

Resistance to Rust and Powdery Mildew in *Lathyrus* Crops

MARIA CARLOTA VAZ PATTO¹ and DIEGO RUBIALES²

¹Instituto de Tecnologia Química e Biológica, Universidade NOVA de Lisboa, Oeiras, Portugal;

²Institute for Sustainable Agriculture, Spanish National Research Council (CSIC), Córdoba, Spain

Abstract

VAZ PATTO M.C., RUBIALES D. (2014): **Resistance to rust and powdery mildew in *Lathyrus* crops.** Czech J. Genet. Plant Breed., **50**: 116–122.

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, 2009; 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. cicera*, 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. baeumleri* 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.



Figure 1. Typical rust (red circular pustules) and powdery mildew (white diffuse spots) symptoms on *Lathyrus cicera* (Photo by N. Almeida)

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. ciceri-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. cicera* Iberian germplasms are usually very resistant against *U. viciae-fabae* ex. *V. sativa* and *U. ciceri-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. ciceri-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-

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 germlings 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. viciae-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. viciae-fabae* based on hypersensitive reaction has been recently identified (RUBIALES & SILLERO 2003) and hypersensitive resistance to *U. viciae-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. cicera* accessions to *U. pisi*, but also to *U. ciceris-arietini* and to *U. viciae-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 sporelings 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. cicera* 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. cicera* (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. cicera* 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 (HAMPHRY *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. cicera* 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 polygenetic 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 *er1* 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 (SCHAEFER *et al.* 2012), increasing the available array of resistance mechanisms to rust and powdery mildew fungi.

Acknowledgements. We would like to acknowledge financial support from Integrated Portuguese-Spanish Action, Conselho de Reitores das Universidades Portuguesas, Portugal/Ministerio de Ciencia y Tecnologia, Spain (E-95/04, AGL2011-22524). M.C. Vaz Pato was supported by Fundação para a Ciência e a Tecnologia, Lisboa, Portugal (Research Contracts by the Ciência 2008 program and PTDC/AGR-GPL/103285/2008 project).

References

- ALLKIN R., GOYDER D.J., BISBY F.A., WHITE R.J. (1986): Names and Synonyms of Species and Subspecies in the *Vicieae*. Issue 3. *Vicieae* Database Project. Southampton University, Southampton.
- ALMEIDA N.F., SARDINHA J., SATOVIC Z., RUBIALES D., VAZ PATTO M.C. (2009): Molecular aspects of Iberian grass pea germplasm diversity. In: Proc. 19th Eucarpia Conf. on Genetic Resources Section, Ljubljana, Slovenia, 26.
- ALMEIDA N.F., LEITÃO S.T., CAMINERO C., TORRES A.M., RUBIALES D., VAZ PATTO M.C. (2013): Transferability of molecular markers from major legumes to *Lathyrus* spp. for their application in mapping and diversity studies. *Molecular Biology Reports*, **41**: 269–283.
- ASTHANA A.N., DIXIT G.P. (1998): Utilization of genetic resources in *Lathyrus*. In: MATHUR P.N., RAO V.R., ARORA R.K. (eds): *Lathyrus* Genetic Resources Network. Pro IPGRI-ICARDAICAR Regional Working Group Meeting, New Delhi, India, 64–70.
- ATTANAYAKE R.N., GLAWE D.A., MCPHEE K.E., DUGAN F.M., CHEN, W. (2010): *Erysiphe trifolii* – a newly recognized powdery mildew pathogen of pea. *Plant Pathology*, **59**: 712–720.
- BARILLI E., SILLERO J.C., MORAL A., RUBIALES D. (2009): Characterization of resistance response of pea (*Pisum* sp.) against rust (*Uromyces pisi*). *Plant Breeding*, **128**: 665–670.
- CAMPBELL C.G. (1997): Grass Pea. *Lathyrus sativus* L. Promoting the Conservation and Use of Under-utilized and Neglected Crops. 18. Institute of Plant Genetics and Crop Plant Research. Gatersleben/International Plant Genetic Resources Institute, Rome, Italy.

- CAMPBELL C.G., MEHRA R.B., AGRAWAL S.K., CHEN Y.Z., EL ALI A.M.A., KHAWAJA H.I.T., YADAV C.R., TOY J., ARAYA W.A. (1994): Current status and future strategy in breeding grass pea (*Lathyrus sativus*). *Euphytica*, **73**: 167–175.
- COOK R.T.A., FOX R.T.V. (1992): *Erysiphe pisi* var. *pisii* on faba beans and other legumes in Britain. *Plant Pathology*, **41**: 506–512.
- EK M., EKLUND M., VON POST R., DAYTEG C., HENRIKSSON T., WEIBULL P., CEPTILIS A., ISSAC P., TUVESSON S. (2005): Microsatellite markers for powdery mildew resistance in pea (*Pisum sativum* L.). *Hereditas*, **142**: 86–91.
- EMERAN A.A. (2003): Studies of the genetic resistance and alternative control methods against rust in faba bean. [PhD. Thesis.] Córdoba University, Córdoba, Spain. (in Spanish)
- FARR D.F., ROSSMAN A.Y. (2013): Fungal databases, systematic mycology and microbiology laboratory. ARS, USDA. Available at <http://nt.ars-grin.gov/fungaldatabases/> (accessed June 19, 2013).
- FERNÁNDEZ-APARICIO M., FLORES F., RUBIALES D. (2009): Field response of *Lathyrus cicera* germplasm to crenate broomrape (*Orobanche crenata*). *Field Crops Research*, **113**: 321–327.
- FERNÁNDEZ-APARICIO M., RUBIALES D. (2010): Characterisation of resistance to crenate broomrape (*Orobanche crenata* Forsk.) in *Lathyrus cicera* L. *Euphytica*, **173**: 77–84.
- FERNÁNDEZ-APARICIO M., FLORES F., RUBIALES D. (2012): Escape and true resistance to crenate broomrape (*Orobanche crenata* Forsk.) in grass pea (*Lathyrus sativus* L.) germplasm. *Field Crop Research*, **125**: 92–97.
- FONDEVILLA S., RUBIALES D. (2012): Powdery mildew control in pea. A review. *Agronomy for Sustainable Development*, **32**: 401–409.
- FONDEVILLA S., CARVER T.L.W., MORENO M.T., RUBIALES D. (2006): Macroscopical and histological characterization of genes *er1* and *er2* for powdery mildew resistance in pea. *European Journal of Plant Pathology*, **115**: 309–321.
- FONDEVILLA S., CARVER T. L.W., MORENO M.T., RUBIALES D. (2007): Identification and characterisation of sources of resistance to *Erysiphe pisi* Syd. in *Pisum* spp. *Plant Breeding*, **126**: 113–119.
- FONDEVILLA S., CUBERO J.I., RUBIALES D. (2011): Confirmation that the *Er3* gene, conferring resistance to *Erysiphe pisi* in pea, is a different gene from *er1* and *er2* genes. *Plant Breeding*, **130**: 281–282.
- FONDEVILLA S., CHATTOPADHYAY C., KHARE N., RUBIALES D. (2013): *Erysiphe trifolii* is able to overcome *er1* and *Er3*, but not *er2*, resistance genes in pea. *European Journal of Plant Pathology*, **136**: 557–563.
- HAMPHRY M., REINSTADLER A., IVANOV S., BISSELING T., PANSTRUGA R. (2011): Durable broad spectrum powdery mildew resistance in pea *er1* plants is conferred by natural loss-of-function mutations in *PsMLO1*. *Molecular Plant Pathology*, **12**: 866–878.
- HANBURY C.D., WHITE C.L., MULLAN B.P., SIDDIQUE K.H.M. (2000): A review of the potential of *Lathyrus sativus* L. and *L. cicera* L. grain for use as animal feed. *Animal Feed Technology*, **87**: 1–27.
- HEATH M.C. (1974): Light and electron microscope studies of the interactions of host and nonhost plants with cowpea rust – *Uromyces phaseoli* var. *vignae*. *Physiological Molecular Plant Pathology*, **4**: 403–414.
- JOHNSON L.E.B., BUSHNELL W.R., ZEYEN R.J. (1982): Defense patterns in nonhost higher plant species against two powdery mildew fungi. I. Monocotyledonous species. *Canadian Journal of Botany*, **60**: 1068–1083.
- MADRID E., RUBIALES D., MORAL A., MORENO M.T., MILLÁN T., GIL J., RUBIO J. (2008): Mechanism and molecular markers associated with rust resistance in a chickpea interspecific cross (*Cicer arietinum* L. × *Cicer reticulatum* Lad.). *European Journal of Plant Pathology*, **121**: 43–53.
- MCDONALD B.A., LINDE C. (2002): Pathogen population genetics, evolutionary potential and durable resistance. *Annual Review of Phytopathology*, **40**: 349–79.
- MENDGEN K. (1978): Attachment of bean rust cell wall material to host and non-host plant tissue. *Archives of Microbiology*, **119**: 113–117.
- MMBAGA M.T., STEADMAN J.R., ROBERTS J.J. (1994): Interaction of bean leaf pubescence with rust urediniospore deposition and subsequent infection density. *Annals of Applied Biology*, **125**: 243–254.
- NIKS R.E. (1986): Variation of germling morphology between species and *formae speciales* of rust fungi of cereals and grasses. *Canadian Journal of Botany*, **64**: 2976–2983.
- NIKS R.E. (1990): Effect of germ tube length on the fate of sporelings of *Puccinia hordei* in susceptible and resistant barley. *Phytopathology*, **80**: 57–60.
- NIKS R.E., RUBIALES D. (2002): Detection of potentially durable resistance mechanisms in plants to specialised fungal pathogens. *Euphytica*, **124**: 201–216.
- ONDŘEJ M., DOSTÁLOVÁ R., ODSTRČILOVÁ L. (2005): Response of *Pisum sativum* germplasm resistant to *Erysiphe pisi* to inoculation with *Erysiphe baeumleri*, a new pathogen of peas. *Plant Protection Science*, **41**: 95–103.
- PANSTRUGA R. (2003): Establishing compatibility between plants and obligate biotrophic pathogens. *Current Opinion in Plant Biology*, **6**: 320–326.
- PARLEVLIET J.E. (1979): The co-evolution of host-parasite systems. In: HEDBERG I. (ed.): *Proc. Symp. Parasites as Plant Taxonomists. Symbolae Botanicae Upsalienses*, **22**: 39–45.
- PEÑA-CHOCARRO L., ZAPATA PEÑA L. (1999): History and traditional cultivation of *Lathyrus sativus* L. and *Lathyrus cicera* L. in the Iberian Peninsula. *Vegetation History and Archaeobotany*, **8**: 49–52.
- POULTER R., HARVEY L., BURRITT D.J. (2003): Qualitative resistance to powdery mildew in hybrid sweet peas. *Euphytica*, **133**: 349–358.
- 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.
- PRATS E., LLAMAS M.J., JORRÍN J., RUBIALES D. (2007): Constitutive coumarin accumulation on sunflower leaf surface prevents rust germ tube growth and appressorium differentiation. *Crop Science*, **47**: 1119–1124.
- RAI R., SINGH A.K., SINGH B.D., JOSHI A.K., CHAND R., SRIVASTAVA C.P. (2011): Molecular mapping for resistance to pea rust caused by *Uromyces fabae* (Pers.) de-Bary. *Theoretical and Applied Genetics*, **123**: 803–813.
- ROBERTSON J.R., ABD EL-MONEIM A.M. (1996): *Lathyrus* Germplasm Collection, Conservation and Utilization for Crop Improvement at ICARDA. In: ARORA R.K., MATHUR P.N., RILEY K.W., ADHAM Y. (eds): Proc. Regional Workshop *Lathyrus* Genetic Resources in Asia. Indira Gandhi Agricultural University, Raipur, IPGRI, Office for South Asia, New Delhi, India, 97–111.
- RUBIALES D., NIKS R.E. (1995): Characterization of *Lr34*, a major gene conferring nonhypersensitive resistance to wheat leaf rust. *Plant Disease*, **79**: 1208–1212.
- RUBIALES D., SILLERO J.C. (2003): *Uromyces viciae-fabae* haustorium formation in susceptible and resistant faba bean lines. *European Journal of Plant Pathology*, **109**: 71–73.
- RUBIALES D., MORAL A. (2004): Prehaustorial resistance against alfalfa rust (*Uromyces striatus*) in *Medicago truncatula*. *European Journal of Plant Pathology*, **110**: 239–243.
- RUBIALES D., CASTILLEJO M.A., MADRID E., BARILLI E., RISPAIL N. (2011): Legume breeding for rust resistance: lessons to learn from the model *Medicago truncatula*. *Euphytica*, **180**: 89–98.
- RUBIALES D., ROJAS-MOLINA M.M., SILLERO J.C. (2013a): Identification of pre and posthaustorial resistance to rust (*Uromyces viciae-fabae*) in lentil (*Lens culinaris*) germplasm. *Plant Breeding*, **132**: 676–680.
- RUBIALES D., SILLERO J.C., EMERAN A.A. (2013b): Response of vetches (*Vicia* spp.) to specialized forms of *Uromyces viciae-fabae* and to *Uromyces pisi*. *Crop Protection*, **46**: 38–43.
- SARDINHA J., ALMEIDA N., VAZ PATTO M.C. (2007): Molecular characterization of *Lathyrus sativus* using AFLP markers. In: Proc. 6th European Conf. Grain Legumes. Lisbon, Portugal, 131.
- SCHAEFER H., HECHENLEITNER P., SANTOS-GUERRA A., SEQUEIRA M.M.D., PENNINGTON R.T., KENICER G., CARINE M.A. (2012): Systematics, biogeography, and character evolution of the legume tribe *Fabeae* with special focus on the middle-Atlantic island lineages. *BMC Evolutionary Biology*, **12**: 250.
- SILLERO J.C., RUBIALES D. (2002): Histological characterization of the resistance of faba bean to faba bean rust. *Phytopathology*, **92**: 294–299.
- SILLERO J.C., FONDEVILLA S., DAVIDSON J., VAZ PATTO M.C., WARKENTIN T., THOMAS J., RUBIALES D. (2006): Screening techniques and sources of resistance to rusts and mildews in grain legumes. *Euphytica*, **147**: 255–272.
- SINGH S.P., SCHWARTZ H.F. (2010): Breeding common bean for resistance to diseases: A review. *Crop Science*, **50**: 2199–2223.
- SKIBA B., FORD R., PANG E.C.K. (2004): Genetics of resistance to *Mycosphaerella pinodes* in *Lathyrus sativus*. *Australian Journal of Agricultural Research*, **55**: 953–960.
- VAZ PATTO M.C., RUBIALES D. (2009): Identification and characterization of partial resistance to rust in a germplasm collection of *Lathyrus sativus*. *Plant Breeding*, **128**: 495–500.
- VAZ PATTO M.C., FERNÁNDEZ-APARICIO M., MORAL A., RUBIALES D. (2006a): Characterization of resistance to powdery mildew (*Erysiphe pisi*) in a germplasm collection of *Lathyrus sativus*. *Plant Breeding*, **125**: 308–310.
- VAZ PATTO M.C., SKIBA B., PANG E.C.K., OCHATT S.J., LAMBEIN F., RUBIALES D. (2006b): *Lathyrus* improvement for resistance against biotic and abiotic stresses: from classical breeding to marker assisted selection. *Euphytica*, **147**: 133–147.
- VAZ PATTO M.C., FERNÁNDEZ-APARICIO M., MORAL A., RUBIALES D. (2007): Resistance reaction to powdery mildew (*Erysiphe pisi*) in a germplasm collection of *Lathyrus cicera* from Iberian origin. *Genetic Resources and Crop Evolution*, **54**: 1517–1521.
- VAZ PATTO M.C., FERNÁNDEZ-APARICIO M., MORAL A., RUBIALES D. (2009): Pre and posthaustorial resistance to rusts in *Lathyrus cicera*. *Euphytica*, **165**: 27–34.
- VAZ PATTO M.C., HANBURY C.D., VAN MOORHEM M., LAMBEIN F., OCHATT S., RUBIALES D. (2011): Grass Pea. In: PEREZ DE LA VEGA M., CUBERO J.L., TORRES A.M. (eds): Genetics, Genomics and Breeding of Cool Season Grain Legumes. CRC Press, Boca Raton, Science Publishers, Enfield, 151–204.
- WOJCIECHOWSKI M., LAVIN M., SANDERSON M.J. (2004): A phylogeny of legumes (*Leguminosae*) based on analysis of the plastid *matK* gene resolves many well-supported subclades within the family. *American Journal of Botany*, **91**: 1846–1862.
- WYNN W.K. (1976): Appressorial formation over stomates by bean rust: Response to a surface contact stimulus. *Phytopathology*, **66**: 136–146.
- WYNN W.K., STAPLES R.C. (1981): Tropisms of fungi in host recognition. In: STAPLES R.C., TOENNIENSEN G.H. (eds): Plant Disease Control: Resistance and susceptibility. Wiley Interscience, New York, 45–69.

Received for publication June 20, 2013

Accepted after corrections November 27, 2013

Corresponding author:

Dr. MARIA CARLOTA VAZ PATTO, Ph.D., Universidade NOVA de Lisboa, Instituto de Tecnologia Química e Biológica, Apt. 127, 2781-901 Oeiras, Portugal; e-mail: cpatto@itqb.unl.pt
