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Medicago truncatula

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4 *Medicago truncatula*

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21
22 **Abstract**

23
24 Rusts are major biotic constraints of legumes worldwide. Breeding for rust resistance is
25 regarded as the most cost efficient method for rust control. However, in contrast to
26 common bean for which complete monogenic resistance exists and is efficiently used,
27 most of the rust resistance reactions described so far in cool season food legumes are
28 incomplete and of complex inheritance. Incomplete resistance has been described in
29 faba bean, pea, chickpea and lentil and several of their associated QTLs have been
30 mapped. However, the relatively large distance between the QTLs and their associated
31 molecular markers hampers their efficient use for MAS. Their large genome size
32 drastically hampers the development of genomic resource and limits the saturation of
33 their genetic maps. The use of model plants such as the model legume *Medicago*
34 *truncatula* may circumvent this drawback. The important genetic and genomic
35 resources and tools available for this model legume can considerably speed up the
36 discovery and validation of new genes and QTLs in resistance to legume pathogens.

1 Here, the potential of *M. truncatula* as a model to study rust resistance in legumes, and to
2 transfer rust resistance genes to cool season grain legumes is reviewed.

3

4 **Rusts of legume crops**

5 There are about 5000 species of rust that attack an extremely wide range of crops
6 worldwide. Several rust species can infect grain and forage legumes, most of them
7 belonging to the genus *Uromyces*, such as *U. appendiculatus* (Pers.) Unger on common
8 bean (*Phaseolus vulgaris* L.), *U. ciceris-arietini* Jacz. in Boyer & Jacz. on chickpea
9 (*Cicer arietinum* L.), *U. lupinicolus* Bub. on lupine (*Lupinus* sp.), *U. pisi* ([Pers.] D.C.)
10 Wint. on pea (*Pisum sativum* L.) and grasspea (*Lathyrus* sp.), *U. striatus* J. Schröt. on
11 alfalfa (*Medicago sativa* L.), *U. viciae-fabae* (Pers.) J. Schröt. on faba bean (*Vicia faba*
12 L.), lentil (*Lens culinaris* Medik.) and common vetch (*V. sativa* L.) and *U. vignae*
13 Barclay on cowpea (*Vigna unguiculata* (L.) Walp.). Rust species belonging to other
14 genera can also be major problems on legumes such as *Phakopsora pachyrhizi* Sydow
15 and *P. meibomiaae* (Arthur) Arthur on soybean (*Glycine max* (L.) Merr.) or *Puccinia*
16 *arachidis* Speg. on groundnut (*Arachis hypogaea* L.) (Rubiales et al. 2002; Sillero et al.
17 2006; Emeran et al. 2008).

18 Breeding for rust resistance is regarded as the most cost efficient method for rust
19 control. In tropical legumes such as common bean and soybean, complete monogenic
20 resistance reactions have been described. Due to their economic importance, these
21 sources have been largely studied leading to the identification of their associated rust
22 resistance genes and closely linked markers that are readily used in marker-assisted
23 backcrossing (Faleiro et al. 2004; Miklas et al. 2006; Hyten et al. 2007; García et al.
24 2008) (Table 1). By contrast, most of the rust resistance reactions described so far in
25 cool season food legumes are incomplete. Phenotypic expression of rust resistance is

1 usually poorly described. As a consequence of this, and of the poorly developed
2 genomic resources usually available in most cool season legumes, genetic basis of
3 resistance is, in most cases, largely unknown. Although QTL mapping studies have
4 been performed for most cool season legumes such as chickpea (Millán et al. 2006;
5 Madrid et al. 2008), faba bean (Torres et al. 2006), lentil (Muehlbauer et al. 2006) or
6 pea (Barilli et al. 2010), in most cases no markers are yet readily available for QTL
7 selection and Marker Assisted Selection (MAS) (Table 1).

8 Incomplete rate reducing resistance not based on hypersensitivity is very
9 common in cool season legumes and is often the only type of resistance available
10 (Sillero et al. 2006). Several sources of resistance against *U. viciae-fabae* have been
11 reported in faba bean in the last decades, being mainly of incomplete expression and not
12 based on hypersensitivity (Sillero et al. 2010). Information on the genetic basis of this
13 incomplete resistance is still scant. A number of race-specific genes has been postulated
14 causing reduced pustule size (Conner and Bernier 1982; Rashid and Bernier, 1986).
15 Mapping studies using a recombinant inbred line (RIL) population to identify QTLs and
16 to develop molecular markers useful in MAS for the non-hypersensitive resistance
17 (Torres et al. 2006), but no results are available yet. On the other hand, hypersensitive
18 resistance was recently described in faba bean germplasm (Sillero et al. 2000; Rubiales
19 and Sillero 2003). It is controlled by genes with major effects (Sillero et al. 2000). Use
20 of Bulk Segregant Analysis (BSA) allowed identifying three Random Amplified
21 Polymorphic DNA (RAPD) markers linked to resistance gene (*Uvf1*) (Avila et al.
22 2003). Three RAPD markers (OPD13₇₃₆, OPL18₁₀₃₂ and OPI20₉₀₀) were mapped in
23 coupling phase to the resistance gene *Uvf-1*. No recombinants between OPI20₉₀₀ and
24 *Uvf-1* were detected. Two additional markers (OPP021₁₇₂ and OPR07₉₃₀) were linked to
25 the gene in repulsion phase at a distance of 9.9 and 11.5 cM, respectively. The

1 simultaneous use of both types of markers allows their use as a codominant marker.
2 Different genes might be available in the different accessions displaying
3 hypersensitivity reported so far (Sillero et al. 2000; Sillero and Rubiales 2002; Rubiales
4 and Sillero 2003), but genetic analysis has so far been performed only with one of them
5 (Avila et al. 2003). Obviously, this preliminary work ought to be complemented with
6 the identification of the different genes and the associated markers before an efficient
7 pyramidization programme can be achieved.

8 In pea, only incomplete resistance has been described against both *U. viciae-*
9 *fabae* (Chand et al. 2006) and *U. pisi* (Barilli et al. 2009a, b). Preliminary mapping
10 studies have yielded identification of several QTLs for resistance to *U. viciae-fabae*
11 (Vijayalakshmi et al. 2005) and to *U. pisi* (Barilli et al. 2010) but results are far for
12 being usable in MAS (Table 1). Partial resistance to *U. viciae-fabae* has been justified
13 as the expression of a single major gene (*Ruf*) (Vijayalakshmi et al. 2005). Two RAPD
14 markers, *SC10-82₃₆₀* (10.8 cM) and *SCRI-71₁₀₀₀* (24.5 cM), were detected flanking the
15 gene *Ruf*, but these markers were not close enough to allow a reliable MAS approach
16 for rust resistance (Vijayalakshmi et al. 2005). A QTL explaining 63% of the resistance
17 to *U. pisi* has been located in the linkage group 3. Two RAPDs markers, *OPY11₁₃₁₆*
18 (26.9 cM) and *OPV17₁₀₇₈* (46.3 cM) showed significant association with rust resistance
19 (Table 1). These results must be validated across diverse locations and genetic
20 backgrounds before the application of MAS in pea breeding programs. Inclusion of new
21 standard markers and transformation into SCARs of the RAPDs tightly linked to the
22 detected QTLs is needed to enhance their applicability for MAS.

23 Similarly, only incomplete resistance was identified in chickpea against *U.*
24 *ciceris-arietini* (Rubiales et al. 2001). A QTL explaining 81% of the resistance in adult
25 plants was located on linkage group 7 of the chickpea genetic map (Madrid et al. 2008).

1 It was hypothesized to correspond to a single gene (*Uca1/uca1*) according to the
2 segregation analysis. Two STMS markers were identified that flank this resistance gene.
3 In this particular case, the distance between the STMS markers and the resistance gene
4 is short enough (3.9cM apart) to allow reliable MAS for rust resistance in chickpea
5 (Table 1).

6 Lentil rust resistance has been reported mainly as partial resistance, although
7 some hypersensitive resistant sources have also been described (Rojas et al. 2004;
8 Negussie et al. 2005). Monogenic resistance has been described (Erskine et al. 1994)
9 and preliminary information on chromosome location and associated molecular markers
10 is being produced (Kant et al. 2004; Table 1). More recently, a sequence related
11 amplified polymorphism (SRAP) marker, F7XEM4a, has been identified at 7.9 cM
12 from the gene for resistance (Saha et al. 2010) (Table 1). The F7XEM4a marker could
13 be used for MAS but additional markers closer to the resistance gene are needed.

14 Resistance to rust has also been identified in *L. sativus* (Vaz Patto and Rubiales
15 2009) and *L. cicera* (Vaz Patto et al. 2009) germplasm but genetic studies have only
16 recently been initiated by generation of proper mapping populations (unpublished).

17 In peanuts, genetic studies indicated that resistance to the rust fungus *Puccinia*
18 *arachidis* is complex and of polygenic nature. In this sense, Khedikar et al. (2010)
19 recently identified and located 12 QTLs associated with resistance to rust of the TAG24
20 genotype. Among them, the QTL_{rust}01 was detected in all environmental conditions
21 tested and explained up to 55.2% of the phenotypic variation. This QTL co-localized
22 with the SSR marker IPAHM103 (Khedikar et al. 2010). Using the same resistant
23 genotype, Mondal and co-workers (2008) found one RAPD marker, J7₁₃₀₀, closely
24 associated with rust resistance. In addition, these authors exploited the natural genetic
25 variation existing in cultivated peanuts to identify three additional SSR markers PM 35

1 PM 50 and PM 179 associated with rust resistance (Mondal and Badigannavar, 2009).
2 All these molecular markers are promising tool for future peanuts breeding against rust
3 although effort should be made to reduce the still important genetic distance separating
4 the rust resistance QTL and the existing molecular marker.

5 In general, the scarce genomic resources developed for cool season legumes and
6 the limited saturation of the genomic regions bearing putative QTLs makes it difficult to
7 identify the most tightly-linked markers and to determine the accurate position of QTLs
8 (Torres et al. 2006; Rubiales et al. 2009; Rispaill et al. 2010). Effectiveness of MAS
9 might soon increase with the adoption of the new improvements in marker technology
10 together with the integration of comparative mapping and functional genomics. But rust
11 resistance breeding is not only slow due to the difficulty and the relatively low
12 investment on genetics, genomics and biotechnology of the legume crops, but also, and
13 mainly because of the little knowledge on the biology of the rust pathogens.
14 Comprehensive studies on host status and virulence of the various rust species are often
15 missing, and in most of the examples listed above, there is little agreement on the
16 existence of races and on their distribution. This is a major limitation for any breeding
17 programme. Also, available information on levels of resistance and on the responsible
18 mechanisms is often incomplete. Only after significant input to improve existing
19 knowledge on biology of the causal agents as well as on the plant, resistance breeding
20 will be efficiently accelerated.

21 Current progress in the genomic and biotechnological research will soon provide
22 important understanding of some crucial developmental mechanisms in both the
23 parasites and their host plants. Transcriptomic and proteomic approaches developed for
24 model plants can be used to understand the molecular components and identify
25 candidate genes involved in defence against rust pathogens. Traditional breeding efforts

1 will be greatly enhanced through collaborative approaches using functional,
2 comparative and structural genomics. Molecular genetic and genomic analyses promise
3 the transfer of technology from model to crop legumes.

4

5 ***Medicago truncatula* as a model legume**

6 The development of *Arabidopsis thaliana* as a unique model improved greatly our
7 understanding of complex biological processes (Jones and Dangl 2006; De Smet and
8 Jurgens 2007). However, *A. thaliana* is not the best suited model to study plant defence
9 mechanisms to rust. Indeed, there is no available fungus that causes a natural rust
10 disease in *A. thaliana*, although the *A. thaliana* - *U. viciae* system has been used to
11 characterize the nonhost signalling pathway (Mellersh and Heath 2003). Other
12 alternative species such as the legume species *Medicago truncatula* and *Lotus japonicus*
13 have been more recently developed as model to address specific issues of legumes. *M.*
14 *truncatula* (barrel medic) is an annual, self-fertile, diploid legume species that has
15 become a model for studying various aspects of legume genomics and biology (Cook
16 1999; Ané et al. 2008; Young and Udvardi 2009; Rispaill et al. 2010).

17 Several germplasm collections of *M. truncatula* are available to search for
18 genetic polymorphism for particular traits which lead to the generation of several
19 genetic and cytogenetic maps instrumental for map-based cloning, genome sequencing
20 and comparative genomics (Ané et al. 2008; Kulikova et al. 2001). In addition, *M.*
21 *truncatula* genome sequencing is near completion with more than 250 Mb already
22 sequenced and annotated (<http://www.medicagohapmap.org/>; release 3.5) and more than
23 260,000 expressed sequence tags (ESTs) are available from public DNA database (Ané
24 et al. 2008). In parallel postgenomic tools such as transcriptomic and proteomic
25 platforms as well as several reverse genetic and functional analysis approaches

1 including the creations of several chemical and insertional mutant collections, TILLING
2 platforms, RNA interference or VIGS technologies have been developed for *M.*
3 *truncatula* (Young and Udvardi 2009; Rispaill et al. 2010).

4

5 **Application of *M. truncatula* to rust resistance**

6 The fact that *M. truncatula* is susceptible to alfalfa (*U. striatus*) and chickpea rusts (*U.*
7 *ciceris-arietini*) (Skinner and Stuteville 1995; Stuteville et al. 2010) opens the way for
8 its use to unravel legume-rust interactions. *U. striatus* is an important disease of
9 worldwide distribution, being particularly damaging in alfalfa (*Medicago sativa*) grown
10 for seed (Koepper 1942; Leath et al. 1988). It has a broad host range comprising many
11 species from the tribes Trifolieae, Cicereae, and Vicieae, including alfalfa and annual
12 medics including barrel medic (Skinner and Stuteville 1995).

13 A range of resistance mechanisms against *U. striatus* are operative in *M.*
14 *truncatula* accessions. Once the fungus has successfully penetrated the stoma, and
15 formed a first haustorium, nutrients are taken from the invaded plant cell to allow
16 further intercellular growth and haustoria formation. Previous studies comparing host
17 and nonhost resistance to rust fungi have shown that nonhost resistance is typically
18 expressed before the formation of the first haustorium (Heath 1981). By contrast, *R*
19 gene-controlled host resistance is almost invariably expressed after the formation of the
20 first haustorium, often in the form of hypersensitive death of invaded cell. Histological
21 investigations, revealed significant differences in resistance to rust among *M. truncatula*
22 accessions that were more evident once the stomata were penetrated by the infection
23 structures (Rubiales and Moral 2004; Kemen et al. 2005). Similarly to most rust hosts
24 (Niks and Rubiales 2002), prepenetration resistance mechanism including reduction of
25 urediospore germination and fungal development on the leaf surface in *M. truncatula*

1 are of marginal importance against *U. striatus*, at best, in reducing infection levels
2 (Rubiales and Moral 2004). Prehaustorial resistance can also be identified in host
3 interactions, playing a major role in the so-called partial resistance, which may be more
4 durable than resistance controlled by *R* genes (Niks and Rubiales 2002). A significant
5 proportion of infection units fails to form any haustoria in some *M. truncatula*
6 genotypes. Posthaustorial resistance was clear in other genotypes (Rubiales and Moral
7 2004; Kemen et al. 2005).

8 *M. truncatula* is already being studied to unravel resistance to a broad number of
9 pathogens, from parasitic plants (Fernández-Aparicio et al. 2008), bacterial pathogens
10 (Vailleau et al. 2007), nematodes (Moussart et al. 2007) to fungal and oomycete
11 pathogens (O'Neill and Bauchan 2000; Yaege and Stuteville 2000; Barbetti and Allen
12 2005; Ellwood et al. 2006; Tivoli et al. 2006; Barbetti 2007; Moussart et al. 2007; Prats
13 et al. 2007). Microarray analysis have been performed to determine genes involved in
14 defence mechanisms against *Erysiphe pisi* (Curto et al. 2007; Foster-Hartnett et al.
15 2007), *Orobanche crenata* (Dita et al. 2009) or to *Mycosphaerella pinodes* (Fondevilla
16 et al. 2009). In addition, Affymetrix chips are also commercially available for *M.*
17 *truncatula* (<http://www.affymetrix.com>) and a novel generation of *M. truncatula* gene
18 chip complemented with 1,850 *M. sativa* transcripts will be soon available to facilitate
19 transcriptomic analysis of closely related species (Ané et al. 2008). All these
20 transcriptomic platforms will allow large improvements in our understanding of legume
21 rust interaction.

22 In parallel, expression of more than 1000 transcription factors (TFs) have been
23 monitored by quantitative real-time PCR during resistance reaction to rust in *M.*
24 *truncatula* (Madrid et al. 2010), in order to refine hypothesis about TFs function in
25 defense response as well as in the regulation of cross-talk between different signaling

1 pathways. A total of 107 putative TF genes were differentially expressed between the
2 susceptible and resistant genotypes. Thirteen of these TFs are known to be relevant in
3 cellular defense. Some of the TFs are pathogenesis-related transcription factors,
4 ethylene response factor (PR-ERF), and WRKY TFs which are involved in the response
5 to biotic stress in plant (Singh et al. 2004). These data suggest that resistance could be
6 mediated both by genes that are constitutively expressed and by genes which are
7 induced/repressed when plants are inoculated. These TFs could be candidates for future
8 experiments to elucidate the genes that control this agronomically important trait.
9 However, the role they play in the interaction need to be clarified in order to completely
10 understand the pathways involved in the plant's defense against this pathogen. On the
11 other hand, taking advantage of the synteny between *Medicago* and *Cicer* (Cannon et al.
12 2006) these defense related TFs sequences were amplified in chickpea DNA.
13 Amplification analysis of the tested primers showed high transferability between both
14 *M. truncatula* and *C. arietinum*. Two of these genes were mapped on the linkage group
15 4 of the chickpea map (Madrid et al. 2010). In this linkage group two QTLs for
16 ascochyta blight resistance have been reported (Tekeoglu et al. 2002; Iruela et al. 2006).
17 These TFs could be candidates for future experiments to elucidate the genes that control
18 this agronomically important trait.

19 Postgenomic approaches are also being applied to tackle other pathogens.
20 Subtractive Suppression Hybridisation (SSH) libraries allowed the identification of
21 defence genes to *Aphanomyces eusteiches* (Nyamsuren et al. 2003), or to *O. crenata*
22 (Die et al. 2007). The range of application of proteomic approaches has been broadened
23 to include *M. truncatula* - *U. striatus* (Castillejo et al. 2010) as well as interactions with
24 other pathogens such as *Aphanomyces* (Colditz et al. 2004, 2005, 2007; Trapphoff et al.
25 2009), *E. pisi* (Curto et al. 2008) and *O. crenata* (Castillejo et al. 2009). Comparison of

1 the proteome between susceptible and resistant accessions of *M. truncatula* upon rust
2 inoculation revealed significant changes in the expression pattern of several proteins
3 (Castillejo et al. 2010). For instance, several enzymes of the energetic metabolism
4 pathway and many stress-related proteins including the ascorbate peroxidase were
5 expressed at higher level in the resistant genotype (Castillejo et al. 2010). Similar results
6 have been observed in other systems studied, such as *M. truncatula*–*O. crenata*
7 (Castillejo et al. 2009).

8 Efficient transfer to legume crops of the knowledge gained on the *M. truncatula*
9 – rust interaction requires the identification of the actual function of the candidate genes
10 identified by genomics and post-genomic approaches (Rispaill et al. 2010). To this
11 purpose, it may be worth exploring the different chemical and insertional mutant
12 collections and the TILLING and RNAi platforms developed for *M. truncatula* that can
13 also help identifying new genes involved in *M. truncatula* resistance to rust (Rispaill et
14 al. 2010).

15 Discovery of markers linked to rust resistance in *M. truncatula* may provide a
16 tool to identify the same characteristic in the otherwise unexplored legume crop in
17 which genomic studies are hampered by the large genome size and complex ploidy. It
18 therefore becomes critical that molecular linkage maps of legume crops include both
19 ESTs and phenotypes (including QTLs) relating to rust resistance, and that variation for
20 these phenotypes is mapped to such conserved EST markers. The nearly completed
21 genome sequences of *M. truncatula* will greatly aid in this area of research
22 (<http://www.medicagohapmap.org/>).

23

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1 **Table 1.** List of QTLs identified in legumes against rust diseases.

Rust species	Legume species	Gene(s)/QTL	Associated Markers	Marker type	Linkage group	References
<i>Uromyces appendiculatus</i>	<i>Phaseolus vulgaris</i>	<i>Ur3</i>	OK14 _{e20}	RAPD	B11	Haley <i>et al.</i> 1994
		<i>Ur4</i>	OA14 _{t100}	RAPD	B6	Miklas <i>et al.</i> 1993
		<i>Ur5</i>	OI19 ₄₆₀	RAPD	B4	Haley <i>et al.</i> 1993
		<i>Ur-6</i>	SOBC06.308	SCAR	B11	Park <i>et al.</i> 2004
		<i>Ur7</i>	OAD12.550 and OAF17.900	RAPD	B11	Park <i>et al.</i> 2003
		<i>Ur9</i>	OA4.1050	RAPD	B1	Park <i>et al.</i> 1999
		<i>Ur11</i>	OAC20 ₄₉₀	RAPD	B11	Johnson <i>et al.</i> 1995
		<i>Ur12</i>			B7	Kelly <i>et al.</i> 2003
		<i>Ur13</i>	KB126 and KB4 <i>Hha</i> I	SCAR and CA	B8	Mienie <i>et al.</i> 2005
		<i>Ur-Dorado</i>			B4	Kelly <i>et al.</i> 2003
		<i>Ur-Ouro Negro</i>	SCARBA08 and SCARF10	SCAR	B11 B4	Miklas <i>et al.</i> 2006 Correa <i>et al.</i> 2000
<i>Uromyces viciae-fabae</i>	<i>Vicia faba</i>	<i>Uvf-1</i>	OPI20 ₉₀₀	RAPD		Avila <i>et al.</i> , 2003
	<i>Pisum sativum</i>	<i>Ruf</i>	SC10-82 ₃₆₀ and SCRI-71 ₁₀₀₀	RAPD		Vijayalakshmi <i>et al.</i> 2005
	<i>Lens culinaris</i>		F7XEM4a OPX-15 ₇₆₀ and OPX-17 ₁₀₇₅	SRAP RAPD	LG-3	Saha <i>et al.</i> 2010 Kant <i>et al.</i> 2004
<i>Uromyces pisi</i>	<i>Pisum fulvum</i>	<i>Up1</i>	OPY11 ₁₃₁₆ and OPV17 ₁₀₇₈	RAPD	LG-3	Barilli <i>et al.</i> 2010
<i>Uromyces ciceris-arietini</i>	<i>Cicer arietinum</i>	<i>Uca1/uca1</i>	TA18 and TA180	STMS	LG-7	Madrid <i>et al.</i> 2008
<i>Uromyces vignae</i>	<i>Vigna unguiculata</i>	<i>Rr1</i>	ABRS _{AAgICTG98}	SCAR		Li <i>et al.</i> 2007
<i>Puccinia arachidis</i>	<i>Arachis hypogaea</i>	QTL _{rust} 01	IPAHM103 and pPGSseq19D6	SSR	LG-6	Khedikar <i>et al.</i> 2010
		QTL _{rust} 02	PM436 and Lec-1	SSR	LG-1	Khedikar <i>et al.</i> 2010
		QTL _{rust} 03	TC11A04 and IPAHM524	SSR	LG-2	Khedikar <i>et al.</i> 2010
		QTL _{rust} 04	TC1B02 and TC9F04	SSR	LG-3	Khedikar <i>et al.</i> 2010
		QTL _{rust} 05	TC4E09 and IPAHM121	SSR	LG-7	Khedikar <i>et al.</i> 2010
		QTL _{rust} 06	pPGSseq13E6 and PM3	SSR	LG-8	Khedikar <i>et al.</i> 2010
		QTL _{rust} 07	pPGSseq19G7 and TC2C07	SSR	LG-8	Khedikar <i>et al.</i> 2010
		QTL _{rust} 08	TC2G05 and TC9H09	SSR	LG-9	Khedikar <i>et al.</i> 2010
		QTL _{rust} 09	GM624 and TC4G10	SSR	LG-9	Khedikar <i>et al.</i> 2010
		QTL _{rust} 10	PM434 and TC4F02	SSR	LG-8	Khedikar <i>et al.</i> 2010
		QTL _{rust} 11	TC9H09 and GM624	SSR	LG-9	Khedikar <i>et al.</i> 2010
		QTL _{rust} 12	PM377 and TC1A01 J7 ₁₃₀₀	SSR RAPD	LG-10	Khedikar <i>et al.</i> 2010 Mondal <i>et al.</i> 2008
<i>Phakopsora pachyrhizi</i>	<i>Glycine max</i>	<i>Rpp1</i>	Sct_187 and Sat_064	SSR	LG-G	Hyten <i>et al.</i> 2007
		<i>Rpp2</i>	Sat_255 and Satt620	SSR	LG-J	Silva <i>et al.</i> 2008
		<i>Rpp3</i>	Satt460 and Sat_263	SSR	LG-C2	Hyten <i>et al.</i> 2009
		<i>Rpp4</i>	Satt288 and AF162283	SSR	LG-G	Silva <i>et al.</i> 2008
		<i>Rpp5</i>	Sat_275 and Sat_280	SSR	LG-N	Garcia <i>et al.</i> 2008

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