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1 **Pathogenicity of animal and plant parasitic *Aphanomyces* spp and their economic**
2 **impact on aquaculture and agriculture**

3

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21

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23 sugarbeet, crayfish, fish

24

25

26 **Abstract**

27

28 Parasitic *Aphanomyces* species are a global threat to agri- and aquaculture, causing
29 multimillion USD damage every year. Via the global trade, *Aphanomyces* has spread across all
30 continents with exception of South America and Antarctica, and has become a major problem in
31 pea, sugar beet, fish and crayfish production. The widespread *A. euteiches* and *A. cochlioides*
32 induce root rot diseases in leguminous species and sugar beet respectively. The fish pathogen *A.*
33 *invadans* is the causative agent of Epizootic Ulcerative Syndrome in various fish species whilst
34 *A. astaci* infects crayfishes causing crayfish plague. *Aphanomyces* have developed an efficient
35 transmission and infection mechanism which allows a rapid colonization and disruption of the
36 host's infected tissues. This review presents an overview on the current research on
37 *Aphanomyces* genus. We summarise the latest research efforts on four pathogenic *Aphanomyces*
38 species, shedding light on the biology of these microorganisms, the pathogenicity factors of these
39 parasites, the diseases which they cause, their distribution and finally the strategies to control the
40 diseases.

41 **1. Introduction**

42 One of the major threats for both agriculture and aquaculture industries are the
43 pathogenic oomycetes, a group known to be responsible for many outbreaks of natural host
44 population (van West, 2006). These oomycetes, which belong to the Stramenopile Kingdom, are
45 filamentous eukaryotic microorganisms that have spread in both terrestrial and aquatic
46 ecosystems (Beakes et al., 2012). Morphologically and ecologically similar to fungus, this
47 phylum was historically considered as a basal fungal lineage (Lévesque, 2011), however genetic
48 studies revealed that they are phylogenetically related to brown algae (Baldauf et al., 2000;
49 Gleason et al., 2018). The most studied and notorious species belong to the genus *Phytophthora*,
50 such as *Phytophthora infestans*, responsible for the Irish potato famine (Erwin and Ribeiro,
51 1996; Haas et al., 2009), *Phytophthora palmivora*, the causative agent of the cocoa black pod
52 (Drenth et al., 2013) or *Phytophthora sojae* which is mainly destructive to soybean (Erwin and
53 Ribeiro, 1996; Tyler, 2007). Beside this famous oomycete genus, other devastating pathogens
54 have been identified, such as those belonging to the genus *Aphanomyces*. Much less studied than
55 *Phytophthora* genus (more than 4,900 articles versus less than 350 articles referenced in
56 Pubmed, consulted in 01-2021), the genus *Aphanomyces* appears to be an economically major
57 threat that can affect both plants and aquatic animals (Diéguez-Uribeondo et al., 2009).

58 Here we reviewed the recent studies about four *Aphanomyces* species causing devastating
59 diseases in agri- and aquaculture. We firstly present the biology of these four species and their
60 distribution in the world, before depicting pathogenicity factors involved in host adaptation. We
61 then discuss the economic impact of *Aphanomyces spp.* and recent advances in management of
62 the diseases. To conclude we propose perspectives for further studies of *Aphanomyces spp.*

63

64 **2. Biology of *Aphanomyces* genus**

65

66 *Aphanomyces* is a monophyletic genus within Saprolegniales order, it has unique features
67 in its lifecycle and host range. In this section we review the phylogenetic position of
68 *Aphanomyces* genus, describe the different lifestyles and focus on the host range of parasitic
69 species.

70 **2.1 Phylogeny**

71 Phylogenetic studies placed the *Aphanomyces* genus in the Saprolegnial lineage, an order
72 that includes also numerous pathogenic species in both plants and aquatic animals (Diéguez-
73 Uribeondo et al., 2009), such as the fish pathogen *Saprolegnia*, also known as “cotton mould”
74 (Hulvey et al., 2007). This lineage is in contrast with the Peronosporalean lineage, which mainly
75 includes plant pathogenic species and diverged from the Saprolegnial lineage in the Early
76 Mesozoic era (Riethmuller et al., 2002; Beakes et al., 2012; Jiang and Tyler, 2012; Matari and
77 Blair, 2014). Phylogenetic analysis revealed that the *Aphanomyces* genus appears to be
78 monophyletic (Leclerc et al., 2000; Diéguez-Uribeondo et al., 2009) and is clustered in three
79 major lineages, composed by plant pathogens, aquatic animal pathogens, and saprotrophic or
80 opportunistic parasites, respectively (Diéguez-Uribeondo et al., 2009) (Figure 1). To date around
81 40 *Aphanomyces* species are described occurring in various ecological niches and ranging from
82 highly specialized parasites to saprotrophic species developing on plant residues or dead animals
83 (Scott, 1961; Dick, 2001; Johnson et al., 2002).

84 **2.2 *Aphanomyces* host range**

85 The pathogenic species belonging to the genus *Aphanomyces* are known to infect a wide
86 range of different hosts. Depending on the species considered, the host spectrum varies from
87 plants to vertebrates, and also invertebrates.

88 On one hand, many plant taxa are susceptible to infection by *Aphanomyces* species. The
89 plant pathogen *Aphanomyces euteiches*, is specialized on perennial or annual plants of the
90 Fabaceae family, including peas (*Pisum sativum* L.), alfalfa (*Medicago sativa* L.), common bean
91 (*Phaseolus vulgaris* L.), broad bean (*Vicia faba* L.), red and white clover (*Trifolium pratense* L.
92 and *T. repens* L., respectively) (Gaulin et al., 2007). Another oomycete plant parasite,
93 *Aphanomyces cochlioides* is specialized to parasitize roots of sugar beet (*Beta vulgaris* L.),
94 spinach (*Spinacia oleracea* L.), cockscomb (*Celosia argentea* L.), and other various species of
95 Chenopodiaceae and Amaranthaceae (Scott, 1961).

96 On the other hand, several animal taxa are susceptible to infection by *Aphanomyces*
97 species. Firstly *Aphanomyces invadans*, the causative agent of the Epizootic Ulcerative
98 Syndrome (EUS), has been reported to interact with more than 160 species of fish (Herbert et al.,
99 2019). It may infect a wide range of estuarine and freshwater fish species (Chinabut, 1998;
100 Blazer et al., 1999) and is especially virulent to catfish (Roberts et al., 1993) and murrels

101 (Chondar and Rao, 1996). Secondly *Aphanomyces astaci* the causative agent of the crayfish
102 plague, is known to associate with crayfish species from Asia, Australia and Europe. *A. astaci* is
103 an obligate parasite specialized on freshwater crayfish (Söderhäll and Cerenius, 1999; Diéguez-
104 Uribeondo, 2006). This oomycete is known to have a North American origin, and could
105 occasionally also be harboured by other decapods such as freshwater crabs or shrimps (Putra et
106 al., 2016; Svoboda et al., 2017; Martín-Torrijos et al., 2021a). *Aphanomyces frigidophilus* is
107 known to infect the eggs of several salmonid species (Ballesteros et al., 2006). The impact of
108 these pathogens is major since they may cause the devastation of both natural and cultured stocks
109 of freshwater animals (Söderhäll and Cerenius, 1999; Collas et al., 2016). Lastly, *Aphanomyces*
110 *sinensis* is a pathogen known to infect the Japanese turtle *Pelodiscus sinensis*, causing small
111 whitish maculae on the carapace (Takuma et al., 2011). These four *Aphanomyces* species are the
112 most notable animal-pathogenic members of the genus. Of these, *A. invadans* and *A. astaci* have
113 by far the greatest economic impact – both of which cause significant losses within the global
114 aquaculture industry (Iberahim et al, 2018; CABI, 2020a). Hence, the primary focus in terms of
115 animal-pathogenic *Aphanomyces* shall be upon these two species.

116 In several other species belonging to the *Aphanomyces* genus, some are predominantly
117 saprotrophic (i.e., *Aphanomyces laevis*, *Aphanomyces stellatus*, *Aphanomyces helicoides* or
118 *Aphanomyces repetans*), but may turn as opportunistic pathogens with no host specialization
119 (Royo et al., 2004; Patwardhan et al., 2005).

120

121 **2.3 Life cycle**

122 The typical life cycle of *Aphanomyces* spp. includes both asexual and sexual phases for
123 the plant pathogens while sexual reproduction in animal pathogens is rare or completely absent
124 (Diéguez-Uribeondo et al., 2009).

125 Sexual reproduction involves specialized reproductive structures, oogonia and
126 antheridia, in which meiosis occurs and gametes are formed. The oogonium produces one to
127 several oospheres, cellular structures containing haploid nuclei (Malloch, 2007). Antheridia are
128 structures in which male nuclei are formed (Dick, 1969; Malloch, 2007). *Aphanomyces* species
129 such as *A. euteiches* and *A. cochlioides* are homothallic, presenting male and female reproductive
130 structures on the same thallus. Fertilization begins when antheridia develop a fertilization tube

131 which penetrates the oogonium. Male nuclei pass through this tube and enter the oogonium
132 where they fuse within the oospheres to produce a diploid (Malloch, 2007).

133 In phytopathogenic *Aphanomyces* spp. fertilization of the oogonium results in the
134 formation of oospores, thick-walled zygotes, 18-25 µm in size, which function as resting spores
135 to survive unfavourable winter conditions (Heffer, 2002; Wu et al., 2018). They are produced in
136 plant infected tissue and are released in the soil when the plant degrades (Heffer, 2002).
137 Oospores can remain dormant in the soil for years in the absence of a host, representing a long-
138 lived source of inoculum (Papavizas and Ayers, 1974; Gaulin et al., 2007). Under warm and
139 moist soil conditions oospore germination is stimulated by the host exudates (Dyer and Windels,
140 2003). Oospores form a germ tube which develops vegetative hyphae that can directly infect the
141 host (Dyer and Windels, 2003).

142 In the asexual stage of plant pathogenic species, vegetative hyphae differentiate to
143 sporangia in which motile uninucleate zoospores are produced. Primary zoospores equipped with
144 an anterior “tinsel” flagellum and a posterior “whiplash” flagellum are released in the soil
145 (Walker and van West, 2007). After evacuation from the zoosporangium primary zoospores
146 encyst and give rise to secondary zoospores (Papavizas and Ayers, 1974; Sivachandra Kumar et
147 al., 2020). Secondary zoospores which also present an anterior and posterior flagellum are motile
148 for a longer period and are determinant for a successful infection (Walker and van West, 2007).
149 Zoospores swim in water film around soil particles through the root surface where in a few
150 minutes they adhere, encyst developing a germ tube, penetrate and colonize the tissue (van West
151 et al., 2003). The invasion events of *A. euteiches* in pea roots has been described by Papavizas
152 and Ayers (1974). The germ tube invades the host tissue in the intercellular spaces within 2
153 hours. In some cases, it enters the cell wall with the formation of an appressorium-like structure.
154 Within a few hours *A. euteiches* penetrates the host cortical cells and develops hyphae that
155 rapidly spread mainly in the intercellular spaces of the root cortex and eventually colonize the
156 entire root system (Wu et al., 2018). Antheridia and oogonia are formed in the invaded tissue
157 within few days, likewise in sugar beet once *A. cochlioides* zoospores have encysted on the root
158 surface the resulting germ tubes penetrate the host directly or via appressoria (Islam et al., 2003)
159 leading to a rapid infection within 30-40 minutes after the zoospores adhesion to the root surface
160 (Islam, 2010). The presence of *A. cochlioides* mycelia has been observed in the intercellular
161 spaces of the cortex (Papavizas and Ayers, 1974).

162 In animal pathogenic species zoospores are produced from clusters of primary cysts at the
163 hyphal tips. As soon as the primary spores are ejected, they immediately cluster around the
164 sporangial opening and form an achlyoid cluster or “spore ball” at the apical tip of the sporangia
165 from where secondary flagellated zoospores are released (Vrålstad et al. 2011a). Secondary
166 zoospores swim in the water column and adhere on the surface of a suitable host. Once they
167 have settled, they discard flagella and encyst. Cysts subsequently germinate and develop a germ
168 tube which penetrates the host (Vrålstad et al., 2011b). Hyphae invade deeper tissue or organs of
169 a susceptible host, differentiate to zoosporangia which release zoospores prior to or just after the
170 host’s death (Vrålstad et al. 2011b).

171 Encysted zoospores of pathogenic *Aphanomyces* species have also the ability to release a
172 new generation of zoospores instead of germinating. This event is known as repeated zoospore
173 emergence (RZE) (Diéguez-Uribeondo et al. 2009). It has been observed that if encystment
174 occurs in the absence of a favorable host, the crayfish pathogen *A. astaci* can produce three
175 consecutive generations of new zoospores before the spore ceases to live (Cerenius and
176 Söderhäll, 1984).

177

178 **2.4 Distribution and diversity**

179 Pathogenic *Aphanomyces* species are widely spread around the hemisphere with
180 cases also reported in South-East Asia, Australia and South Africa (Figure 2). Plant pathogenic
181 *Aphanomyces* spp. are detected in the majority of regions where suitable crops are cultivated.
182 Occurrence of crayfish pathogen *A. astaci* is mainly found in North America, Europe and Japan
183 whereas fish pathogen *A. invadans* is spread around the world except for Europe and South
184 America.

185

186 **2.4.1 *Aphanomyces euteiches***

187 Since its first report in peas in Wisconsin by Drechsler in 1925 (Jones and Drechsler,
188 1925), *A. euteiches* has been reported as one of the major yield limiting factors in the US
189 (Gossen et al., 2016), Canada (Wu et al., 2018) France (Quillévéré-Hamard et al., 2018) and
190 Sweden (Levenfors et al., 2003). Cases of *A. euteiches* detection were also reported in Australia
191 (van Leur et al., 2008), China, India, territory of former USSR, former Czechoslovakia, Poland,

192 Italy, Germany (CABI, 2019) and the Netherlands (Oyarzun and van Loon, 1989) (Figure 2).
193 Unfortunately, no quantitative data on *A. euteiches* distribution is known for major producing
194 countries as India, China and Russia.

195 *A. euteiches* has a broad host range within the family Fabaceae such as pea, alfalfa,
196 trifolium, lentil, etc. (Gaulin et al., 2007; Malvick et al., 2009) and cause the greatest economic
197 damage to pea and lentil crops (Gaulin et al., 2007; Malvick et al., 2009; Ma et al., 2020). The
198 ability of different *A. euteiches* pea strains to infect plants was used to identify two pathotypes (I
199 and III). While both pathotypes are present in North America, only the pathotype I is reported in
200 France (Wicker et al., 2001). A recent study also indicates that pathotype I is prevalent in
201 Canadian prairies (Kumar et al 2021). *A. euteiches* strains isolated from alfalfa fields are
202 designated as races: the less aggressive race 1 is able to infect susceptible alfalfa genotype
203 Saranac, but not the tolerant genotype WAPH-1; the more aggressive race 2 genotype overcomes
204 resistance of WAPH-1 and is able to infect both genotypes (Malvick et al., 2009, Grau et al
205 1991; Malvick and Grau, 2001). Studies on *A. euteiches* isolates from US alfalfa fields
206 demonstrate the emergence of new races (Seitz and Rouse 2012) and the prevalence of the
207 aggressive race 2, which represents around 45% of all strains, while race 1 represents 11%
208 (Samac et al., 2017).

209

210 **2.4.2 *Aphanomyces cochlioides***

211 It was 1929 when *A. cochlioides* was first identified as the causal agent of the black rot
212 disease in sugar beet in Michigan (Dreschler, 1929). Despite the restricted host range, this
213 pathogen has a worldwide distribution and its presence has been reported especially in major
214 sugar beet producing areas in North America such as The River Valley of Minnesota, North
215 Dakota, Nebraska and Wyoming, in Canada, Chile, Europe and Japan (Harveson, 2000; Beale et
216 al., 2002). Although *A. cochlioides* represents a major constraint in sugar beet production, little
217 attention has been given to the genotypic variation among *A. cochlioides* strains in comparison to
218 the intensively-studied *A. euteiches*.

219

220 **2.4.3 *Aphanomyces invadans***

221 *A. invadans* was first isolated in Japan, 1971, from a freshwater fish farm (Egusa and
222 Masuda, 1971). Over the past half-century, this fish-pathogenic oomycete has spread globally
223 and has now been isolated from the continents of Asia, North America, Africa and Australia
224 (OIE, 2016; Iberahim et al., 2018). Recently, molecular techniques for the identification of *A.*
225 *invadans* have been developed and refined (Vandersea et al., 2006; Kamilya and Kollanoor,
226 2020). Therefore, the global distribution of *A. invadans* is closely monitored and currently listed
227 in 28 countries.

228 *A. invadans* is a specialized pathogen of fish exclusively (Diéguez-Uribeondo et al.,
229 2009), with over 125 species of fish currently known to be susceptible to infection (Kamilya and
230 Baruah, 2014), a further 38 additional susceptible fish genera having been recognized since the
231 authors' previous study (Baruah et al., 2012). To date, only one genotype of *A. invadans* has
232 been recorded (OIE, 2016), with all isolates tested demonstrating fish pathogenicity –
233 encompassing those from North America (Sosa et al., 2007), Europe (Oidtmann et al., 2008) and
234 Asia (Yadav et al., 2014). Several *Aphanomyces* isolates were obtained from Malaysian fish
235 farms and found to be non-pathogenic to fish under laboratory conditions, however these were
236 not identified to species level (Afzali et al., 2013). This species propagates solely via asexual
237 reproduction (Kiryu et al., 2005; Diéguez-Uribeondo et al., 2009). The lack of a sexual life stage
238 has given rise to the global spread of *A. invadans*, as a single highly virulent clone, worldwide
239 over the past 50 years (Lilley et al., 2003; Iberahim et al., 2020).

240

241 **2.4.4 *Aphanomyces astaci***

242 *A. astaci* is originally a specific parasite of crayfish originating from the North American
243 continent (Martín-Torrijos et al., 2021b). North American crayfish species are known to be
244 healthy carriers, for example such as *Procambarus clarkii* (red swamp crayfish), *Pacifastacus*
245 *leniusculus* (signal crayfish) and *Faxonius limosus* (spiny-cheek crayfish) (Souty-Grosset et al.,
246 2006). For several decades, phylogenetic analyses have been performed to better describe and
247 understand the relationship between *A. astaci* and its North American hosts. Thus, the Random
248 Amplification of Polymorphic DNA–Polymerase Chain Reaction (PCR-RAPD) was the first
249 molecular technique which enabled the description of the genetic diversity of *A. astaci*, and

250 enabled the characterization of 5 distinct genetic groups. Group A was isolated from specimens
251 of the native European crayfish *Astacus astacus*, and is probably related to the first introduction
252 of *A. astaci* in Europe during the 19th century (Huang et al., 1994). Group B was isolated from
253 signal crayfish *P. leniusculus* Swedish specimens (originally from Canada) (Huang et al., 1994),
254 and appears to be responsible for many outbreaks in native European species so far (Cerenius et
255 al., 2008). Group C was also isolated from *P. leniusculus* Swedish specimens (Huang et al.,
256 1994); however, it has never been observed again since its detection (Söderhäll and Cerenius,
257 1999). Group D was isolated from introduced Spanish specimens of red swamp crayfish *P.*
258 *clarkii* (Diéguez-Urbeondo et al., 1995), whereas group E was isolated from the spiny-cheek
259 crayfish *F. limosus* introduced in Czech Republic (Kozubíková et al., 2011). Over the last ten
260 years, the number of genotyping methods to characterize *A. astaci* has been constantly
261 increasing, facilitating the identification of genotypes involved in outbreaks. In order to evaluate
262 the genetic diversity of the pathogen *A. astaci*, studies have focused on the sequencing of
263 chitinase genes (Makkonen et al., 2012a), but also Amplified Fragment Length Polymorphism
264 (AFLP) markers (Rezinciuc et al., 2014), and recently on Single Nucleotide Polymorphisms
265 (SNP) diversity based on mitochondrial DNA (Minardi et al., 2019). The genetic markers
266 currently most used to characterize the pathogen strains responsible for outbreaks have focused
267 on microsatellite sequencing (Grandjean et al., 2014) and mitochondrial haplotyping (Makkonen
268 et al., 2018) approaches. It was possible to distinguish 4 mitochondrial haplogroups: a
269 (corresponding to the RAPD-group A and C), b (corresponding to the RAPD-group B), d
270 (corresponding to the RAPD-group D) and e (corresponding to the RAPD-group E) (Makkonen
271 et al., 2018). These findings were also congruent with the genetic diversity observed on
272 microsatellites, since the same genetic groups were found between RAPD initial markers: SSR-
273 A, SSR-B, SSR-C, SSR-D and SSR-E corresponding to RAPD-groups A, B, C, D and E,
274 respectively (Grandjean et al., 2014). Furthermore, these results underline the mitochondrial
275 diversity observed within the different *A. astaci* strains, since 2 different mitochondrial
276 haplotypes were described within the RAPD-group D (d1 and d2, Makkonen et al., 2018). The
277 author also differentiated the *A. astaci* strains in 2 lineages: lineage 1 which includes a, b and e
278 mitochondrial haplotypes (RAPD-groups A, B and E) and lineage 2 corresponding to the d1 and
279 d2 mitochondrial haplotypes (RAPD-group D) (Makkonen et al., 2018). Recently, six new
280 haplotypes have been characterized in North American species belonging to both lineage 1

281 (called *usa1* and *usa2*) and lineage 2 (*usa3* to *usa6*) (Martín-Torrijos et al., 2021b). The
282 development of these different markers will increase our knowledge of the genetic diversity of *A.*
283 *astaci* strains, which is still relatively unknown. Thus, microsatellite markers have allowed the
284 characterization of a new genotype, isolated in North America from the rusty crayfish *Faxonius*
285 *rusticus* (Panteleit et al., 2019). The newly described strain presented the same RAPD and
286 mitochondrial haplogroup profiles as RAPD-group A. Although additional combination of
287 chitinase-like markers attached this new strain to group C. All these results illustrate the
288 complementarity of the different markers developed, as well as the need to use a combination of
289 these approaches in order to better understand the diversity and the evolutionary history of *A.*
290 *astaci*.

291 **3. Pathogenicity determinants of *Aphanomyces* spp.**

292 Pathogenic *Aphanomyces* spp. are distributed around the world and are able to infect
293 various host ranges. In this section we review current knowledge of the factors which make the
294 *Aphanomyces* genus the global threat for agriculture and aquaculture.

295

296 **3.1 Zoospores as a key pathogenicity factor**

297 Oomycetes zoospores play a key role in the infection process and in the pathogen
298 transmission from host to host (Walker and van West, 2007). Spore production rate is an
299 important trait to determine the aggressiveness and the ability of the pathogen to disperse and
300 successfully infect new hosts (Delmas et al., 2014). In plant pathogenic oomycetes zoospores
301 motility is influenced by tactic and electrotactic signals generated by root exudates which drive
302 the zoospores throughout a suitable infection site (Appiah et al., 2005). Attractants of *A. raphani*
303 and *A. euteiches* zoospores such as indole-3-aldehyde and prunetin have been identified in
304 cabbage seedlings and pea seedlings respectively (Yokosawa et al., 1986), while a potent
305 attractant substance to *A. cochlioides* zoospores, cochliophilin A (5-hydroxy-6,7-
306 methylenedioxyflavone, 1) has been isolated from one of its host roots *Spinacia oleracea* (Horio
307 et al., 1992) and it is known to be present also in sugar beet roots. This flavonoid is considered a
308 species-specific attractant compound since it has the capacity to attract *A. cochlioides* zoospores
309 but it has no effect on zoospores motility of other *Aphanomyces* species (Islam and Tahara,
310 2001). When attracted by cochliophilin A, *Aphanomyces* zoospores encyst in few minutes and
311 germinate within 30-60 minutes (Sakihama et al., 2004). Another important step towards a

312 successful infection is the differentiation of zoospores from a motile form into cyst, the immobile
313 form capable of infecting the host. Several studies have provided evidence that changes in
314 cations concentration such as calcium (Byrt et al., 1982a, 1982b; Morris et al., 1995) and
315 potassium (Appiah et al., 2005) play an important role in zoospores taxis and encystment of plant
316 pathogenic oomycetes. Chemotaxis has been reported also on the animal pathogenic *A. astaci*
317 where chemotactic responses were observed within few minutes mainly towards parts of the
318 crayfish where the cuticle is soft such as the tip and the junction of the legs (Cerenius and
319 Söderhäll, 1984). However, no recent studies have confirmed the role of chemotaxis in *A. astaci*
320 zoospores attraction and information about zoospores motility in *A. invadans* and other animal
321 pathogenic *Aphanomyces* species remains still unknown.

322 **3.2 Genetic determinants of pathogenicity**

323 When *Aphanomyces* starts colonization of the host, it has to cope with host immunity and
324 defence reactions. Oomycetes widely exploit the repertoire of secreted proteins called effectors
325 to modulate host physiology and immune reactions (Bozkurt et al., 2012). Based on subcellular
326 localization within the host, effectors are reported as extracellular when they act within the
327 apoplast while intracellular effectors are able to reach the intracellular space of the host cells
328 (Gaulin et al., 2008; Schornack et al., 2010). These proteins are generally induced during
329 infection and generally harbour a signal peptide to be secreted by the pathogen (Bozkurt et al.,
330 2012). Availability of the whole genome sequence of four *Aphanomyces* strains allowed *in silico*
331 prediction of putative secreted proteins in *A. astaci* and *A. invadans* (strain NJM9701) - animal
332 pathogens; *A. euteiches* (strain ATCC201684) plant pathogen and *A. stellatus* (strain CBS
333 578.67) saprophyte (Gaulin et al., 2018; Iberahim et al., 2018). The genome size of
334 *Aphanomyces spp.* are estimated at 50-70 Mb, having 16,000-25,000 predicted genes. Secreted
335 proteins correspond respectively to 10% and 6% of the total proteome of plant and animal
336 pathogens (Gaulin et al. 2018).

337

338 **3.2.1 Extracellular effectors**

339 A large majority of extracellular effectors concern cell wall degrading enzymes for plant
340 pathogens such as *A. euteiches*. Indeed, to get through plant cell wall plant-associated pathogens
341 release a set of cell-wall degrading enzymes (CWDE), which mostly consist of glycosyl

342 hydrolases families (GH), GlycosylTransferases (GT), PolysaccharideLyases (PL) and
343 Carbohydrate-Esterase (CE) also regrouped as CAZymes (Lombard et al. 2014). *A. euteiches* has
344 over 300 secreted carbohydrate-active enzymes (CAZy) and carbohydrate-binding modules
345 (Gaulin et al., 2018). They include protein families targeting plant-specific polysaccharides (e.g.,
346 hemicellulases: GH 10, 11, CE4 families and pectinases: GH 28, PL1, 3, 4 families), which
347 might be involved in penetration of plant cell wall (Lanver et al. 2014). Interestingly, animal
348 pathogen *A. astaci* lacks those plant-specific families in its secretome but harbours enzymes able
349 to interact with chitinous exoskeleton of the crayfish (Gaulin et al. 2018). Indeed, during
350 infection, chitinase may play a major role in the penetration of the hyphae through the chitinous
351 wall following spore germination (Söderhäll et al., 1978). While several species of *Aphanomyces*
352 show chitinase activity in the presence of chitin, *A. astaci* has been shown to be capable of
353 producing chitinases even in the absence of substrate (Andersson and Cerenius, 2002). However,
354 to date, no strain-specific or genotype-specific expression has been found in the chitinase
355 activities of *A. astaci* (Andersson and Cerenius, 2002). Moreover, it has been suggested that this
356 expression pattern may be the result of an adaptation of the pathogen to a purely parasitic
357 lifestyle (Unestam, 1966; Andersson and Cerenius, 2002). Genomic work has identified three
358 major chitinase groups (CHI1, CHI2 and CHI3) existing in the different strains of *A. astaci*.
359 Depending on the strain considered, these genes showed structural differences in their coding
360 region, thus highlighting the variations in the epidemiological properties of the different
361 genotypes studied (Makkonen et al., 2012a).

362 Whole genome sequencing of *A. invadans* (strain NJM9701) in 2014 has enabled initial
363 exploration of the effector repertoire for this species (Makkonen et al., 2016). Recent analysis of
364 effectors encoded within the genome indicate that *A. invadans* encodes a sizeable number of
365 effector proteins, bearing more similarity to animal-pathogenic as opposed to plant-pathogenic
366 saprolegniales (Iberahim et al., 2018). Firstly, CAZymes are thought to play an important part in
367 *A. invadans* infection – although potentially not having such a pivotal role as during plant-
368 pathogenic *Aphanomyces* infections. Specifically, key CAZyme gene families, encoding CE1-
369 and CE10, are induced primarily in plant-pathogenic oomycetes (de Vries and de Vries, 2020).
370 Also of considerable interest are those effector classes typically associated with pathogenic
371 *Aphanomyces* species but lacking in *A. invadans*. Specifically, the *A. invadans* genome was
372 found to lack two major extracellular effectors: disintegrins and haemolysin-E (Iberahim et al.,

373 2018). These peptides are key protease effectors often secreted by animal-pathogenic oomycetes,
374 such as *Saprolegnia parasitica* (Banfield and Kamoun, 2013; Rzeszutek, 2019), both known to
375 play a significant role in oomycete virulence via mediation of host-cell binding (Banfield and
376 Kamoun, 2013). Proteases overall have long been recognized as key effectors of pathogenic
377 oomycetes (Schornack et al., 2009). Recent analysis of extracellular protease products from *A.*
378 *invadans* has found that, of these, serine proteases constitute the vast majority hence likely are of
379 central importance to virulence (Majeed et al., 2017).

380

381 **3.2.2 Intracellular effectors**

382 Intracellular oomycete effectors, meaning molecules that are addressed within the
383 cytoplasm of the host cell, were predicted years ago based on comparative genomics of known
384 virulence genes of oomycetes genomes (Tyler 2002). Two main protein families have been
385 predicted based on the presence of RxLR or LxLFLAK amino acid motif after the predicted
386 signal peptide in the plant pathogen *Phytophthora sp.* (Birch et al., 2008; Schornack et al., 2010).
387 Hundreds of genes encoding RxLR and CRN effectors are predicted and characterized in
388 Peronosporales oomycetes especially in *Phytophthora* genus (Rehmany et al., 2005; Schornack
389 et al., 2010).

390 In plant pathogenic *Aphanomyces* no RxLRs were found during the genome analysis, but
391 numerous CRNs were identified (Gaulin et al. 2018). In contrast the *A. invadans* genome was
392 found to lack those two major classes of effectors (Iberahim et al., 2018), while around 31 CRN-
393 like genes were identified in *A. astaci* (Gaulin et al., 2018). The first reported putative
394 intracellular effector from *A. euteiches* AeCRN5 was described in 2010 (Schornack et al., 2010)
395 although its function within the cell is still unknown. Another member of CRNs effectors in *A.*
396 *euteiches*, AeCRN13, was found to target host nuclei and possesses DNA damage activity
397 (Ramirez-Garcés et al., 2016). The triggered DNA damage response induces severe plant
398 necrosis. Interestingly, the homolog of AeCRN13 from the batracian pathogen *Batrachochytrium*
399 *dendrobatidis* also targets host nuclei and induces DNA-damage responses (DDR). It seems that
400 nuclear targeting and DNA damage is an important strategy of pathogenesis for *Aphanomyces*
401 spp. (Camborde et al., 2019). A third class of oomycete effectors was recently reported in the
402 genus *Aphanomyces* (Gaulin et al. 2018). *Aphanomyces* SSPs for Small Secreted Proteins were
403 named in analogy with fungal SSPs (Rep, 2005) and characterized as proteins with a signal

404 peptide, <300 amino acids in size and without any functional domain predicted. In *A. euteiches*
405 296 SSPs are predicted, and numerous are organized in cluster (Gaulin et al. 2018). SSPs have
406 also been detected in *A. astaci*. Functional studies have shown that SSPs from *A. euteiches* can
407 target plant nuclei and modify activity of plant DEAD-box RNA helicase to enhance *A. euteiches*
408 infection (Camborde et al., 2020). These effectors appear to be a promising area of research to
409 improve our understanding of the molecular factors involved in the virulence of *A. euteiches*.

410 Recently, the intracellular chaperone Lhs1 has also been identified as an important
411 modulator of virulence in *A. invadans* (Iberahim et al., 2020). This study of RNAi-based Lhs1
412 silencing demonstrated significantly reduced virulence in a *Galleria melonella* infection model,
413 likely due to the role of Lhs1 as an important regulator in oomycete and fungal zoospore
414 production (Chen et al., 2019; Iberahim et al., 2020). Due to limited knowledge of both
415 extracellular and intracellular *A. invadans* effectors, further research in this field is warranted.
416 Specific to *A. invadans*, a contemporary study successfully targeted the serine protease gene of
417 this species using single-guide RNAs via the Crispr/Cas9 editing system (Majeed et al., 2018).
418 Zoospores genetically edited in this manner did not produce clinical signs of EUS during *in-vivo*
419 infection trials of the ornamental fish *Trichogaster lalius* (Majeed et al., 2018), suggesting the
420 viability of genome editing as a potential technique for combatting epizootic ulcerative syndrome
421 specifically.

422

423 **4. Economic impact of *Aphanomyces* spp.**

424 *Aphanomyces* spp. cause a dramatic economic impact on various sectors of agri- and
425 aquaculture businesses. In general, it is very difficult to precisely calculate the impact caused by
426 *Aphanomyces* spp. as it includes direct yield loss, implementation of protective measures such as
427 crop rotation in the fields and conservation strategies in aquatic environments.

428

429 **4.1 Damage to agriculture**

430 Among the most relevant *Aphanomyces* species in agriculture special attention must be
431 given to *A. euteiches* and *A. cochlioides* being responsible for the root rot disease in two of the
432 most economically important crops such as pea and sugar beet, respectively. Pea is the second
433 most important food legume crop in the world (Ali et al., 1994) and is cultivated primarily in

434 Canada, Russia, the United States, France, and Australia (Tulbek et al., 2016). Sugar beet is a
435 major crop in temperate regions providing about 20% of sugar worldwide and it dominates the
436 market in the European Union and the United States (Finkenstadt, 2014). Although crop losses
437 caused by these two species can be difficult to estimate, the majority of yield loss in pea and
438 sugar beet can be attributed to root rot rather than other diseases (Papavizas and Ayers, 1974).
439 Very raw estimation of pea yield loss due to root rot complex is around 10% (Allmaras et al.,
440 1998), which in the current market could cost up to 600 million US dollars (transparency market
441 research). The root rot disease complex of legumes is usually an association of *A. euteiches* with
442 *Fusarium* spp., *Pythium* spp. and *Rhizoctonia solani*. This complex triggers damping-off, root rot
443 and reduces root development and nitrogen fixation (Gossen et al., 2016). *A. euteiches* is present
444 in over 90% of fields diagnosed with root rot in Canada (Wu et al., 2018). The yield loss caused
445 by *A. euteiches* could be as high as 70-80% in heavily infested fields (Pfender and Hagedorn,
446 1982; Bogdan, 2019). *A. cochlioides* has a great impact on sugar beet production and has a
447 world-wide distribution representing a big threat in many areas of the United States, Europe and
448 Asia (CABI, 2020b). About 51% of 293.000 ha of sugar beet field was estimated to be infested
449 with *A. cochlioides* in Minnesota and North Dakota in 1999 (Beale et al., 2002). In USA 42.8
450 million dollars per year is lost to *A. cochlioides* with current management practices such as
451 application of the fungicide Tachigaren on seeds, whereas 243.5 million dollar is lost when no
452 treatment or agronomic practices are used (information given by the Beet Sugar Development
453 Foundation, BSDF, 2020). *A. cochlioides* is also often part of a root rot complex in association
454 with *Fusarium* spp and *Rhizoctonia solani* (Harveson and Rush, 2002).

455

456 **4.2 Damage to aquaculture**

457 *A. invadans* is the causative agent of Epizootic Ulcerative Syndrome (EUS)
458 (Huchzermeyer and Van der Waal, 2012), a seasonal oomycete disease affecting both wild and
459 farmed fish within fresh and brackish water (OIE, 2016). EUS due to *A. invadans* is
460 economically devastating to aquaculture at a global level, with losses from this disease at
461 infected farms frequently reaching one hundred percent (Iberahim et al., 2018). While no
462 worldwide data exists from the past three decades, within the Asia-Pacific region alone the most
463 recent estimates indicate that EUS caused a loss of circa USD 110 million between the late 1980s
464 and early 1990s. (Lilley et al., 1998; Majeed et al., 2017).

465 Since 1990, the global aquaculture industry has expanded enormously (FAO, 2020). In
466 1990, the global output of the aquaculture sector was circa 14 million tons (FAO, 1991) and has
467 since increased fivefold to 81.8 million tons in 2018 (FAO, 2020). Furthermore, the region with
468 greatest recent growth in aquaculture, warmwater Asia, is also the region that is most susceptible
469 to *A. invadans* (FAO, 2020). Due to both above factors, alongside minimal effective treatment
470 options, contemporary global aquaculture losses to EUS are likely huge. Nationally, culturing of
471 major carps in India (Pradhan et al., 2008; Kamilya and Kollanoor, 2020) and various
472 snakeheads (*Channa* sp.) in Thailand (Lilley et al., 2003; Arshad and Arockiarai, 2020) are most
473 adversely impacted by EUS. Non-Asian countries tend to provide a less suitable climate and
474 temperature for *A. invadans*, hence outbreaks in aquaculture non-Asian countries are often less
475 costly (Kamilya and Kollanoor, 2020). Within North America, *A. invadans* is often present in
476 freshwater bodies (Saylor et al., 2010). However, EUS outbreaks seldom occur and a 2010 mass
477 mortality in Florida of 300 captive snakehead fish (*Channa marulius*) was highly unusual
478 (Saylor et al., 2010).

479 The source of introduction of the crayfish plague pathogen *A. astaci* in Europe during the
480 19th century was never established. This pathogen has caused devastating damage to native
481 European crayfish populations, mainly concerning the species *Austropotamobius pallipes* (white-
482 clawed crayfish), *Austropotamobius torrentium* (stone crayfish), *A. astacus* (noble crayfish) and
483 *Pontastacus leptodactylus* (narrow-clawed crayfish) (Holdich et al., 1995; Westman, 1995;
484 Alderman, 1996; Machino and Diéguez-Uribeondo, 1998). Nevertheless, data on the real
485 economic impact of this disease are rather unknown. Historically, native European crayfish have
486 been widely used as a food source (especially in poor areas, since the catch was not regulated),
487 mainly through the cropping of the native species *A. astacus* and *P. leptodactylus* (CABI,
488 2020a). However, the crayfish plague has drastically reduced the production of native species,
489 reducing stocks by up to 90% in some countries, mainly in Scandinavia, Germany, Spain and
490 Turkey (Lodge et al., 2000). For instance, data from the beginning of the 20th century report that
491 noble crayfish *A. astacus* exports from Sweden dropped from 90 tons in 1908 to only 30 tons in
492 1910 (Brinck, 1975). Similarly, in Finland, exports fell from 16 million *A. astacus* individuals in
493 1880 to less than 2 million in 1910 (Westman, 1991). The economic impact of the crayfish
494 plague is best described since its introduction in Turkey in the 1980s, where fished crayfish
495 stocks declined from 8,000 tons in 1984 to less than 500 tons between 1990 and 1994 as a result

496 of the disease (Ackefors, 2000). Thus, even though no native European species has been
497 extinguished by the disease, the range and local abundance of populations has drastically
498 decreased due to *A. astaci* (CABI, 2020a). *A. astaci* is moreover considered as one of the “100 of
499 the World’s Worst Invasive Alien Species”, according to the Global Invasive Species Database
500 (Lowe et al., 2000).

501 Another direct economic impact of *A. astaci* to consider is the cost of native crayfish
502 conservation strategies, which are directly impacted by the spread of crayfish plague through the
503 European continent. Currently, crayfish plague has been detected and potentially implicated in
504 outbreaks in at least 20 countries, spreading over 3,500 km from North (Finland) to South
505 (Spain) and over 3,000 km from East (Turkey) to West (Spain) (Ungureanu et al., 2020),
506 highlighting its presence and impact throughout entire Europe. Furthermore, over the past 20
507 years, the cost of conservation programs has reached several million US dollars to the economies
508 of most European countries (CABI, 2020a). However, the budget allocated to the conservation of
509 native European crayfish has never been recorded to our knowledge.

510

511 **5. Diseases caused by *Aphanomyces* spp. and management strategies**

512 The next section reported on the diseases due to *Aphanomyces* spp. and strategies to limit
513 the impact of the microorganism on agri and aquaculture.

514 **5.1 *Aphanomyces* root rot in peas, alfalfas and lentils**

515 *A. euteiches* induces root rot of the host plant and dramatically decreases the yield or
516 even induces death of plants in the fields. Legumes are susceptible to *A. euteiches* throughout
517 their life cycle and the first symptoms can be seen 3-4 days after infection (Papavizas and Ayers,
518 1974). The primary inoculum of *A. euteiches* in the field are oospores, which keep germination
519 ability for ten years (Schren, 1960). The most favourable conditions for *A. euteiches* pea
520 infection appears in wet periods, when moisture in soil induces massive production of swimming
521 zoospores and their spread within the field (Hoch and Mitchell 1973; Gaulin et al., 2007; Wu et
522 al., 2018). At early-stages of infection *A. euteiches* induces softened and water-soaked zones on
523 roots (Hughes and Grau 2007). At the later stages of infection, roots impair in function and in
524 nodulation therefore secondary symptoms appear such as chlorosis, necrosis and wilting of the
525 foliage (Papavizas and Ayers, 1974, Hughes and Grau 2007) (Figure 3A).

526 No efficient chemical protection against *A. euteiches* is known, in addition it seems that effective
527 fungicides against individual soilborne pathogens as *Aphanomyces* spp. are less efficient against
528 soilborne pathogens complexes (You et al., 2020). Without chemical control available, several
529 microorganisms have been tested for biological control of *A. euteiches*. Promising effects have
530 been observed *in vitro*, but slight effects on root rot emergence are generally observed in field
531 conditions (Wakelin et al., 2012 ; King and Parke 2013). Thereby crop management remains the
532 most effective tool to limit legumes root rot. One recommendation to improve management of *A.*
533 *euteiches* root rot in legumes field is crop rotation with different periods to diminish the
534 pathogen level in soils overtime. Nevertheless the diversity of alternative hosts in combination
535 with the extraordinary longevity of *A. euteiches* oospores in soil, reduces the efficiency of this
536 method (Schren, 1960, Moussart et al., 2009). Another recommendation is to seed plants into soil
537 rich in phosphorus, as it delays disease development (Bødker et al., 1998). Finally there are DNA
538 tests to check the presence of *A. euteiches* in suspect soils, root tissues or seeds (Gangneux et al.,
539 2014; Barker 2018). While improved procedures and reproducibility of DNA testing are needed,
540 these tools are useful for implementing disease management practices when the pathogen is
541 present.

542 For the past two decades, the obtention of resistant pea cultivars has been considered as a major
543 objective in France to secure the yields (Quillévéré-Hamard et al, 2021). The strategy of the pea
544 breeding program launched in 1995 relies on pyramidizing of different genetic loci from partially
545 resistant pea lines (Gritton, 1990; Kraft, 1992; Pilet-Nayel et al., 2017). The first Quantitative
546 Trait Loci (QTL) of resistance were described in some pea accessions by Pilet-Nayel et al. in
547 2002 and 2005, and the first varieties with partial *A. euteiches* resistance were registered in 2012
548 (McGee et al., 2012). Genome-wide association mapping using 175 lines of pea validated 52
549 QTL of small size-intervals associated with resistance to *A. euteiches* (Desgroux et al., 2016).
550 Among them six major QTL were verified. These studies along with the availability of GenoPea
551 SNP Array (Tayeh et al., 2015) will facilitate the development of resistant cultivars. One of the
552 major QTLs in pea is Ae-Ps7.6 which explains over 50% of phenotypic variations using a
553 collection of reference *A. euteiches* strains (Hamon et al., 2011, 2013). Combination of Ae-Ps7.6
554 with other QTLs delays symptom onset and slows down root colonization (Lavaud et al., 2016).
555 The effect and stability of the QTL were validated using the large collection of *A. euteiches*
556 strains from different regions of France (Quillévéré-Hamard et al., 2021), therefore the

557 AeD990SW45-8-7 line, which harbours the combination of 4 major QTL Ae-Ps1.2, Ae-Ps2.2,
558 Ae-Ps3.1 and Ae-Ps7.6 might be used as a source of resistance in further pea breeding programs
559 (Desgroux et al. 2016). In alfalfa, there are at least two significant races (*i.e.*, race1 and race2)
560 that are detrimental to the crop. Alfalfa resistant cultivars to race 1 were released in the 1990's
561 (Grau, 1992), but the resistance was rapidly overcome by the pathogen leading to the discovery
562 of the race 2 and the development of race2-resistant alfalfa cultivars. By now *A. euteiches*
563 isolates able to knock out race1 and race2-resistance have been identified in the US (Samac et
564 al., 2012; Seitz and Rouse 2012). The emergence of a putative new race of the pathogen reveals
565 the difficulties to obtain alfalfa cultivars displaying a durable resistance to *Aphanomyces* root rot.
566 In lentil, the first QTL mapping and genome-wide association studies identify seven QTL
567 clusters and 15 putative genes within the cluster associated with *Aphanomyces* resistance (Ma et
568 al., 2020). This finding, in association with image-based phenotyping approaches on roots
569 (Marzougui et al., 2019), will enhance the development of lentil cultivars with partial resistance
570 to *A. euteiches*.

571 The complete genome sequence of reference pea 'Cameor' line became available in 2019
572 (Kreplak et al., 2019) and chromosome-level genome of alfalfa in 2020 (Chen et al., 2020).
573 There are no doubts that these resources will facilitate research in resistance mechanisms of these
574 crops and transfer of knowledge previously obtained using closely related model legume
575 *Medicago truncatula*. As a legume model *M. truncatula* offers various techniques for molecular
576 studies such as high-quality genome, transient and stable transformation, and fast generation
577 cycle (Bruijn, 2020). An *in vitro* system which allows to test susceptibility of 157 *M. truncatula*
578 lines against *A. euteiches* and demonstrates natural variation of susceptibility was reported
579 (Djébali et al., 2009; Bonhomme et al., 2014). From the study one susceptible (F83005.5) and
580 two tolerant lines (Jemalong A17 and DZA45.15) were selected for molecular studies (Badis et
581 al., 2015; for review see Jacquet and Bonhomme, 2019) to decipher tolerant mechanisms. One
582 of the major features of tolerant Jemalong A17 line is the development of 'ring of lignin' which
583 protects central cylinder from invasion of *A. euteiches* into vascular tissue and therefore ensures
584 the maintenance of nutrient and water supply in the plant (Djébali et al., 2009). Pathogen attack
585 induces complex remodelling of the host metabolism such as phenolic compounds. One of the
586 most induced genes of the tolerant A17 *M. truncatula* line under *A. euteiches* infection is
587 isoliquiritigenin 2'-O-methyltransferase transforming isoliquiritigenin to 2'-O-

588 methylisoliquiretin. The latter was shown to inhibit *A. euteiches* zoospores germination by
589 72-86% (Badis et al., 2015). Genome-wide association studies of quantitative resistance to *A.*
590 *euteiches* identified two major loci on the chromosome 3 of *M. truncatula* (Djébali et al., 2009).
591 A candidate gene encoding an F-box protein was characterized as a negative regulator of
592 resistance to *A. euteiches* (Bonhomme et al., 2014). In addition significant SNPs were identified
593 within an adenylate isopentenyltransferase (IPT) involved in cytokinin biosynthesis, and/or a
594 MYB transcription factor regulated by gibberellin and abscisic acid (GAMYB) (Bonhomme et
595 al., 2014; Jacquet and Bonhomme, 2019). Thus the integration of genomic and genetic
596 technologies with adapted breeding designs will accelerate legume improvement needed to
597 counter *Aphanomyces* root rot.

598

599 **5.2 *Aphanomyces* root rot in sugar beet**

600 *A. cochlioides* is the causal agent of the black root rot in sugar beet. The disease can lead
601 to the loss of entire sugar beet fields and to a drastic reduction of sugar yield (Papavizas and
602 Ayers, 1974; Taguchi et al., 2010). The infection can occur in two separate phases during the
603 sugar beet life cycle: an early, acute phase, known as damping-off, on 2- to 5-week-old seedlings
604 and a chronic phase, later in the season on mature roots (Papavizas and Ayers, 1974). The acute
605 phase generally occurs in post-emergence and it is favoured by warm soil temperature (20-30°C)
606 and moist conditions (Panella and Lewellen, 2005). Infected hypocotyls turn into a dark, thin
607 thread (Harveson, 2006) and seedlings may fall over and die (Taguchi et al., 2009). If warm and
608 wet conditions persist in the soil, the damage can lead to total crop failure (Luterbacher et al.,
609 2005) but if the soil dries and temperature decreases, young roots may recover by developing
610 later roots and survive (Papavizas and Ayers, 1974). The chronic phase occurs on older plants in
611 late June to August (Buchholtz, 1944). Infected roots appear soft and water-soaked and are
612 characterized by a dark brown discoloration on the affected area (Papavizas and Ayers, 1974)
613 (Figure 3B, C). Roots can be severely stunted and often show rotted, tasselled root tip (Windels,
614 2000). The infection, when severe, results in the death of the plants, however older roots that
615 recover from damping-off infection or that are infected in a later stage can survive but are
616 characterized by reduced yield and low sugar content (Windels, 2000). While the effects of
617 *Aphanomyces* damping-off can be overcome by the application of fungicides such as hymexazol,
618 no effective strategies have been developed for the control of the chronic phase of the black rot

619 disease (Taguchi et al., 2010). Cultivation practices such as early planting, enhanced drainage or
620 application of “spent lime” (calcium carbonate) in sugar beet field as pH adjustment in the soil
621 can help to reduce the effect of *Aphanomyces* on sugar beet yield (Bresnahan et al., 2001;
622 Brantner and Chanda, 2016). However, in highly infested soils these practices are inadequate for
623 economic yields. Crop rotation is also not efficient because of the persistence of the pathogen in
624 the soil (Takenaka and Ishikawa, 2013). The development of resistant varieties remains the only
625 valuable solution to control the disease but the genetic basis of resistance to *A. cochlioides* is still
626 unclear. Bockstahler et al. (1950) indicated that the resistance to *Aphanomyces* is heritable and
627 dominant, but important details such as number, map position and products of resistance genes
628 remain unknown (Taguchi et al., 2009). Taguchi et al. (2010) have identified a single dominant
629 gene, *Acr1* (*A. cochlioides* resistance 1) that confers resistance to *Aphanomyces* root rot in both
630 greenhouse conditions and in *Aphanomyces*-infested field and such gene has been located on
631 chromosome III in sugar beet genome. Several genes and major QTLs associated with the
632 resistance to important sugar beet diseases such as Rhizomania and Cercospora leaf spot have
633 been mapped on the same chromosome (Barzen et al., 1997; Schäfer-Pregl et al., 1999; Scholten
634 et al., 1999; Setiawan et al., 2000; Gidner et al., 2005; Grimmer et al., 2007) highlighting the
635 importance of *Acr1* in sugar beet breeding to *Aphanomyces*-caused disease.

636

637 **5.3 Epizootic ulcerative syndrome (EUS) caused by *A. invadans***

638 *A. invadans* typically infects the juvenile and young adult stages of fishes, with no
639 documented pathogenicity towards larvae and fry (OIE, 2016). The severity of EUS infection
640 varies considerably depending on culture conditions of affected fish. Mortality and morbidity
641 within a typical aquaculture scenario, snakehead species (*Channa* sp.), are both highest
642 (exceeding 50%) when water temperatures remain between 18-22°C for an extended time (OIE,
643 2016). Therefore, protracted periods of low (sub-22°C) temperature throughout summer
644 alongside heavy rainfall appear to be the major environmental factors which increase severity of
645 EUS outbreaks.

646 Characteristic external clinical signs of EUS are uniform across the majority of affected species
647 and in order of diagnostic significance include: dermal ulceration, erratic swimming and
648 inappetence, with increasing symptoms as the disease progresses (Blazer et al., 2002; Saylor et

649 al., 2010). Due to the non-specific external clinical signs, a molecular approach to diagnosis
650 involving PCR-based internal transcribed spacer sequencing (Vandersea et al., 2006; Kamilya
651 and Kollanoor, 2020) is used to positively identify *A. invadans* at fish farm outbreaks.
652 Nonetheless, the characteristic dermal ulceration caused by *A. invadans* has been deemed an
653 appropriate presumptive diagnosis for EUS (Bondad-Reantaso, 1992). Death, generally caused
654 by internal mycosis or loss of osmotic balance, typically occurs within 1-4 days post-infection
655 (Saylor et al., 2010). Internal clinical signs of EUS are similarly uniform across infected fish
656 species: mycotic granulomas form as *A. invadans* hyphae penetrate through dermal tissue and
657 into the target organ of the host – skeletal muscle (OIE, 2016). Mycotic granulomas, the typical
658 internal pathology associated with EUS, may also be present throughout other internal organs.

659 EUS is a highly difficult disease to treat within commercial aquaculture, therefore the
660 most common approach currently undertaken by farmers is immediate destruction of infected
661 stock (Herbert et al., 2019). No antibiotic treatments are commercially available for *A. invadans*
662 (Iberahim et al., 2018). Furthermore, the two chemotherapeutics with demonstrated efficacy
663 against *A. invadans*, malachite green and formalin, are tightly regulated globally and hazardous
664 to human health and the environment (Srivastava et al., 2004; Iberahim et al., 2018). Use of
665 malachite green in aquaculture is currently prohibited worldwide (Zhou et al., 2019).
666 However, recent *in-vitro* testing of antifungals against *A. invadans* has yielded encouraging
667 results. Formalin, KMnO₄ and Fluconazole show considerable inhibitory action against zoospore
668 germination and hyphal growth of *A. invadans* at 10ppm, 100ppm and 1ppm respectively (Paria
669 et al., 2020). The activity of KMnO₄ and Fluconazole against *A. invadans* had been little-studied,
670 with these candidates currently showing the greatest promise in the search for chemical EUS
671 treatments.

672 Regarding immunostimulants, use of pro- and prebiotics for disease management in
673 aquaculture is an emerging field (Verschuere et al., 2000), with strong potential in the shrimp
674 sector and industry-wide (Lara-Flores, 2011; Kumar et al., 2016). Regarding *A. invadans*, two
675 recent immunostimulant trials have demonstrated efficacy as in-feed treatments for EUS (Devi et
676 al., 2019a, 2019b).

677

678 **5.4 Crayfish plague caused by *A. astaci***

679 When a native European crayfish population is affected by *A. astaci*, one of the first
680 observable symptoms is often the presence of numerous crayfish visible in broad daylight
681 (whereas crayfish are most often active at night). Indeed, clinical symptoms at the individual
682 level are manifested by behavioural changes (such as changes in feeding behaviour, in swimming
683 movement, lethargy), as well as the appearance of visible lesions (Figure 3E) on the cuticle
684 (CABI, 2020a). However, these lesions are not specific to aphanomycosis and may be caused by
685 mechanical injury or infection with other fungal or bacterial pathogens (Persson and Söderhäll,
686 1983). However, unless aquatic environments are particularly monitored, the first sign of
687 infection at the population level is the presence of many dead crayfish observed (Figure 3D),
688 with no mortality in other aquatic animal species (which could be possibly due to pollution effect
689 or to a less specific pathogen) (Alderman et al., 1987). Currently, the most reliable and
690 commonly used diagnostic techniques are based on PCR tests, either followed by a sequencing
691 step (Oidtmann et al., 2006) or directly by real time PCR approaches from the cuticle of dead
692 individuals found in the wild (Vrålstad et al., 2009). In recent years, the development of
693 techniques based on environmental DNA (eDNA) has been a promising tool for the detection of
694 plague directly in water samples, allowing an early management of this pathogen potentially
695 present in aquatic systems, as well as a better understanding of the spread of this disease in the
696 natural environment (Strand et al., 2014; Wittwer et al., 2018, 2019).

697 These recent detection techniques have made it possible to identify several populations of
698 native European crayfish (*A. astacus*, *P. leptodactylus* and *A. torrentium*) that are chronically
699 infected by the crayfish plague, notably in Finland, Turkey, Slovenia or Spain (Jussila et al.,
700 2011; Kokko et al., 2012; Kušar et al., 2013; Maguire et al., 2016). When it was verified, it turns
701 out that haplogroups A and B were involved in these chronic infections (Maguire et al., 2016).
702 These observations raised the question of the potential virulence of the different strains of *A.*
703 *astaci*, but also the question of the potential immunological resistance developed by natural
704 populations of European crayfish. Thus, following infections carried out in a controlled
705 environment using *A. astacus* crayfish to estimate mortality rates, it was also shown that RAPD-
706 groups B and E were more virulent than the RAPD-group A. A recent study revealed resistance
707 and susceptibility of European crayfish to *A. astaci* could depend on the population origin

708 (Jussila et al., 2020). In the case of resistant North American crayfish, they have developed
709 immune defences that prevent a fatal *A. astaci* infection.

710

711 **6. Conclusion and perspectives**

712 *Aphanomyces* genus comprises a vast number of species including both plant and animal
713 pathogenic species and saprophytic species (Diéguez-Uribeondo et al., 2009). Due to their
714 remarkable economic impact on agriculture and aquaculture systems, their worldwide
715 distribution, species belonging to this genus have been receiving growing attention from the
716 oomycete research community with a major focus on pathogenicity and host resistance
717 mechanisms.

718 To secure the production of economically important *Aphanomyces* spp. hosts we suggest several
719 directions for further studies:

- 720 ● Enhance our understanding of *Aphanomyces* spp. pathogenesis on molecular level and
721 elucidate the role of effectors and their interaction with the host during infection;
- 722 ● Exploit the natural variation of resistance against *Aphanomyces* spp. in commercial
723 breeding;
- 724 ● For plant pathogenic species, begin studying the role of soil microbiome in stimulation or
725 protection against *Aphanomyces*-induced diseases.
- 726 ● For animal pathogenic species, combine the analysis of *Aphanomyces* spp. effectors with
727 the immunological response of the host to better understand and control the spread of
728 those pathogens in natural environments.

729 **7. References**

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1357 **Conflict of Interest**

1358 The authors declare that they have no conflict of interest.

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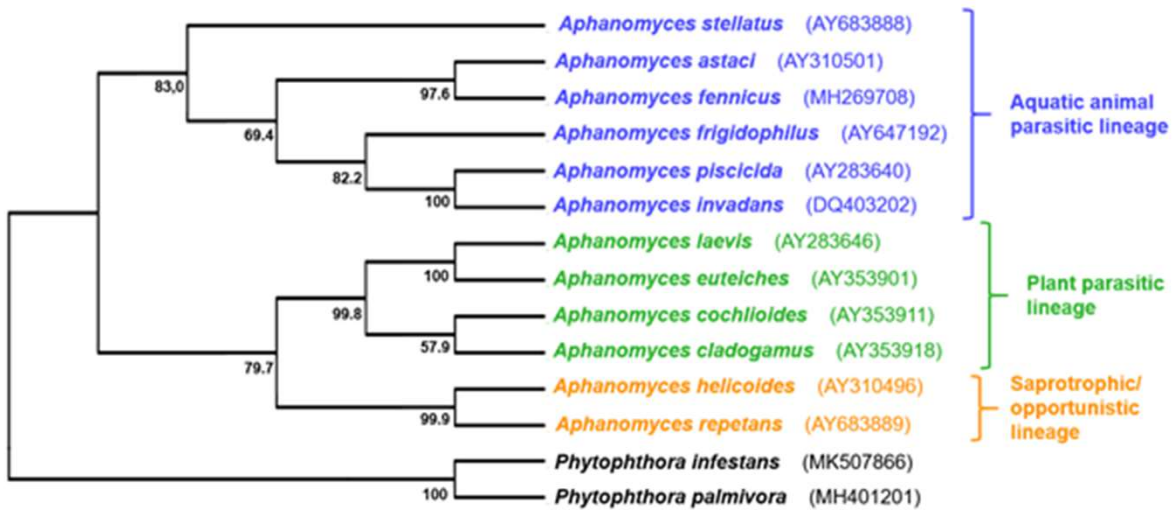


Figure 1: Cladogram of *Aphanomyces* species showing the three major lineages based on the host category. The phylogeny is based on 5.8S ribosomal RNA gene with a 691 nucleotides alignment length. Phylogenetic reconstruction was performed with PhyML 3.0- (Guindon et al., 2010), under the GTR + G substitution model (assessed with jModelTest 2.1.7, (Darriba et al., 2012)) and was tested with the Bootstrap method (1,000 replicates). The identifier written between brackets correspond to the NCBI accession number of the used sequences.

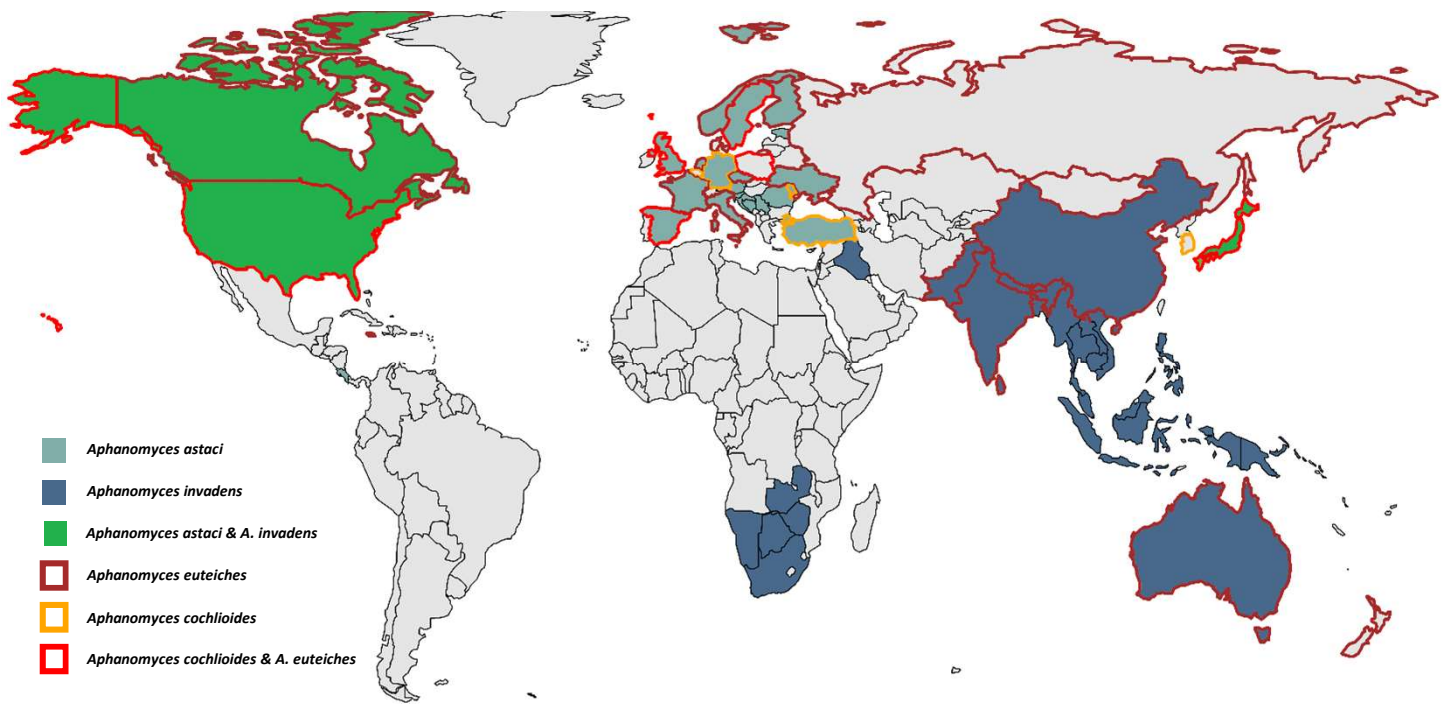


Figure 2: Occurrence of *A. astaci*, *A. invadans*, *A. euteiches* and *A. cochlioides* worldwide. Countries are labelled in colours according to *Aphanomyces* species presence. *A. astaci* is actually founded in 24 countries (North America and Europe), and 28 countries have experienced an outbreak caused by *A. invadans* (North America, South Africa, South East of Asia and Oceania), 21 countries have experienced an outbreak caused by *A. euteiches* (North America, South America, Europe, Asia and Oceania) and 11 countries have experienced an outbreak caused by *A. cochlioides* (North America, Europe and Asia). To summarize, a total of 56 countries are known to have experienced an outbreak caused by one of the four *Aphanomyces* species studied in this review. All these countries are listed in the supplementary table 1.

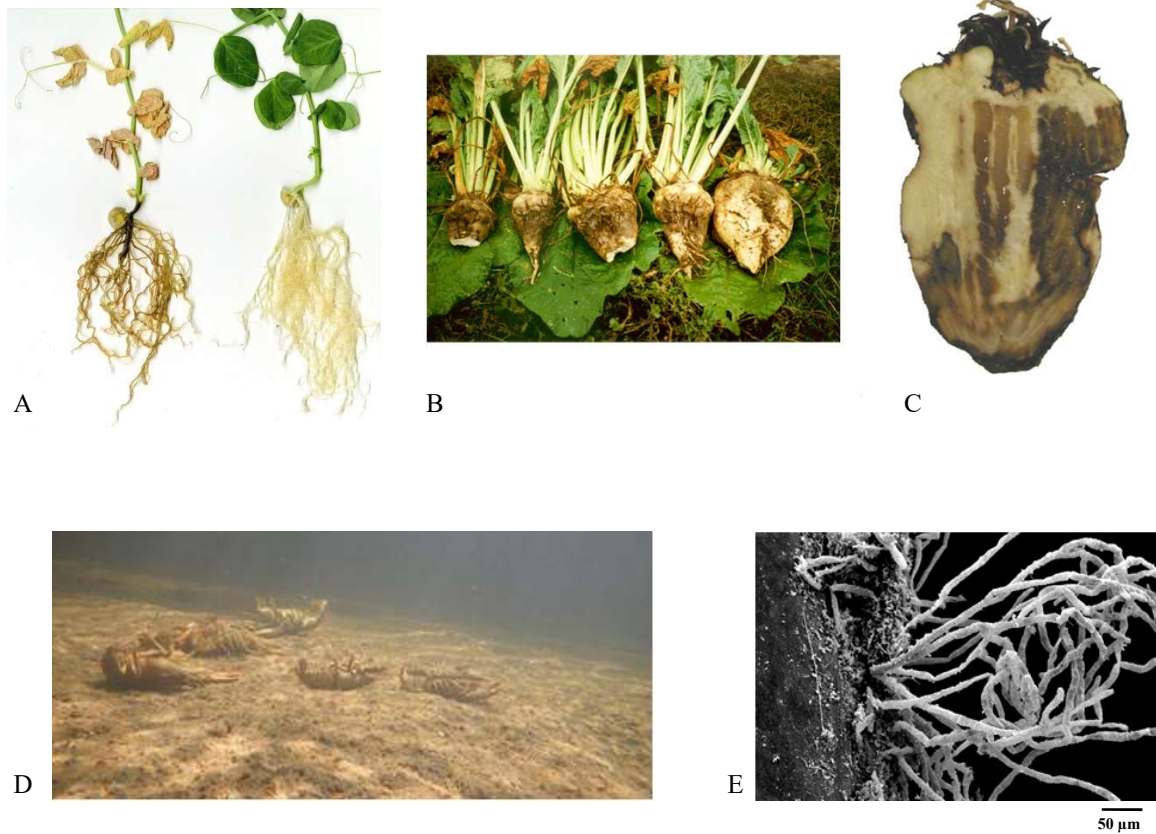


Figure 3: Symptoms of diseases induced by *Aphanomyces* genus. (A) *A. euteiches* root rot symptoms on dry pea (*Pisum sativum*) cv. Cameor. At 34 days after inoculation with zoospore suspension at root level, *A. euteiches* induces browning of roots; impaired root growth and induces yellowing of leaves Left : infected. Right: control, non-infected (pictures, A. Kiselev, LRSV, France). (B,C) *A. cochlioides* root rot on sugar beet: dark-brown and scabby lesions on sugar beet roots infected in field and longitudinal section of a sugar beet root with water-soaked lesions (pictures provided by Maribo Hillesthög Research AB, Sweden). (D, E) White-clawed crayfish mass mortality in Lucelle brook (France) (Collas et al., 2016) and *A. astaci* hypha (in white) in naive infected crayfish (pictures from scanning electron microscope provided by UMR CNRS 7267, France).