191
	RVS	1585	AGTCCTTTCACCCAGTCAAGCAA	
Solyc05g005140.2.1	FWD	228	GTGTCTGCTCTAGCACTACCTA	197
	RVS	425	GGAAGTGGGTATTTCGCCTTCA	
Solyc05g010400.2.1	FWD	164	TGTTGATCCATGTAGCTGGAATA	144
	RVS	308	GCTCTGCAGAAGCAGTAGATT	
Solyc05g056370.2.1	FWD	89	TGATGTTGAAGGTCATGCTTTA	119
	RVS	208	CATGTAACATGAGACCAACTGAA	
Solyc07g006110.2.1	FWD	107	AAGGAGAAGTTTGGATGACCCAA	128
	RVS	235	TGACTTGGAGCTCCTAGTGCAA	
Solyc10g047140.1.1	FWD	427	TACGCTTCCTGAGGCTCAATAAT	122
(SlBAK1)	RVS	549	TGACTGGAACTAGTCCTGTCA	
Solyc11g008960.1.1	FWD	608	TGACAGTGAAGGTTCTCCCAGTA	186
	RVS	794	TTGACCAAATGGAATTCGTCTGT	
Solyc04g077970.2.1	FWD	581	GAACAGACAAGATTGAGATGCATGTA	61
(APT1*)	RVS	640	CCACGAGGGCACGTTCA	

*APT1 (Adenine Phosphoribosyltransferase) was used as endougenous control