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Reaction of genotypes from several species of grain and forage legumes to infection with a French pea isolate of the oomycete *Aphanomyces euteiches*

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Abstract The susceptibility/resistance to *Aphanomyces euteiches* of various genotypes (cultivars and breeding lines) of several grain legume species was assessed in controlled conditions. A total of 279 genotypes from the major grain legumes grown in temperate climates (faba bean, chickpea, lentil, lupin and common vetch) and three other legumes frequently cultivated in France (French bean, clover and alfalfa) were screened with one pea-infecting isolate from France. Four different categories of susceptibility/resistance were identified among the legume species/cultivars tested with the pea *A. euteiches* isolate: (1) susceptible legume species (lentil, alfalfa, French bean) among which low levels of partial resistance was observed; (2) legume species including susceptible genotypes and genotypes with high levels of resistance (common vetch, faba bean and clover), (3) species with a very high level of resistance (chickpea) and (4) species displaying no symptoms (lupin). It is therefore important to consider pathogen-species and pathogen-genotype interactions when defining the host specificity of *A. euteiches* and considering the possible role of different legume species in increasing or decreasing the soil inoculum potential.

Keywords Specific resistance · Partial resistance · Cool season grain legumes · Host specificity

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Introduction

Aphanomyces root rot of pea was first described in the 1920s (Jones and Dreschler 1925) in Wisconsin, USA, where peas have been grown intensively since 1889. This new disease, mostly observed during mild, wet seasons, was subsequently detected in other parts of the USA (Papavizas and Ayers 1974) and in other parts of the world, on peas and other legumes: North America (Basu et al. 1973), Australia (Allen et al. 1987), New Zealand (Manning and Menzies 1980), Asia (Yokosawa et al. 1974) and Europe (Persson et al. 1997).

Aphanomyces root rot is considered to be the most damaging root disease of pea crops in France. It was first identified in France, by Labrousse (1933), but the first major losses due to this disease were not observed until 1993 (Didelot et al. 1994), following an intensification of spring pea cropping in the 1980s. The disease was initially detected in the Parisian Basin and has since gradually spread to other regions of pea production. Aphanomyces root rot may cause major yield losses in conditions favourable for the disease (yield losses may reach 100% on some plots

in France) and is now considered the major factor limiting pea cultivation. Resistance to this disease has been studied in pea for several years, but no resistant cultivars are yet available (Pilet et al. 2005; Tivoli et al. 2006; Moussart et al. 2007). The only control measure currently available consists of soil assessment and avoiding infested fields (Moussart et al. 2006). Other legumes, such as faba bean, are often cultivated in fields infested with *A. euteiches* and possible rotations involving several different legume species have been described (Levenfors et al. 2003).

Aphanomyces euteiches has been isolated from a number of legume species: pea (Wicker et al. 2001; Levenfors et al. 2003), faba bean (Salt and Delaney 1985; Lamari and Bernier 1985), vetch (Levenfors et al. 2003), lentil (Lamari and Bernier 1985), alfafa (Malvick et al. 1998), French bean (Salt and Delanay 1985), red clover (Tofte and Smith 1992), subterranean clover (Greenhalgh et al. 1985), barrel medic (Moussart et al. 2007) and several other plants (Chan and Close 1987). Isolates from different species may display some specificity for the species from which they were isolated. Levenfors et al. (2003) identified populations of pea-specific and vetch-specific *A. euteiches* isolates. Malvick and Percich (1999) also showed that alfalfa isolates were highly pathogenic on alfalfa and very weakly pathogenic on pea.

On pea, Wicker and Rouxel (2001) have described two main pathotypes: pathotype I, present in France, European countries and USA, and pathotype III, observed only among American isolates.

Wicker et al. (2001) showed that French isolates originating from pea were also virulent on common vetch, alfalfa, broad been and green bean, in climate chamber experiments. However, no other legumes than pea have been found to carry Aphanomyces infection in field conditions. Therefore, it is unknown whether *A. euteiches* can propagate on other legumes than pea in the crop rotation.

Salt and Delanay (1985) showed that *A. euteiches* could only be isolated from pea and faba bean on the field soils of Rothamsted in the UK. Furthermore, they identified two biological races under controlled conditions: (1) pea isolates which caused severe root rot in pea but not in faba bean, and (2) faba bean isolates which were not pathogenic to pea. Levenfors et al. (2003) also reported that 46 isolates obtained from pea were pathogenic only on pea. About 50% of these isolates induced symptoms on green bean and faba bean, but these symptoms remained below the threshold defining pathogenicity. In pathogenicity tests, authors observed oospores of *A. euteiches* in the root tissues of pea, common vetch, alfalfa, green bean, broad bean, red clover and yellow sweet clover.

Until now, in most studies that focused on the host range of *A. euteiches* at plant species level, only one cultivar was tested per species. Levenfors et al. (2003) used a single cultivar from each species to determine whether *A. euteiches* could infect a given species. Similarly, Malvick et al. (1998) studied the pathogenicity of 62 strains of *A. euteiches* on three cultivars of pea and only one cultivar each of French bean, alfalfa and red clover. Conversely, Lamari and Bernier (1985) investigated whether isolates obtained from faba bean in the field could induce symptoms on different cultivars of several legumes: alfalfa, faba bean, lentil, pea and French bean. They found differences in resistance/susceptibility between the various cultivars studied. For example, in naturally infested faba bean fields, two cultivars were found to be mildly infected, two were moderately infected and three were severely infected. One cultivar of garden pea was found to be mildly infected, two were moderately infected and two were severely infected. These observations suggest that there may be differences between the genotypes or lines of each grain legume and that the choice of cultivar may therefore affect the conclusions drawn about the ability of an isolate to infect a given legume species.

Several studies have screened pea (Malvick and Percich 1999; Wicker et al. 2003; Pilet-Nayel personal communication) and barrel medic (*Medicago truncatula*; Moussart et al. 2007) genotypes for resistance to pea *A. euteiches* isolates. Several isolates were tested against a large pea genotype collection, but only a low level of partial resistance was found in a few genotypes. Conversely, several genotypes of barrel medic responded as highly resistant to one pea isolate. In other studies, alfalfa genotypes were screened for resistance to races 1 and 2 of *A. euteiches* isolated from alfalfa (Vandemark and Grünwald 2004). Allen et al. (1987) screened 11 French bean (*Phaseolus vulgaris*) genotypes in glasshouses, in naturally infested soil. They found that nine genotypes were susceptible and two were resistant.

In infested fields, replacing pea by another legume crop may have deleterious effects if the replacement species serves as a host for this pathogen and/or if the

grower uses a susceptible cultivar. Such replacement has given good results so far, because *Aphanomyces* root rot has not been observed in France on other legumes under field conditions. As we have mentioned above, in published studies usually a large number of isolates were tested on a restricted number of legume species and/or genotypes. Thus, further studies are required to determine, on a large range of legume species and genotypes, inter- and intraspecific variability for resistance to *A. euteiches*. The aim of this study was, therefore, to assess the susceptibility/resistance of different cultivars and/or lines of several grain legume species grown in temperate climates, to one isolate of *A. euteiches* representative of French isolates belonging to pathotype I (Wicker et al. 2001).

Materials and methods

Plant material

We studied the reaction to infection, using a pea isolate of *A. euteiches*, of several genotypes of eight legumes species: faba bean (*Vicia faba*), chickpea

Table 1 Reaction of lentil (*Lens culinaris*) genotypes to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Pisum sativum[b]				
Baccara	France	4.6±0.4 a	4.6±0.3 abcd	4.6±0.0 a
PI180693	Germany	3.8±0.1 ab	3.8±0.2 e	3.8±0.0 b
Lens culinaris				
Rosana	France	4.5±0.3 a	4.7±0.2 abcd	4.6±0.1 a
CFL186	Italy	4.3±0.5 ab	4.8±0.2 ab	4.6±0.3 a
Blondette	France	4.2±0.6 ab	4.9±0.1 a	4.5±0.5 a
Naslada	Spain	4.4±0.3 a	4.6±0.3 abcd	4.5±0.2 a
CFL82	Greece	4.2±0.1 ab	4.8±0.1 ab	4.5±0.5 a
Yoyette	France	4.4±0.3 a	4.5±0.2 abcd	4.5±0.0 a
CFL138.1	Turkey	4.4±0.4 a	4.5±0.3 abcd	4.5±0.4 a
Dora	Spain	4.2±0.4 ab	4.7±0.2 abc	4.5±0.0 a
Nigrican	Spain	4.2±0.2 ab	4.7±0.1 abcd	4.5±0.3 a
CFL41.2	Balkan	4.2±0.4 ab	4.7±0.3 abcd	4.4±0.3 a
Rose	France	4.2±0.4 ab	4.6±0.0 abcd	4.4±0.3 ab
CFL136	Greece	4.3±0.1 ab	4.4±0.2 abcd	4.4±0.1 ab
CFL183	Algeria	4.3±0.2 ab	4.4±0.3 abcd	4.4±0.0 ab
CFL188	Sicily	4.0±0.4 ab	4.7±0.1 abcd	4.3±0.5 ab
Flora	France	4.0±0.2 ab	4.6±0.2 abcd	4.3±0.4 ab
CFL88.1	Afghanistan	4.3±0.1 ab	4.2±0.2 bcde	4.3±0.1 ab
CFL143	Chile	3.9±0.3 ab	4.7±0.3 abcd	4.3±0.6 ab
Cilaos	Reunion	4.2±0.2 ab	4.4±0.3 abcd	4.3±0.1 ab
CFL115	India	4.0±0.0 ab	4.5±0.1 abcd	4.3±0.3 ab
Anicia	France	4.2±0.4 ab	4.3±0.3 abcde	4.2±0.1 ab
CFL79	Greece	4.2±0.2 ab	4.3±0.4 abcde	4.2±0.1 ab
CFL21	Yemen	3.9±0.2 ab	4.5±0.1 abcd	4.2±0.5 ab
CFL242	URSS	4.2±0.2 ab	4.2±0.1 cde	4.2±0.0 ab
Santa	France	4.2±0.2 ab	4.1±0.1 de	4.2±0.0 ab
CFL124.1	Afghanistan	4.1±0.1 ab	4.2±0.1 bcde	4.2±0.1 ab
CFL236	URSS	4.0±0.1 ab	4.2±0.1 bcde	4.1±0.1 ab
CFL233	Argentina	3.8±0.3 ab	4.3±0.4 bcde	4.0±0.3 ab
CFL137	Greece	3.5±0.2 b	4.5±0.2 abcd	4.0±0.7 ab

[a] For each experiment, data are means and standard deviation of four replicates. Five plants were tested in each replicate. Plants were evaluated on a 0–5 scale. Mean values followed by the same letter are not significantly different (Newman–Keuls test $P=0.05$)

[b] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

Table 2 Reaction of alfalfa (*Medicago sativa*) genotypes to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Pisum sativum[b]				
Baccara	France	4.6±0.3 a	4.7±0.1 a	4.6±0.1 a
PI180693	Germany	3.8±0.2 abcd	4.0±0.0 ab	3.9±0.1 ab
Medicago sativa				
Anick[c] (2×)	Canadian cultivar	4.1±0.1 abcd	4.6±0.3 a	4.3±0.3 ab
Villamayor (4×)	Wild Spanish ecotype	4.1±0.2 abcd	4.5±0.2 a	4.3±0.3 ab
Krasnokutskaya[c] (4×)	Ukrainian cultivar	4.3±0.4 abc	4.4±0.4 a	4.3±0.1 ab
Pancrudo (4×)	Wild Spanish ecotype	3.8±0.2 abcd	4.7±0.4 a	4.2±0.6 ab
Maron[c] (4×)	Wild French ecotype	4.4±0.2 ab	3.9±0.5 b	4.2±0.3 ab
Coussouls (4×)	French cultivar	4.0±0.2 abcd	4.1±0.6 ab	4.1±0.0 ab
M. coerulea (2×)	Wild Ukranian ecotype	3.8±0.1 abcd	4.2±0.4 ab	4.0±0.3 ab
Pool 5 (4×)	Pool of landraces of Morocco	4.0±0.2 abcd	4.0±0.0 ab	4.0±0.0 ab
Aragon (4×)	Spanish cultivar	4.0±0.4 abcd	4.0±0.4 ab	4.0±0.0 ab
Mercedes (4×)	French cultivar	4.0±0.2 abcd	3.9±0.5 ab	4.0±0.1 ab
Luzelle (4×)	French cultivar	3.7±0.2 abcd	4.2±0.2 a	4.0±0.3 ab
Flamande (4×)	Landrace from north of France	3.7±0.2 abcd	4.1±0.2 ab	3.9±0.2 ab
Gabes (4×)	Landrace from south of Tunisia	3.9±0.5 abcd	3.9±0.3 ab	3.9±0.0 ab
Provence (4×)	Landrace from south of France	3.7±0.3 abcd	4.1±0.6 ab	3.9±0.2 ab
Comete (4×)	French cultivar	3.6±0.2 bcd	4.1±0.2 ab	3.8±0.3 ab
Zenith (4×)	French cultivar	3.7±0.2 abcd	4.0±0.2 ab	3.8±0.3 bc
Alfagraze (4×)	US cultivar	3.5±0.8 bcd	4.1±0.2 ab	3.8±0.4 bc
Europe (4×)	French cultivar	3.4±0.3 bcd	4.0±0.4 ab	3.7±0.4 bc
Marais de Luçon (4×)	Landrace from west of France	3.6±0.4 abcd	3.8±0.3 ab	3.7±0.1 bc
WL 514 (4×)	US cultivar	3.4±0.2 cd	4.1±0.7 ab	3.7±0.5 bc
Barmed (4×)	French cultivar	3.7±0.3 abcd	3.7±0.4 ab	3.7±0.0 bc
Lodi (4×)	Italian cultivar	3.7±0.1 abcd	3.7±0.2 ab	3.7±0.0 bc
Natsuwakaba (4×)	Japanese cultivar	3.6±0.3 abcd	3.7±0.5 ab	3.7±0.0 bc
Crioula (4×)	Brasilian cultivar	3.2±0.3 d	4.0±0.2 ab	3.6±0.5 bc
Malzeville[c] (4×)	Wild French ecotype	3.2±1.0 d	3.1±1.2 b	3.1±0.1 c

[a] For each experiment, data are means and standard deviation of four replicates. Five plants were tested in each replicate. Plants were evaluated on a 0–5 scale. Mean values followed by the same letter are not significantly different (Newman–Keuls test $P=0.05$)

[b] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

[c] *Medicago sativa* ssp. *falcata*

(*Cicer arienatum*), lentil (*Lens culinaris*), lupin (*Lupinus alba*), common vetch (*Vicia sativa*), French bean (*Phaseolus vulgaris*), clover (*Trifolium repens* and *T. pratense*) and alfalfa (*Medicago sativa*). The genotypes tested were chosen to represent the geographic and genetic diversity available in the collections. As faba bean and lupin are widely grown in France, cultivars from the French and European lists were also assessed. The faba bean, alfalfa and clover collections were provided by INRA Dijon (Mr Marget and Mrs Raffiot) and Lusignan (Dr Julier and Dr Huygue). The chickpea collection was provided by INRAT Tunis, Tunisia (Dr Kharrat). Lentil, French bean, lupin and common vetch collections were provided by several groups of breeders.

We used two pea (*Pisum sativum*) genotypes – Baccara and PI180693 (USDA Plant Introduction Station, Pullman, USA), susceptible and resistant to *A. euteiches* (Wicker et al. 2003), respectively – as controls for comparisons of resistance in pea and other legumes.

Plant inoculation and disease assessment

We used a modified version of the standardized test developed for evaluating pea resistance to *A.*

euteiches (Moussart et al. 2001). Seeds were sown in 500 ml plastic pots containing unsterilised vermiculite (VERMEX, M). Faba bean seeds were soaked in water for 24 h at 25°C in the dark before sowing. We sowed five seeds of lentil, alfalfa, common vetch and clover and four seeds of French bean, faba bean, chickpea and lupin per pot. Each pot constituted a replicate and there were four replicates per genotype. Pots were arranged in a completely randomised design in a controlled environment chamber, under constant conditions (thermoperiod: 25/23°C and 16 h photoperiod).

Seven days after sowing, legume and pea control seedlings were inoculated with a suspension of zoospores from a French strain of *A. euteiches* (RB84). This strain is very aggressive on pea and belongs to the main virulence group present in France (Wicker and Rouxel 2001). Under favourable climatic conditions, this isolate is also able to infect other

Table 3 Reaction of French bean (*Phaseolus vulgaris*) genotypes to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Pisum sativum[b]				
Baccara	France	4.9±0.2 a	4.8±0.0 a	4.8±0.0 a
PI180693	Germany	4.0±0.0 ab	4.0±0.0 ab	4.0±0.0 b
Phaseolus vulgaris				
Kerprim	French list	4.0±0.0 ab	4.0±0.0 b	4.0±0.0 b
Linex	French list	4.0±0.0 ab	3.9±0.1 b	4.0±0.0 b
Pation	French list	4.0±0.0 ab	3.8±0.2 b	3.9±0.1 bc
Safran	French list	3.8±0.1 b	4.0±0.0 b	3.9±0.1 bc
Cocobel	French list	4.0±0.0 ab	3.8±0.4 b	3.9±0.1 bc
Diego	French list	3.9±0.1 b	3.9±0.2 b	3.9±0.0 bc
Booster	French list	3.6±0.1 bc	4.0±0.2 b	3.8±0.1 bc
Saint esprit à œil rouge	French list	3.6±0.2 bc	4.0±0.0 b	3.8±0.3 bc
Antare	French list	3.6±0.4 bc	4.0±0.0 b	3.8±0.3 bc
Rognon de Pont L'Abbé	French list	3.5±0.5 bcd	4.0±0.0 b	3.7±0.3 bcd
Angers	French list	3.4±0.1 bcde	3.9±0.2 b	3.6±0.3 bcde
Lannion	French list	3.2±0.5 bcde	3.9±0.1 b	3.6±0.5 bcde
Triomphe de Farcy	French list	3.3±0.5 bcde	3.7±0.4 b	3.5±0.2 bcdef
Flagrand	French list	3.3±0.4 bcde	3.5±0.1 b	3.4±0.1 bcdefg
Stop	French list	4.0±0.0 ab	2.6±0.6 c	3.3±0.9 bcdefg
Coco jaune de la Chine	French list	3.8±0.2 b	2.6±0.3 c	3.2±0.9 bcdefgh
Lingot	French list	3.4±0.4 bcd	2.7±0.9 c	3.1±0.5 cdefghi
Rigalex	French list	3.4±0.3 bcd	2.7±0.7 c	3.1±0.5 cdefghi
Elsa	French list	3.4±0.3 bcde	2.7±0.7 c	3.0±0.5 cdefghi
Blondor	French list	3.7±0.4 bc	2.3±0.4 cd	3.0±0.9 cdefghi
Aramis	French list	3.3±0.3 bcde	2.7±0.7 c	3.0±0.4 cdefghi
Efesto	French list	3.6±0.3 bc	2.2±0.3 cd	2.9±0.9 defghij
Michelet à longues cosses	French list	3.1±0.1 bcde	2.6±0.4 c	2.8±0.1 efghijk
Fin de Bagnols	French list	3.1±0.5 bcde	2.3±0.2 cd	2.7±0.6 fghijkl
Calypso	French list	3.8±0.2 bcde	2.6±0.5 c	2.7±0.2 fghijkl
Castandel	French list	3.1±0.5 bcde	2.2±0.5 cd	2.6±0.6 ghijkl
Paloma	French list	2.7±0.3 bcde	2.1±0.2 cd	2.4±0.5 hijkl
Aiguillon	French list	2.5±0.7 cde	1.9±0.1 cd	2.2±0.4 ijkl
Fructidor	French list	2.4±0.4 de	2.0±0.0 cd	2.2±0.3 jkl
Miramont	French list	2.4±0.4 de	1.7±0.9 d	2.1±0.4 kl
Coco nain blanc précoce	French list	2.2±0.2 e	1.7±0.5 d	2.0±0.3 l

[a] For each experiment, data are means and standard deviation of four replicates. Four plants were tested in each replicate. Plants were evaluated on a 0–5 scale. Mean values followed by the same letter are not significantly different (Newman–Keuls test $P=0.05$)

[b] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

legume species such as common vetch, alfalfa, broad bean and green bean (Wicker et al. 2001). Zoospores were produced as previously described (Moussart et al. 2001). Seedlings were inoculated by applying 5 ml of inoculum suspension per plant (2.5×10^4 zoospores per plant). Preliminary studies with several zoospore concentrations showed the application of 2.5×10^4 zoospores per plant to be optimal for the observation of disease on several legumes. The vermiculite was saturated with water after inoculation, to favour disease development. In these conditions very favourable to the disease, plants were assessed 10 days after inoculation. Disease index (DI) was assessed visually, according to the following 0 to 5 scale: 0=no symptoms; 1=traces of discolouration on the roots (<25%); 2=discolouration of 25 to 50% of the roots; 3=discolouration of 50 to 75% of the roots; 4=discolouration of >75% of the roots; 5=plant dead. For each legume species, symptoms were described, oospore formation was observed in the diseased root tissues (under the microscope at ×20 magnification) and the oomycete was isolated using a semi-selective medium (MBR; Malvick et al. 1994). Two experiments were performed for each legume species. At the zoospore concentration used, the DIs of all the lentil and alfalfa genotypes were between 4 and 5 (results not shown). For these two species, a second experiment was carried out with the lower zoospore

Table 4 Reaction of common vetch (*Vicia sativa*) genotypes to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Pisum sativum[b]				
Baccara	France	5.0±0.0 a	4.4±0.1 a	4.7±0.3 a
PI180693	Germany	4.0±0.0 b	4.0±0.0 ab	4.0±0.0 b
Vicia sativa				
L9	Chili	4.0±0.0 b	4.0±0.0 ab	4.0±0.0 b
L10	breeding line	4.0±0.0 b	4.0±0.0 ab	4.0±0.0 b
L11	breeding line	4.0±0.0 b	4.0±0.0 ab	4.0±0.0 b
Safran	France	3.9±0.1 b	3.8±0.2 ab	3.9±0.1 b
Amethyste	France	3.8±0.3 c	3.9±0.1 ab	3.9±0.1 b
L1	breeding line	3.3±0.4 c	3.7±0.3 b	3.5±0.3 b
L3	breeding line	3.0±0.0 cd	3.9±0.2 ab	3.4±0.6 b
Granit	France	3.6±0.1 b	3.2±0.5 c	3.4±0.3 b
Cristal	France	3.0±0.3 cd	2.7±0.2 cde	2.8±0.2 c
Opale	France	2.5±0.4 e	2.8±0.2 cd	2.7±0.2 c
Candy	France	2.6±0.3 de	2.7±0.3 cde	2.7±0.1 c
Spinelle	France	2.8±0.2 de	2.3±0.2 de	2.6±0.3 c
Jade	France	2.9±0.5 de	2.2±0.2 e	2.5±0.5 c
L2	breeding line	1.7±0.2 f	1.4±0.1 f	1.6±0.2 d
Platine	France	1.1±0.1 g	1.3±0.3 f	1.2±0.2 e
L6	France	0.8±0.2 gh	1.0±0.0 fg	0.9±0.1 e
Marine	France	0.5±0.5 hij	1.2±0.9 f	0.8±0.5 e
Pepite	France	0.6±0.1 i	0.9±0.3 fgh	0.7±0.2 e
Malachite	France	0.0±0.0 i	0.5±0.2 ghi	0.3±0.4 f
L7	France	0.0±0.0 i	0.5±0.4 ghi	0.3±0.4 f
Corail	France	0.0±0.0 i	0.4±0.2 hi	0.2±0.2 f
Catarina	France	0.1±0.1 i	0.2±0.2 i	0.1±0.1 f
L4	breeding line	0.0±0.0 j	0.2±0.3 i	0.1±0.2 f
Caravelle	France	0.0±0.0 i	0.1±0.2 i	0.1±0.0 f
L5	breeding line	0.0±0.0 i	0.1±0.1 i	0.0±0.0 f
Topaze	France	0.0±0.0 i	0.0±0.0 i	0.0±0.0 f

[a] For each experiment, data are means and standard deviation of four replicates. Five plants were tested in each replicate. Plants were evaluated on a 0–5 scale. Mean values followed by the same letter are not significantly different (Newman–Keuls test $P=0.05$)

[b] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

Table 5 Reaction of faba bean (*Vicia faba*) genotypes to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Pisum sativum[b]				
Baccara	France	4.9±0.1 a	4.6±0.2 a	4.8±0.3 a
PI180693	Germany	3.9±0.0 c	3.9±0.1 ab	3.9±0.0 b
Vicia faba				
Di-340	Sudan	4.2±0.6 b	3.7±0.5 b	4.0±0.3 b
Di-1653	Spain	3.3±1.2 d	3.1±0.4 bc	3.2±0.2 c
Baraca	Spain	2.6±0.8 e	3.2±0.7 bc	2.9±0.4 cd
Alameda	Spain	2.2±0.7 f	2.5±0.5 cde	2.3±0.2 de
Di-713	Maroc	2.1±0.5 fg	2.0±1.1 def	2.0±0.1 ef
Salsa	France	1.8±0.2 g	1.9±0.1 defgh	1.8±0.1 efg
Di-281	France	1.7±0.2 gh	1.8±0.2 defghi	1.8±0.0 efg
Castel	France	1.3±0.3 hi	1.8±0.5 defghi	1.6±0.3 fgh
Albus	Czech Republic	0.9±0.2 ijklmnop	2.0±0.6 defg	1.4±0.7 fghi
Merkur	Czech Republic	1.2±0.4 ijkl	1.5±0.4 efghij	1.4±0.2 fghij
Di-2305	Spain	1.4±0.1 hi	1.1±0.2 fghijk	1.3±0.2 ghijk
Irena	France	1.4±0.4 hi	1.1±0.2 fghijk	1.2±0.2 ghijkl
Lobo	Germany	1.3±0.4 ij	1.1±0.1 fghijk	1.2±0.1 ghijklm
Di-315	Ethiopia	1.2±0.9 ijk	1.2±0.6 fghijk	1.2±0.0 ghijklm
Di-1460	Yemen	1.1±0.1 ijklm	–	1.1 ghijklmn
Di-2405	Estonia	0.9±0.1 ijklmno	1.0±0.3 fghijk	1.0±0.1 hijklmn
Valeria	Austria	1.0±0.7 ijklmn	0.9±0.7 fghijk	0.9±0.1 hijklmn
Di-2384	Austria	0.8±1.1 jklmnopq	1.0±0.5 fghijk	0.9±0.2 hijklmn
Nile	Netherlands	1.0±0.0 ijklmn	0.8±0.2 fghijk	0.9±0.1 hijklmn
Di-34	India	0.7±0.4 klmnopqr	1.1±0.2 fghijk	0.9±0.2 hijklmn
Victoria	France	0.6±0.6 klmnopqrs	1.0±0.3 fghijk	0.8±0.2 hijklmn
Gloria	Austria	1.0±0.8 ijklmn	0.6±0.4 hijk	0.8±0.3 hijklmn
Mistral	Czech Republic	0.7±0.3 klmnopqrs	0.9±0.6 fghijk	0.8±0.1 hijklmn
Fribo	Germany	0.7±0.2 klmnopqr	0.8±0.4 fghijk	0.8±0.0 hijklmn
Divine	France	0.8±0.6 klmnopq	0.7±0.6 fghijk	0.7±0.1 hijklmn
Dixie	France	0.5±0.5 mnopqrs	1.0±0.3 fghijk	0.7±0.3 hijklmn
Hiverna	Germany	0.6±0.6 klmnopqrs	0.8±0.2 fghijk	0.7±0.1 hijklmn
Fuego	Germany	0.6±0.3 lmnopqrs	0.8±0.2 fghijk	0.7±0.2 ijklmn
Tyrol	Germany	0.6±0.4 lmnopqrs	0.8±0.3 fghijk	0.7±0.2 ijklmn
Louxor	Denmark	0.5±0.2 mnopqrs	0.9±0.5 fghijk	0.7±0.3 ijklmn
Di-2310	Austria	0.7±0.2 klmnopqr	0.6±0.3 hijk	0.7±0.1 ijklmn
Di-277	France	0.7±0.3 klmnopqr	0.6±0.1 hijk	0.6±0.1 ijklmn
Di-131	USSR	0.6±0.5 lmnopqrs	0.7±0.5 fghijk	0.6±0.1 ijklmn
Marcel	France	0.5±0.3 mnopqrs	0.8±0.6 fghijk	0.6±0.2 ijklmn
Di-389	China	0.4±0.2 nopqrs	0.9±0.1 fghijk	0.6±0.3 ijklmn
Di-2387	Denmark	0.5±0.4 mnopqrs	0.7±0.5 fghijk	0.6±0.2 ijklmn
Wizzard	UK	0.4±0.3 nopqrs	0.7±0.6 fghijk	0.6±0.2 ijklmn
Disco	France	0.4±0.4 mnopqrs	0.6±0.3 hijk	0.5±0.1 ijklmn
Crisbo	Germany	0.3±0.5 opqrs	0.7±0.5 fghijk	0.5±0.3 ijklmn
Olan	France	0.2±0.1 qrs	0.7±0.4 fghijk	0.5±0.4 jklmn
Hobbit	Germany	0.6±0.3 klmnopqrs	0.3±0.3 jk	0.5±0.2 jklmn
Compass	Germany	0.2±0.2 qrs	0.7±0.5 fghijk	0.4±0.3 jklmn
Di-276	France	0.4±0.1 nopqrs	0.5±0.5 ijk	0.4±0.1 jklmn
Di-1451	Nepal	0.4±0.4 nopqrs	0.5±0.3 ijk	0.4±0.1 jklmn
Lady	France	0.2±0.2 qrs	0.7±0.2 ghijk	0.4±0.3 jklmn
Di-279	France	0.4±0.4 nopqrs	0.5±0.3 jk	0.4±0.1 jklmn

Table 5 (continued)

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Di-2436	Germany	0.3±0.4 opqrs	0.5±0.4 ijk	0.4±0.1 jklmn
Mireille	France	0.2±0.3 qrs	0.6±0.5 hijk	0.4±0.2 klmn
Expresso	Germany	0.4±0.3 nopqrs	0.4±0.1 jk	0.4±0.0 klmn
Diva	France	0.4±0.3 nopqrs	0.3±0.1 jk	0.3±0.0 klmn
Mélodie	France	0.3±0.2 opqrs	0.4±0.3 jk	0.3±0.1 klmn
Di-1216	Netherlands	0.2±0.3 pqrs	0.5±0.6 jk	0.3±0.1 klmn
Di-1197	UK	0.6±0.3 klmnopqrs	0.1±0.2 k	0.3±0.3 klmn
Di-2180	Germany	0.5±0.2 mnopqrs	0.2±0.2 jk	0.3±0.2 klmn
Di-1626	France	0.2±0.3 pqrs	0.4±0.3 jk	0.3±0.1 klmn
Di437	France	0.1±0.1 rs	0.6±0.2 hijk	0.3±0.3 klmn
Vulcain	France	0.2±0.3 pqrs	0.3±0.4 jk	0.3±0.1 klmn
Maya	France	0.1±0.1 rs	0.5±0.4 ijk	0.3±0.3 klmn
Monark	France	0.1±0.1 rs	0.5±0.3 jk	0.6±0.3 lmn
Target	UK	0.0±0.0 s	0.5±0.1 ijk	0.2±0.3 mn
Di-2304	Spain	0.0±0.0 s	0.4±0.1 jk	0.2±0.3 n
Di-2385	Austria	0.1±0.2 qrs	0.1±0.2 k	0.1±0.0 n
Clipper	UK	0.1±0.1 rs	0.2±0.2 jk	0.1±0.1 n

[a] For each experiment, data are means and standard deviation of four replicates. Four plants were tested in each replicate. Plants were evaluated on a 0–5 scale. Mean values followed by the same letter are not significantly different (Newman–Keuls test $P=0.05$)

[b] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

concentration: 10^3 zoospores per plant (Moussart et al. 2001).

Terminology concerning disease reactions to *A. euteiches*

We used the terminology of Parlevliet (1979) and Agrios (2004) to describe the four types of reaction observed on legume species or genotypes. The term non-host resistance was defined by Agrios (2004) as the inability of a pathogen to infect a plant. According to Parlevliet (1979), qualitative resistance interferes with the disease cycle by completely preventing the emergence of symptoms and/or the production of spores. Partial resistance is defined as interference with one or more steps of the epidemic cycle, slowing disease progress and/or reducing pathogen multiplication (Parlevliet 1979). The term susceptibility was defined by Agrios (2004) as the inability of a plant to resist the effect of a pathogen or other damaging factors.

Data analysis

An analysis of variance (ANOVA) was carried out for the screening results, and means were compared, using a Newman–Keuls test ($P<0.05$) in the General Linear Model procedure of SAS (1988; SAS Institute, Cary, NC, USA). Relationships between replicates were tested by Pearson correlation analysis (SAS 1988).

Results

For each legume species tested, the relationship between the results obtained for the two replicates was significant (R^2 from 0.95 for faba bean and vetch to 0.71 for French bean). Four classes of legumes were identified (1) susceptible, (2) genotypes ranging from susceptible to resistant, (3) high level of partial resistance and (4) no visible symptoms.

1. Susceptible

Three legume species were considered susceptible to *A. euteiches*. Lentil and alfalfa genotypes (28 and 25 genotypes, respectively) highly susceptible to *A. euteiches* were treated with a lower zoospore concentration (Tables 1 and 2). The symptoms observed were similar to those on pea roots: brown soft necrosis on rootlets and on the main root, with many oospores in root tissues. At this spore concentration, DIs of 4.0 to 4.6 for lentil genotypes and of 3.1 to 4.3

Table 6 Reaction of clover (*Trifolium repens* and *T. pratense*) genotypes to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin	Disease severity[a]		
		Experiment I	Experiment II	Mean both experiments
Pisum sativum[b]				
Baccara	France	5.0±0.0 a	4.9±0.3 a	4.9±0.0 a
PI180693	Germany	4.0±0.0 a	4.0±0.2 b	4.0±0.0 b
Trifolium				
Podkowa[c]	Polska	2.3±2.5 bc	3.3±1.1 b	2.8±0.7 c
Luclair[c]	France	2.8±0.5 b	2.5±0.2 c	2.7±0.2 cd
Rivendel	Denmark	2.4±0.4 bc	2.1±0.6 cde	2.2±0.2 cde
Aran	Ireland	1.7±0.1 bc	2.3±0.3 cd	2.0±0.4 cdef
Merwi	Belgium	1.5±0.6 bc	2.2±0.8 cd	1.9±0.5 cdef
Grasslands Huia	New Zealand	1.6±0.7 bc	2.0±0.8 cde	1.8±0.3 def
Abercrest	UK	2.0±0.5 bc	1.5±0.4 cdef	1.7±0.3 def
Abervantage	UK	1.2±0.4 bc	2.1±0.8 cde	1.6±0.6 def
California ladino	USA	1.9±0.6 bc	1.3±0.7 cdef	1.6±0.4 def
Grasslands Tahora	New Zealand	1.4±0.5 bc	1.8±0.4 cdef	1.6±0.3 def
Regal	USA	1.4±0.4 bc	1.7±0.2 cdef	1.6±0.2 def
NFG Gigant	Germany	1.4±0.4 bc	1.8±0.6 cdef	1.6±0.3 def
Sonja	Sweden	2.0±0.3 bc	1.2±0.4 cdef	1.6±0.5 def
Grasslands demand	New Zealand	1.5±0.4 bc	1.5±0.3 cdef	1.5±0.0 def
Menna	UK	1.7±0.6 bc	1.2±0.5 cdef	1.5±0.3 def
Seminole	USA	1.3±0.5 bc	1.6±0.2 cdef	1.4±0.2 def
Alberta	Denmark	1.1±0.8 bc	1.7±0.5 cdef	1.4±0.4 ef
Mistral[c]	France	1.1±0.4 bc	1.3±0.1 cdef	1.2±0.1 ef
Larus[c]	Switzerland	1.0±0.9 bc	1.2±0.5 cdef	1.1±0.1 ef
Lune de mai	France	0.9±0.7 bc	1.0±0.2 def	0.9±0.1 ef
Tara	Ireland	1.1±0.5 bc	0.8±0.3 f	0.9±0.2 ef
Sacremento	USA	0.6±0.5 c	1.1±0.4 def	0.8±0.3 f
Lemmon[c]	Belgium	1.1±0.6 bc	0.6±0.1 f	0.8±0.4 f
Merviot[c]	Belgium	0.6±0.5 c	1.0±0.5 def	0.8±0.2 f

[a] For each experiment, data are means and standard deviation of four replicates. Five plants were tested in each replicate. Plants were evaluated on a 0–5 scale. Mean values followed by the same letter are not significantly different (Newman–Keuls test $P=0.05$)

[b] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

[c] *T. pratense*

for alfalfa genotypes were obtained. Some lentil genotypes were more susceptible than the resistant pea line.

All 31 genotypes of French bean assessed were susceptible to *A. euteiches* (Table 3). Typical soft brown necrosis, with many oospores, was observed in all genotypes. However, all genotypes had a DI no higher than that of the resistant pea line PI 180693. Some genotypes showed a certain level of partial resistance ($2<DI<2.2$), namely Coco nain blanc précoce, Miramont, Fructidor and Aiguillon.

2. Genotypes ranging from susceptible to resistant

This class included three legume species. The 26 genotypes of *V. sativa* (common vetch), mostly from France, displayed variable levels of resistance, from genotypes with qualitative resistance (Topaze, L5, Caravelle, Catarina, L4, Corail, L7 and Malachite) to genotypes highly susceptible (Granit, L3, L1, Safran, Amethyste, L11, L10 and L9; Table 4). Genotypes with a $DI<2$ were considered to have a high level of partial resistance. These genotypes displayed brown to red lesions and root tissues were turgescent. In susceptible genotypes, typical soft brown necrosis was observed. Oospores were observed on the root tissues of all genotypes other than those displaying qualitative resistance.

Most of the 63 genotypes of faba bean screened were highly resistant to *A. euteiches* (Table 5). Only a

Table 7 Geographical origin of chickpea (*Cicer arienatum*) genotypestested for their reaction to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin
Pisum sativum[a]	
Baccara	France
PI180693	Germany
Cicer arienatum	
Amdoun1	Tunisia
Beja1	Tunisia
Bouchra	Tunisia
ILC3279	USSR
ILC5275	ICARDA
ILC5312	ICARDA
ILC5461	ICARDA
ILC5494	ICARDA
ILC5550	ICARDA
ILC5921	Bulgaria
ILC6925	Hungaria
ILC72	USSR
ILC8779	Macedonia
ILC8795	Bulgaria
ILC8802	Bulgaria
ILC8806	Bulgaria
ILC8808	Bulgaria
ILC8822	Bulgaria
ILC8839	Bulgaria
ILC8863	Bulgaria
ILC8872	Bulgaria
ILC8882	Bulgaria
ILC8883	Bulgaria
ILC8885	Bulgaria
ILC8889	Bulgaria
ILC8916	Bulgaria
ILC8944	Bulgaria
ILC9946	Palestine
JG62[b]	India/ICRISAT
Neyer	Tunisia
WR315[b]	India/ICRISAT

[a] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

[b] Desi type

few restricted areas of black tissue were observed on rootlets (never on the main roots), with no oospore formation (DI<1). Some typical black soft necrosis, in some cases with oospores, was observed on the rootlets and main root of a few genotypes (DI close to 2): Di-281, Salsa, Di-713, Alameda. However, the symptoms spread no further into the root and the total diseased area covered no more than 25% of the length of the root. Only three cultivars were susceptible: Baraca, Di-1653 and Di-340 (3<DI<4). On these cultivars, many oospores were observed in the root tissues.

The 24 genotypes of clover tested (18 *T. repens* and 6 *T. pratense* genotypes) mainly displayed high levels of partial resistance (Table 6). Symptoms were similar to those observed on pea, lentil and alfalfa. Only five genotypes were moderately susceptible (1.9<DI<2.8): Merwi, Aran, Rivendel, Luclair and Podkowa. Oospores were observed in the root tissues of these genotypes.

3. High level of partial resistance

Two of the 31 chickpea genotypes tested (Table 7) were of the Desi type (JG62 and WR315) and 28 were of the Kabuli type. In both replicates, mild symptoms were observed on only a few rootlets (small, superficial black spots). A few oospores were observed in the rootlet tissue of genotypes ILC8795 and ILC 8822, but it was not possible to recover the pathogen. The disease scores of susceptible and resistant pea lines Baccara and PI180693 were 5.0 and 4.1, respectively.

4. No visible symptoms

No symptoms were observed on the 51 genotypes of lupin assessed (Table 8). Roots were healthy, like those of the non-inoculated controls, in both replicates. No oospores were observed at the end of the experiment. This species may therefore be considered a non-host species. The disease scores of the susceptible and resistant pea lines Baccara and PI180693 were 4.2 and 4.9, respectively.

Discussion

We observed four categories of susceptibility/resistance to the pea *A. euteiches* isolate used among the various legume species/cultivars tested: (1) susceptible legume species (lentil, alfalfa, French bean), in which no more than partial resistance was observed; (2) legume species including both susceptible genotypes and highly resistant genotypes (common vetch, faba bean and clover), (3) species with a very high level of partial resistance (chickpea) and (4) species developing no symptoms (lupin).

The absence of symptoms in lupin may indicate that this species is a non-host species. However, this observation requires confirmation with several *A. euteiches* isolates. Unlike lupin, chickpea may be defined as a host plant under these conditions, but the

Table 8 Geographical origin of lupin (*Lupinus alba*) genotypes tested for their reaction to infection by *Aphanomyces euteiches*

Genotypes	Geographical origin
Pisum sativum[a]	
Baccara	France
PI180693	Germany
Lupinus	
Ac003	Azores
E107	Portugal
E126	Portugal
E2	Spain
E36	Spain
E59	Spain
E80	Portugal
E99	Portugal
Egypte16	Egypt
Egypte22	Egypt
Egypte50	Egypt
Ethiopie1	Ethiopia
GR03	Greece
GR1	Greece
GR30	Greece
GR25	Greece
ITA1	Italy
ITA20	Italy
ITA37	Italy
ITA51	Italy
LA020	Ethiopia
LA198	Madeira
LA259	Turkey
LA406	Israel
LA432	Jordan
LA547	Syria
LA642	Canary Islands
LA656	Kenya
LA673	?
LA680	?
LA686	Algeria
Maroc74	Morocco
Maroc78	Morocco
Soudan1	Sudan
Soudan2	Sudan
Soudan4	Sudan
Soudan5	Sudan
TR16	Turkey
TR17	Turkey
TR21	Turkey
TR7	Turkey
Aster	France
Clovis	France
Lugain	France
Lumen	France
Luxe	France
A00	France
Amiga	Chile
Energy	France
Feodora	Germany
Ludic	France

[a] Standard reference cultivars of *P. sativum* for *Aphanomyces* root rot resistance

genotypes studied displayed a very high level of partial resistance.

The existence of susceptible, partially and highly resistant genotypes within the same species, as observed for common vetch, faba bean and clover in this study, was previously described for *A. euteiches* on barrel medic (*M. truncatula*) by Moussart et al. (2007). These observations suggest that several mechanisms of resistance against *A. euteiches* exist. Furthermore, the results obtained with lentil, alfalfa and French bean genotypes with low levels of partial resistance were similar to those obtained by Wicker et al. (2003) with pea.

Our results clearly demonstrate that a pea isolate may infect several other legume species, inducing severe symptoms on roots and oospore formation. This ability to infect other species depends on the susceptibility of the cultivar used in some species (common vetch, faba bean and clover) and the reaction may therefore be described as cultivar-specific. For other legumes, the reaction could be species-specific because all the cultivars tested were either susceptible (lentil, alfalfa and French bean) or highly resistant (chickpea). As described by Malvick et al. (1998), isolates of *A. euteiches* display two levels of pathogenic variation: (1) isolates causing disease of different levels of severity on different genotypes of the same host (races or virulence phenotypes), and (2) isolates preferentially pathogenic on different plant species (formae speciales).

The use of a single cultivar is not sufficient to determine whether a particular *A. euteiches* isolate can infect a given legume species. Conversely, because we used only one pea isolate in this study it cannot be concluded that lupin is a non-host species. Thus, previous studies on forage and legume crops (Chan and Close 1987; Levenfors et al. 2003) require

confirmation with a range of genotypes for each species. Similarly, the conclusion of Wicker et al. (2001), who described specific susceptibility in common vetch, is also debatable, because we found that some common vetch cultivars displayed qualitative resistance to *A. euteiches*. It is, therefore, essential to consider pathogen–legume species and/or pathogen–plant genotype interactions before drawing conclusions about whether a legume species is a host/non-host or mildly/severely infected. Thus, for each legume species, a differential set of genotypes should be established and screened with different races of *A. euteiches*, as carried out by Carley (1970), with a differential French bean series and eight *A. euteiches* isolates. Such studies might also make it possible to identify resistant genotypes in lentil, alfalfa and/or French bean genotypes and susceptible genotypes in chickpea. For the same reasons, it would also be interesting to enlarge the set of legume species genotypes tested.

The relationship between the results of tests in vermiculite and those obtained in natural soil is an issue of major epidemiological importance. Several authors have shown a poor agreement between the results obtained in vermiculite and those obtained in natural soil. Levenfors et al. (2003) obtained symptoms on broad beans in the vermiculite test, but no symptoms in a test on infested soil. This observation confirms that of Lamari and Bernier (1985), who reported studies carried out by Haensler (1926) showing a lack of infection of faba bean in non-sterile conditions. Similarly, our results for vermiculite tests showed the pea isolate to be highly pathogenic on all alfalfa genotypes tested, but, to our knowledge, no aphanomyces root rot has ever been observed on alfalfa in field conditions in France. As suggested by Salt and Delanay (1985), the microflora or other biotic or abiotic soil factors may play an important role in root rot expression. The conditions used in our study were very favourable for disease development and our results require confirmation under field conditions.

If lupin truly is a non-host to *A. euteiches* as our results suggest, at least in French and maybe European conditions, the use of lupin may have no effect on soil infestation and subsequent disease development. Conversely, the use of lentil, alfalfa or French bean might considerably increase the inoculum potential of the soil, having a deleterious effect on the subsequent pea crop. The use of faba bean or common vetch cultivars with qualitative resistance could be considered, but studies on the risk of resistance breakdown are required. These ideas are supported by the studies of Salt and Delanay (1985), who concluded that pea and faba bean rotations including *Phaseolus* beans suffered more damage due to root diseases than rotations with only one legume species. It would be important to determine if and which species could act as bridging hosts allowing for the crossing of *A. euteiches* isolates from one legume with those from another, as demonstrated by Shang et al. (2000) for pea and French bean *A. euteiches* isolates. This is especially important in light of the plasticity of *A. euteiches* which is highly adaptable under the influence of biotic and abiotic factors (Malvick and Percich 1999; Grünwald and Hoheisel 2006).

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