Resistance to Rust and Powdery Mildew in *Lathyrus* Crops

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**Abstract**


Several *Lathyrus* species, particularly *Lathyrus sativus* and *L. cicera*, have a high potential both as food and fodder crops. Rust and powdery mildew fungi are among the most important pathogens of major grain legumes including *Lathyrus* species. We review and critically discuss available knowledge of the existence of resistance and the underlying resistance mechanisms against rust and powdery mildew in the *L. sativus* and *L. cicera* crop species.

**Keywords:** Erysiphe pisi; Lathyrus sativus; Lathyrus cicera; Uromyces pisi

**Potential of *Lathyrus sativus* and *Lathyrus cicera* for resistance breeding**

The genus *Lathyrus* comprises about 160 annual and perennial species (Allkin et al. 1986), some of which, particularly *Lathyrus sativus* and *L. cicera*, are of agronomic interest (Vaz Patto et al. 2006b). They have a high potential compared to other grain legumes both as food and fodder crops, due to their high nutritional value, capability to fix large amounts of nitrogen and aptitude to withstand drought and excessive soil moisture, salinity and low soil fertility (Hanbury et al. 2000). Furthermore, resistance to serious diseases of important cultivated legume species, such as ascochyta blight (Campbell et al. 1994; Skiba et al. 2004), powdery mildew and rust fungi (Vaz Patto et al. 2006a, b, 2007; Vaz Patto & Rubiales 2009) or broomrape (Fernández-Aparicio et al. 2009, 2012; Fernández-Aparicio & Rubiales 2010), is also an important feature of these species especially in a more sustainable agricultural system.

Due to rapid agricultural mechanization and abandoning of small-scale farming (Peña-Chocarro & Zapata 1999), the use of these species has been regressing, exposing the risk of losing genotypes developed over thousands of years of cultivation. Still, *L. sativus* in particular, is rightly considered to be one of the most promising sources of energy and protein for the vast and expanding populations of drought-prone and marginal areas of Asia and Africa and an interesting alternative for cropping system diversification in marginal lands in Europe, Australia and America (Almeida et al. 2013). The large variation recorded in the *L. cicera* and *L. sativus* germplasm (Vaz Patto et al. 2006b, 2011) offers a considerable potential for the breeding of *Lathyrus* cultivars in general and disease resistance improvement in particular.

Rust and powdery mildew are among the most important pathogens of major grain legumes (Sillero et al. 2006; Rubiales et al. 2011). Powdery mildew is, together with downy mildew (*Peronospora lathipalustris*), a major disease worldwide, affecting *L. sativus* (Campbell et al. 1994) and *L. odoratus* crops (Cook & Fox 1992). Rust is an important disease of *L. sativus* in northwestern Ethiopia (Campbell 1997). These pathogens are obligate biotrophs that are entirely dependent on living tissue for their development and propagation (Panstruga 2003). The initial phases of pathogenesis do not differ fundamentally among them and include spore adhesion, spore germination, appressorium formation and penetration of the epidermal cell wall (for powdery mildew) or stomatal penetration (rust fungi). At later stages, haustoria are established by the pathogen within living plant cells and redirect the host’s metabolism to meet the pathogen own needs (Panstruga 2003) (Figure 1).

In the genus *Lathyrus*, infection by different rust and powdery mildew species has been reported, al-
though on *L. sativus* and *L. cicer*, data only refer to *Uromyces pisi* and *U. viciae-fabae* and *Erysiphe pisi*, *E. communis* and *E. polygoni* (online fungal database – Farr & Rossman 2013). Results from rust species cross-inoculations (Emeran 2003) agreed with the above, where *L. sativus* was infected only by *U. pisi* and slightly by *U. ciceri-arietini* and *U. viciae-fabae* ex. *V. sativa*, but not by *U. viciae-fabae* ex. *V. faba* or other *Uromyces* species. In contrast, the existence of specialized forms or races of powdery mildew infecting *Lathyrus* sp. is still unclear, but differing ability to infect different plant species has been reported. Cook and Fox (1992) reported that a strain of *E. pisi* collected on *L. odoratus* was able to infect *Vicia faba*, but not *Pisum sativum*, whereas a different strain collected on *L. latifolius* was able to infect pea and faba bean. It has recently been found that in addition to *E. pisi*, other mildew species such as *E. trifolii* or *E. baeamleri* cause severe infections on pea (Ondřej et al. 2005; Attanayake et al. 2010; Fondevilla et al. 2013). The response of *Lathyrus* species to these mildew species should be explored.

Breeding for genetic resistance is one of the best methods to handle rust and powdery mildew diseases, as it is the most economical and environmentally friendly control method (Rubiales et al. 2011). However, powdery mildew and rust fungi are among the pathogens with the highest risk for breaking down the effectiveness of resistance genes with rapid changes in virulence in the pathogen populations (McDonald & Linde 2002). Different plant defence mechanisms may be operative at different phases of the infection process, from spore deposition to haustoria formation, with different components that can be grouped into macro- and microscopic types.

The majority of the work published on macroscopic *Lathyrus* resistance, especially on rust and powdery mildew infection, has been developed by Vaz Patto and collaborators who have assessed and described the resistance to various rusts and pea powdery mildew on different *Lathyrus* sp. More precisely, a collection from the native Iberian *Lathyrus* germplasm of 150 accessions of *L. cicera* (Vaz Patto et al. 2007, 2009) and 50 accessions of *L. sativus* (Vaz Patto et al. 2006a; Vaz Patto & Rubiales 2009) was evaluated by these authors for resistance to *U. pisi*, *U. ciceris-arietini* (tested only on the *L. sativus* accessions), *U. viciae-fabae* ex. *V. sativa* and *E. pisi*. A wide range of disease reactions against the different pathogens was revealed in this collection. The only references to the study of the microscopic components of resistance in *Lathyrus* species deal with *U. pisi* resistance described in *L. sativus* and *L. cicera* accessions selected from this Iberian collection (Vaz Patto et al. 2009; Vaz Patto & Rubiales 2009).

**Lathyrus resistance to rusts**

Both *L. sativus* and *L. cicer* Iberian germplasms are usually very resistant against *U. viciae-fabae* ex. *V. sativa* and *U. ciceris-arietini* (tested only on *L. sativus*) (based on strong early acting hypersensitivity), whereas a compatible reaction [susceptibility or a high infection type (IT), a qualitative/quantitative resistance scoring] was the rule against *U. pisi* infection (Vaz Patto et al. 2009; Vaz Patto & Rubiales 2009). Nevertheless, in this case, the level of resistance in terms of disease severity (DS, scored as the percentage of the plant tissue area affected by disease), varied among accessions. More precisely, *L. sativus* accessions were in general more resistant (lower DS) to *U. pisi* than the accessions of *L. cicera*, both under field and growth chamber conditions (Vaz Patto et al. 2009; Vaz Patto & Rubiales 2009). Reduced disease development in spite of a compatible interaction (high IT), indicating levels of partial resistance, was very frequent in *L. sativus* (Vaz Patto & Rubiales 2009), and also present, although much less frequently, in *L. cicera* (Vaz Patto et al. 2009). DS values were positively correlated when comparing growth chamber and field experiments.

The generally found immunity or high resistance to *U. ciceris-arietini* and *U. viciae-fabae* in the majority of the *L. cicera* and *L. sativus* accessions tested may be indicative of a nonhost resistance status. Prehaustorial resistance is typical in nonhosts, but it has also been implicated in partial host resistance (Rubiales & Niks 1995; Sillero & Rubiales 2002). This ap-

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**Figure 1.** Typical rust (red circular pustules) and powdery mildew (white diffuse spots) symptoms on *Lathyrus cicera* (Photo by N. Almeida)
plies especially to the case of *U. ciceris-arietini*, since some *L. cicera* accessions with moderately susceptible phenotypes to *U. viciae-fabae* were identified. This contrasts with the already described and most frequently observed susceptible reaction to *U. pisi*. As regards the resistance detected in *U. pisi*, as in most of the rust resistance reactions described in cool-season food legumes so far (Sillero et al. 2006; Rubiales et al. 2011), the majority of the observed interactions were of incomplete resistance although cases of complete resistance associated with plant cell necrosis (hypersensitivity) were identified on *L. cicera* accessions. This was however never the case for the *L. sativus* accessions.

A clear rust species-specific resistance was observed since the majority of accessions showed a high IT and in some cases also high DS (susceptibility) in response to *U. pisi* inoculations whereas they were generally immune or highly resistant to *U. ciceris-arietini* and *U. viciae-fabae* inoculations. Nevertheless, some sporulation was observed on *L. cicera* accessions when inoculated either with *U. ciceris-arietini* or with *U. viciae-fabae*. However, this was not always associated with higher *U. pisi* infection (Vaz Patto et al. 2009). Mixed disease reactions (accessions segregating plants with the total absence of symptoms and plants with well-formed colonies and no associated macroscopically visible chlorosis or necrosis) were detected only in some *L. cicera* accessions with cases of hypersensitive reaction (Vaz Patto et al. 2009).

In most rust pathosystems, spore germination and appressorium formation are independent of the host plant genotype (Heath 1974), but once the appressorium and the substomatal vesicle have been successfully formed, plant genotypes differ in the extent to which pre- and post-haustorial mechanisms of resistance operate (Niks 1986; Rubiales & Niks 1995; Rubiales & Moral 2004). Remarkably, germination of *U. pisi*urediospores, orientation of germings and appressorium formation observed in the majority of the selected *Lathyrus* accessions were lower or poorer compared to the susceptible pea control (Vaz Patto et al. 2009; Vaz Patto & Rubiales 2009). This result was unexpected since rust spores usually germinate equally well on hosts and nonhosts (Niks & Rubiales 2002). Nevertheless, cases of irregular or reduced germination due to chemical inhibition, poor leaf wettability or abundance of leaf hairs have been reported (Heath 1974; Johnson et al. 1982; Prats et al. 2002, 2007) and might be present on these *L. sativus* and *L. cicera* accessions, which merits further investigation.

Other mechanisms of rust exclusion may act after spore germination, but prior to stomatal penetration. Such defence mechanisms can be due to poor germling adhesion to the leaf surface (Mendgen 1978; Wynn & Staples 1981), deviating micromorphology of the epidermal surface (Wynn & Staples 1981), stomatal guard cell morphology (Wynn 1976) or leaf pubescence (Mmbaga et al. 1994). The less oriented germ tube growth observed on the *Lathyrus* accessions when compared with the pea cultivar could probably be due to one of the causes described above. This might be relevant for reducing the infectiousness by reducing the number of infection units (appressorium over stoma). Also even when an appressorium is finally formed over a stoma, those germlings that take longer to find a stoma will be depleted of reserves and thus will have less chances to successfully form an haustorium (Niks 1990). However, the differences in germination, oriented germ tube growth and appressorial differentiation were in general of marginal importance for explaining resistance among the *Lathyrus* accessions.

Differences between the selected *Lathyrus* accessions became more evident once the stomata were penetrated by the infection structures (Vaz Patto et al. 2009; Vaz Patto & Rubiales 2009). Resistance to *U. pisi* was detected only microscopically after stoma penetration and both pre-haustorial and post-haustorial resistance mechanisms were identified. In the partially resistant *L. cicera* and *L. sativus* accessions, resistance was due to a restriction of haustorium formation with a high frequency of early abortion of the colonies, a reduction in the number of haustoria per colony and in some cases also with a reduction in the intercellular growth of infection hyphae, representing a clear example of pre-haustorial resistance with no associated necrosis. In some *L. cicera* accessions, post-haustorial resistance with necrosis of the host cells associated with infection hyphae and reduced growth of the colony were identified. Hence, the resistance reaction to *U. pisi* showed not only typical host resistance reactions such as hypersensitivity, but also pre-haustorial resistance based both on hampered haustoria formation and low spore germination and poor germ tube orientation with no associated necrosis (partial resistance sensu Parlevliet 1979). In some *L. cicera* accessions and a few *L. sativus* accessions, a restriction of haustorium formation with a high level of early abortion of the colonies and a reduction in the number of haustoria per colony were observed. In *L. cicera*, necrosis of the host cells associated with infection hyphae was also detectable in some accessions from the beginning of
colony development both in early aborted and established colonies (Vaz Patto et al. 2009). In L. sativus a reduction in the intercellular growth of infection hyphae was also recorded (Vaz Patto & Rubiales 2009).

Once a U. pisi colony was successfully established, it reached a similar size to that on the pea control in most Lathyrus accessions studied, but genetic variation in colony size existed within L. cicera germplasm (Vaz Patto & Rubiales 2009; Vaz Patto et al. 2009). U. ciceris-arietini colonies were very small in all Lathyrus accessions and mainly associated with host cell necrosis. However, U. vicie-fabae colonies ranged from small to big (as big as the vetch control), but were always associated with necrosis.

Although partial resistance against rusts, not associated with host cell necrosis, is common in major grain legumes, hypersensitive reactions to the rust fungus are also found on certain legume species (Sillero et al. 2006; Rubiales et al. 2011). In Phaseolus vulgaris, hypersensitive reaction is the most frequent resistance mechanism reported against U. appendiculatus (Singh & Schwartz 2010). Also in faba bean, incomplete resistance to U. vicie-fabae based on hypersensitive reaction has been recently identified (Rubiales & Sillero 2003) and hypersensitive resistance to U. vicie-fabae has been reported in common vetch, in other species of the genus Vicia (Rubiales et al. 2013b), and in lentil (Rubiales et al. 2013a). However, no hypersensitive resistance against U. pisi has been described so far in pea (Barilli et al. 2009) or in chickpea against U. ciceris-arietini (Madrid et al. 2008). Hypersensitive resistance was observed in some L. cicer accessions to U. pisi, but also to U. ciceris-arietini and to U. vicie-fabae together with some L. sativus accessions (Vaz Patto & Rubiales 2009; Vaz Patto et al. 2009). However, in these plant/pathogen interactions the importance of a potential pre-haustorial resistance mechanism with no associated necrosis cannot be dismissed and awaits a more detailed evaluation in the future.

**Lathyrus resistance to powdery mildews**

For powdery mildew little is known about the availability of resistance in the genus Lathyrus and the mechanisms responsible, but a few more reports are available than for rust. Qualitative resistance to E. pisi, characterized by a collapse of sporplings shortly after germination, associated with collapse of the contacted epidermal host cells was reported on L. belinensis and its hybrids with L. odoratus (Poulter et al. 2003). Lathyrus odoratus × L. belinensis hybrid plants, and those produced by backcrossing to L. odoratus were resistant to E. pisi (Poulter et al. 2003). Continued backcrossing resulted in introgressed plants that closely resembled the L. odoratus parent, but segregated for complete resistance/susceptibility to E. pisi, with a ratio of 2.5:1 resistant to susceptible plants, suggesting the presence of a single dominant resistance gene.

Lathyrus sativus lines showing moderate resistance to powdery mildew have been reported in India and Syria (Campbell et al. 1994; Robertson & El-Moneim 1996; Asthana & Dixit 1998), but the disease reactions were not critically studied. Only recently have the L. sativus and L. cicer germplasm with powdery mildew resistance been comprehensively characterized both under field and growth chamber conditions (Vaz Patto et al. 2006a, 2007). Under growth chamber conditions, both species showed in most cases a compatible reaction of high IT with no macroscopically visible hypersensitivity. However, DS varied significantly among accessions and low DS values were far more frequent in L. sativus than in L. cicer (Vaz Patto et al. 2006a, 2007). Partially resistant accessions with reduced DS of high-IT powdery mildew have been identified both under growth chamber and field conditions (Vaz Patto et al. 2006a, 2007); resistance which was expressed in the case of some L. cicer accessions only at the adult plant stage (Vaz Patto et al. 2007).

Incomplete resistance to E. pisi has also been described in P. sativum and in wild relatives (Fondevilla et al. 2007). In some situations it is known that these moderate levels of resistance are controlled by one single recessive gene er1 (Fondevilla & Rubiales 2012). Nevertheless, this er1 gene can also provide complete resistance in some locations and due to its prolonged durability it is widely used in pea breeding programs (Fondevilla et al. 2006). A recent study indicates that resistance provided by er1 is due to a loss of the function of PdMLO1, an MLO (Mildew Resistance Locus O) gene (Hampiry et al. 2011). Other independent genes are known to confer E. pisi resistance in pea. This is the case of the er2 gene that also confers high levels of resistance in some locations, but is ineffective in others. The expression of er2 is influenced by temperature and leaf age (Fondevilla et al. 2006). The Er3 gene was recently identified in Pisum fulvum, conferring complete resistance (Fondevilla et al. 2011).

Mixed disease reactions were much more common on L. sativus than on L. cicer in the case of the powdery mildew inoculation (Vaz Patto et al. 2006a, 2007). As for rust inoculation, if this is due to a certain level
of heterogeneity affecting the polygenic partial resistance, it will be possible for breeders to select plants with higher levels of resistance within these accessions. From these accessions, selected resistant plants were self-pollinated and crossed with susceptible accessions (Vaz Patto et al. 2009, 2006a; Vaz Patto & Rubiales 2009). The obtained progeny will allow the study of the inheritance of this resistance.

CONCLUSIONS

Screening Lathyrus germplasm for disease resistance may result in the discovery of alternative non-hypersensitive, and hopefully more durable, defence mechanisms.

Evidence of physiological specialization in different species, as already confirmed for the legume rusts, suggests that the use of single resistance genes in cultivars is unlikely to result in a durable degree of control (Sillero et al. 2006). Furthermore, both rust and powdery mildew show a quick and effective air dispersal and coexistence of asexual and sexual reproduction cycles being among the pathogens with the highest risk for breaking down the effectiveness of resistance genes (McDonald & Linde 2002). The combination/pyramiding into new varieties of these alternative plant protective mechanisms discovered in the L. sativus and L. cicera germplasm, some of which may impose lower selection pressure due to partial expression, will confront such mutable pathogens with potentially extended durability.

The selected resistant plants were already introduced into crossing schemes and the study of the resistance inheritance is underway. For the selection of the appropriate parental accessions of segregating populations, not only the disease resistance levels but also the genetic distance (Sardinha et al. 2007; Almeida et al. 2009) were taken into consideration to increase the present genetic diversity, facilitating the development of the respective molecular linkage maps. These molecular tools will allow the identification and location of the responsible resistance gene/genes and of associated molecular markers useful for future marker-assisted selection in Lathyrus breeding programs. Additionally, molecular markers linked to E. pisi and U. pisi resistance genes or QTLs are already available in pea, and due to the phylogenetic proximity between P. sativum and L. sativus or L. cicera (Wojciechowski et al. 2004), could potentially be shared for Marker-Assisted Selection (MAS) in Lathyrus. Nevertheless until now, although molecular marker cross amplification studies have been quite successful between these three related species (Almeida et al. 2013), none of the SSR markers associated with pea resistance such as that conferred by erl for E. pisi (Ek et al. 2005) or conferred by the QTL Qruf for U. fabae resistance (Rai et al. 2011) was cross amplifiable to L. sativus or L. cicera (Almeida et al. 2013).

Likewise, once the genes controlling Lathyrus resistance mechanisms have been identified, they can be of great interest not only for accelerating and increasing the efficiency of Lathyrus resistance improvement, but also for Lens and Vicia sp. and especially to the breeding support of phylogenetically close Vavilovia and Pisum more related species (Schafer et al. 2012), increasing the available array of resistance mechanisms to rust and powdery mildew fungi.

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References


Prats E., Rubiales D., Jorrín J. (2002): Acibenzolar-S-methyl-induced resistance to sunflower rust (Puccinia helianthi) is associated with an enhancement of cou-
marins on foliar surface. Physiological Molecular Plant Pathology, 60: 155–162.


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