Mycopathologia (2010) 169:403–412
DOI 10.1007/s11046-010-9272-y

Morphological and Molecular Characterization of the Causal Agent of Downy Mildew on Quinoa (*Chenopodium quinoa*)

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Received: 19 March 2009 / Accepted: 9 January 2010 / Published online: 27 January 2010

Abstract Downy mildew is an economically important and widespread disease in quinoa (*Chenopodium quinoa*) growing areas. Although in many studies *Peronospora farinosa* is most commonly regarded as the causal agent of the disease, identification and classification of the pathogen remain still uncertain due to its taxonomic confusion. Thirty-six *Peronospora* isolates from quinoa with different geographic origins including Argentina, Bolivia, Denmark, Ecuador, and Peru were morphologically and molecularly compared with *Peronospora* species from other *Chenopodium* species. The morphology of three herbarium specimens was similar to that of *P. variabilis*, which originated from *C. album*, characterized by flexuous to curved ultimate branchlets and pedicellated conidia. Phylogenetic analysis based on ITS rDNA sequences also placed the quinoa pathogen within the same clade as *P. variabilis*. Within the ITS rDNA sequences of the quinoa pathogens, two base substitutions were found, which separated the majority of the Danish isolates from isolates from South America, but no sequence difference was found among the isolates from different cultivars of quinoa. The present results indicate that the pathogen responsible for the quinoa downy mildew is identical to *Peronospora variabilis* and that it should not be lumped with *P. farinosa* as claimed previously by most studies.

Keywords Chenopodiaceae · Geographic origin · ITS rDNA · Morphology · Peronosporaceae · Phylogenetic analysis

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Introduction

Quinoa (*Chenopodium quinoa* Willd.) is an important grain crop, which has been cultivated for more than 5,000 years in the Andean region of South America [1]. This ancient crop has recently gained worldwide

attention because of its high nutritional value and tolerance to various stress conditions like soil salinity, soil acidity, drought, and frost [2, 3]. It is now being cultivated in Africa, Asia, Europe, and North America [4], and many European countries are members of a major project entitled 'Quinoa-A multipurpose crop for EC's agricultural diversification (AIR2-CT92-1426)'. Downy mildew caused by a *Peronospora* sp. (Peronosporales, Oomycota) is the most damaging disease of quinoa in Argentina, Bolivia, Colombia, Ecuador, and Peru, and causes considerable yield loss of 33–58% even in the most resistant cultivars [5]. Reports of the disease from India [6] in Asia, Canada [7] in North America, and Portugal [8] and Denmark [9] in Europe have revealed its worldwide occurrence and spread.

Despite the economic importance and wide distribution of this disease, identification and classification of the causal agent are still uncertain due to taxonomic confusion of the pathogen. In most reports, it is classified as *Peronospora farinosa*, but recent morphological and molecular analyses have revealed that *P. farinosa* s.l. is a polyphyletic species complex with biological specialization toward specific genera or species within the family of Chenopodiaceae (now belonging to Amaranthaceae) [10–12]. Choi et al. [12] noted the existence of host-specific *Peronospora* species infecting *Chenopodium*. Therefore, the precise identification of the causal agent of downy mildew on *C. quinoa* is required to diagnose the disease correctly and to develop appropriate control strategies. Sequence analysis of the ITS rDNA has previously shown to be a very useful tool to compare closely related species within *Peronospora* [10–14]. The present study was undertaken to identify and characterize the pathogen responsible for downy mildew on quinoa by morphological and molecular traits.

Materials and Methods

Oomycete Isolates

Thirty-six isolates of *Peronospora* from *Chenopodium quinoa* were collected or loaned from Argentina (2), Bolivia (1), Denmark (22), Ecuador (7), and Peru (4). For comparison, further 30 sequences (Table 1), representing 25 isolates of *Peronospora farinosa* s.l. from *Atriplex*, four *Peronospora* species previously regarded as *P. farinosa*, namely *P. boni-henrici*, *P. chenopodii*, *P. chenopodii-polyspermi*, *P. variabilis*, and one unnamed species were included in the analyses. New ITS sequences were registered in GenBank. Herbaria abbreviations are those from Holmgren and Holmgren [15].

Morphological Analysis

Three herbarium specimens from Argentina and Bolivia were moistened with 70% alcohol and transferred to 60% lactic acid on a slide. The microscope preparations were heated, covered with cover slips, and examined in brightfield- and DIC- light microscopy, using a Olympus BX51 microscope (Olympus, Tokyo, Japan) for measurements and a Zeiss AX10 microscope (Carl Zeiss, Göttingen, Germany) mainly for photographs. Measurements were performed at 1000× for conidia and at 100–200× for other organs. They are reported as maxima and minima in parentheses, and the mean plus and minus the standard deviation of a number of measurements given in parenthesis. The means were given in italic in the center of the data.

Molecular Analysis

Genomic DNA was extracted from the 36 *Peronospora* isolates from quinoa using conidiophores and conidia formed on the lower surface of the infected host leaves. The DNA extraction was undertaken according to the method of Lee and Taylor [16] or a modified version of the protocol described by Griffith and Shaw [17]. The DC6 [18] and ITS4 [19] primers were used for the selective amplification of the complete ITS region of the rDNA with PCR conditions as described by Cooke et al. [18]. The PCR products were visualized on 1% agarose gels and purified using a QIAquick Gel Extraction Kit (Qiagen, Hilden, Germany). Purified DNA was directly sequenced on an automatic sequencer (ABI Prism TM 377 DNA Sequencer), using the BigDye^{TM} (Applied Biosystems, Foster City, CA, USA) Cycle Sequencing Kit, version 3.1, with primers ITS1, ITS2, ITS3, and ITS4 [19]. Sequences were edited with the DNASTAR computer package (Lasergene, Madison, WI), version 5.05. An alignment of the sequences was initially performed using the

Table 1 Information about the specimens used in this study

Species	Host (cultivar)	Geographic origin/year of collection (herbarium or isolate number)	GenBank accession no.
Peronospora boni-henrici	*Chenopodium bonus-henricus*	Austria, Tirol, 2000 (WU22886)	AY198286
	C. bonus-henricus	Bulgaria, Rhodopes, 1982 (SOMF15654)	EF614952
	C. bonus-henricus	Germany, Westfalen, 1920 (BPI787221)	EF614953
	C. bonus-henricus	Switzerland, Granbunden, 1971 (BPI787219)	EF614954
P. chenopodii	*C. hybridum*	Germany, Sachsen-Anhalt, 2001 (HAL) (ex H. Jage 3550/01)	EF614955
P. chenopodii-polyspermi	*C. polyspermum*	Austria, Upper Austria, 2000 (WU22891)	AY198291
	C. polyspermum	Germany, Mittelfranken, 1946 (BPI787538)	EF614956
P. farinosa s.l.	*Atriplex* sp.	Argentina, Dorrego, 2000 (RD 1459)	EU571109
	A. sp.	Iceland, Reykjavik, 1962 (UPS)	DQ643840
	A. littoralis	Sweden, Oland, 1959 (BPI789214)	DQ643841
	A. patula	Sweden, Västergötland, 1962 (UPS)	DQ643842
P. sp.	*Chenopodium ambrosioides*	Australia, N.S.W., 1965 (UPS) (ex DAR45530)	EF614957
	C. ambrosioides	Korea, Jeju, 2003 (KUS-F20063; BPI877765)	EF614958
P. sp.	*C. quinoa* (−)	Argentina, Villarino, 1997 (RD 1436)	EU571113
	C. quinoa (−)	Argentina, Jujuy, 1997 (RD 1437)	EU571114
	C. quinoa (−)	Bolivia, Colomi, 1953 (BPI788269a)	EU571108
	C. quinoa (Carmen)	Denmark, Give, 2001 (DK01)	EU113308
	C. quinoa (Atlas)	Denmark, Give, 2002 (DK02)	FJ638472
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK03)	FJ638473
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK04)	EU113306
	C. quinoa (Atlas)	Denmark, Taastrup/Rørrende, 2001 (DK05)	FJ638474
	C. quinoa (Carmen)	Denmark, Taastrup/Rørrende, 2001 (DK06)	FJ638475
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK07)	FJ638476
	C. quinoa (Atlas)	Denmark, Taastrup/Rørrende, 2001 (DK08)	FJ638477
	C. quinoa (Carmen)	Denmark, Taastrup/Rørrende, 2001 (DK10)	FJ638478
	C. quinoa (Carmen)	Denmark, Taastrup/Rørrende, 2001 (DK11)	FJ638479
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK12)	FJ638480
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK13)	FJ638481
	C. quinoa (Atlas)	Denmark, Taastrup/Rørrende, 2001 (DK14)	FJ638482
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK16)	FJ638483
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK18)	FJ638484
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK19)	FJ638485
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK20)	FJ638486
	C. quinoa (G205)	Denmark, Taastrup/Rørrende, 2001 (DK21)	FJ638487
	C. quinoa (Atlas)	Denmark, Taastrup/Rørrende, 2001 (DK22)	FJ638488
	C. quinoa (Atlas)	Denmark, Taastrup/Rørrende, 2001 (DK23)	EU113305
	C. quinoa (Carmen)	Denmark, Taastrup/Rørrende, 2001 (DK24)	FJ638489
	C. quinoa (Carmen)	Denmark, Taastrup/Rørrende, 2001 (DK25)	FJ638490
	C. quinoa (Ecu-251)	Ecuador, Pichincha, 2002 (EC04)	EU113303
	C. quinoa (Ecu-273)	Ecuador, Pichincha, 2002 (EC05)	FJ638491
	C. quinoa (Ecu-280)	Ecuador, Pichincha, 2002 (EC06)	FJ638492

Table 1 continued

Species	Host (cultivar)	Geographic origin/year of collection (herbarium or isolate number)	GenBank accession no.
	C. quinoa (Ecu-285)	Ecuador, Pichincha, 2002 (EC07)	FJ638493
	C. quinoa (Ecu-629)	Ecuador, Pichincha, 2002 (EC09)	FJ638494
	C. quinoa (Tunkahuan)	Ecuador, Pichincha, 2002 (EC10)	FJ638495
	C. quinoa (Oriental)	Ecuador, Pichincha, 2002 (EC11)	EU113309
	C. quinoa (Rosada de Junin)	Peru, Pasco, 2002 (PE01)	FJ638496
	C. quinoa (Mantaro)	Peru, Pasco, 2002 (PE03)	FJ638497
	C. quinoa (Amarilla)	Peru, Pasco, 2002 (PE04)	EU113304
	C. quinoa (Quillahuaman)	Peru, Pasco, 2002 (PE05)	FJ638498
P. variabilis	*C. album*	Argentina, Necochea, 1986 (RD90)	EU571110
	C. album	Argentina, Necochea, 1986 (RD774)	EU571111
	C. album	Argentina, Villarino, 1997 (RD1438)	EU571112
	C. album	China, Heilungjiang, 1981 (HMAS57036)	EF614959
	C. album	Germany, Oberhessen, 1964 (BPI791617)	EF614961
	C. album	Ireland, Dublin Co., 1935 (UPS)	EF614962
	C. album	Italy, Montesilvano, – (BPI791615)	EF614963
	C. album	Korea, Chunchon, 2000 (KUS-F17266)	AF528556
	C. album	Korea, Chunchon, 2000 (KUS-F17547)	AY211017
	C. album	Korea, Chunchon, 2002 (KUS-F18830)	EF614964
	C. album	Korea, Chunchon, 2003 (KUS-F19787)	EF614965
	C. album	Korea, Pyeongchang, 2000 (KUS-F17768)	EF614966
	C. album	Korea, Samchok, 2000 (KUS-F17289)	AF528557
	C. album	Latvia, Vidzema, 1932 (BPI791620)	EF614967
	C. album	Romania, 2000 (UPS)	AF465762
	C. album	The Netherlands, Zuid-Holland, 1932 (UPS)	EF614968
P. manshurica	*Glycine soja*	Korea, Chunchon, 1999 (KUS-F17669)	AY211019

Acronym: RD, R. Delhey (private collections) in the Phytopathology Lab of Bahía Blanca, Argentina

CLUSTAL X [20] program, and visually checked and refined with Se-Al version 2.0 (A. Rambaut, University of Oxford, UK). Phylogenetic trees were obtained from the data using maximum likelihood (ML), maximum parsimony (MP), and Bayesian methods (MCMC). For ML inference, RAxML version 7.0.3 [21] was used with all parameters set to default values, using the GTRCAT variant. A MP heuristic search was performed with 1000 random sequence additions and branch swapping by tree bisection-reconnection (TBR), using PAUP version 4b10. The relative robustness of the individual branches was estimated by bootstrapping (BS) using 10K replicates, each with ten rounds of heuristic searches with TBR branch swapping on trees generated by random sequence addition. The MCMC analysis was performed using the MRBAYES version 3.0b4 [22]. The general time reversible model (GTR) with rates estimated based on a γ distribution (α-parameter estimated from the data) was chosen for a given dataset using Modeltest 3.06 [23] and PAUP version 4b10 [24]. Four incrementally heated simultaneous Markov chains were run for 1M generations, with a tree saved every 100th generation. The first 1K trees generated via this method were ignored. MRBAYES was used to compute a 50% majority rule consensus of the remaining trees to obtain estimates for the posterior probabilities (PP) of groups. A *Peronospora manshurica* sequence was used as outgroup based on result of Choi et al. [10].

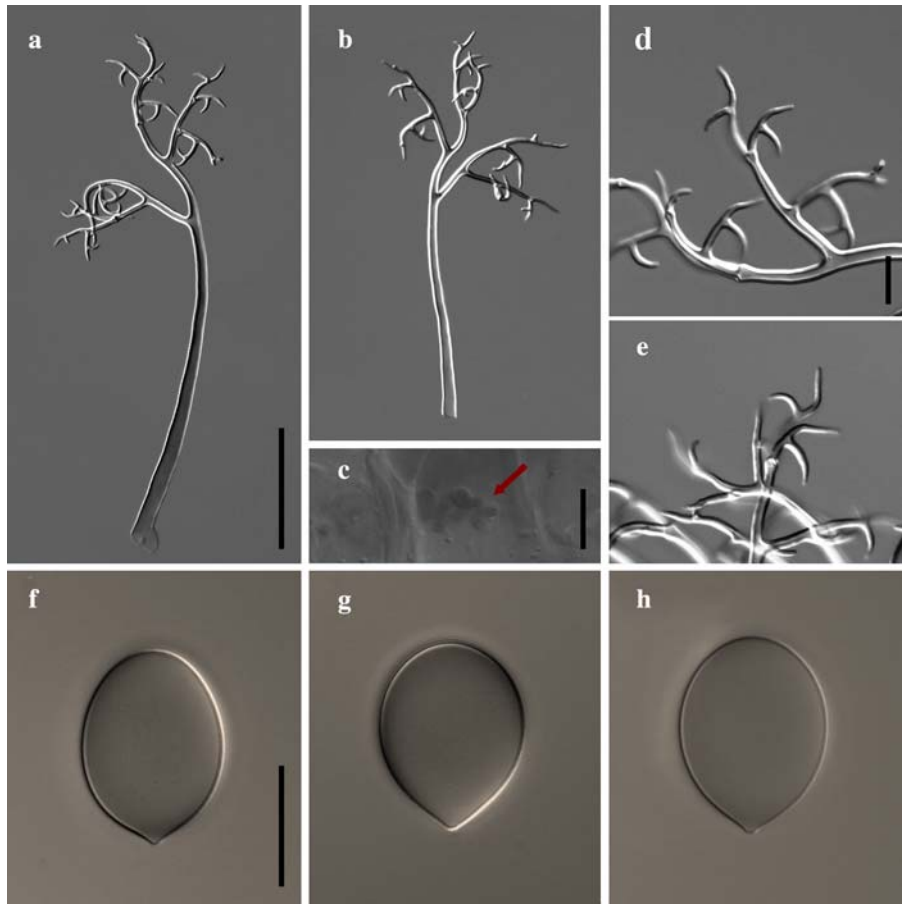

Fig. 1 *Peronospora variabilis* on *Chenopodium quinoa*. **a**, **b** Conidiophores, **c** haustorium, **d**, **e** branches, **f**, **g**, **h** conidia. *Scale bar* is 100 μm for **a**, **b**, 10 μm for **c**, and 20 μm for **d**–**h**

Results

Morphological Analysis

The morphological features of the quinoa downy mildew pathogen are summarized as follows (Fig. 1): *Haustoria* hyphal, often branched, without sheaths. *Conidiophores* emerging through stomata, colorless, straight to slightly curved, (320-)430-*480*-530(-600) μm long ($n = 89$); trunk substraight to slightly curved, (180-)270-*315*-360(-390) μm long ($n = 81$), basal end not differentiated, rarely bulbous, 12–17 μm wide at the base, 8–14 μm wide below the first branch, often slightly tapering upward, callose plugs rarely present; branches subdichotomously or monopodially branched in (4-)5-7 orders, slightly curved, elaborate, wall often thickening, callose plugs mostly absent; ultimate branchlets mostly in pair, with different lengths, (10-)14-*19.5*-25(-32) μm long in axial ($n = 60$), (5-)10-*12.0*-14(-17) μm in abaxial ($n = 62$), 2–3 μm wide at the base, from flexuous to curved, wall often thickening, apex obtuse or subtruncate. *Conidia* pale brown to olivaceous, varied in shape, mostly broadly ellipsoidal to ellipsoidal, sometimes appearing as obovoid or napiform due to distinct pedicel, subglobose in young, greatest width median or submedian, (24.5-)28.7-*30.7*-32.6(-35) μm long, (20.5-)22.3-*23.8*-25.3(-27.3) μm wide, length/width ratio = (1.18-)1.22-*1.31*-1.36(-1.56) ($n = 96$), tip rounded, base rounded or gradually narrowed; pedicel mostly present, short-conical or cylindrical, 1–1.5 μm long, 1–2 μm wide. *Resting organ* not seen.

Peronospora from *C. quinoa* were easily distinguished from *P. boni-henrici* on *C. bonus-henricus* and *P. chenopodii-polyspermi* on *C. polyspermum* by

Table 2 Morphological comparison between *Peronospora* species from *Chenopodium quinoa*, *C. album*, and *Atriplex patula*

Fungus	*Peronospora* sp.	*P. variabilis*	*P. farinosa* s.l.
Host species	*Chenopodium quinoa*	*C. album*	*Atriplex patula*
Conidiophores			
Length	320–630 µm	240–580 µm	150–450 µm
Trunk width (below the first branch)	8–14 µm	8–10 µm	5–10 µm
Branch type	Subdichotomous to monopodial	Subdichotomous	Monopodial
No. of branch orders	(4-)5-7	5-6(-7)	4-6
Callose plugs	Rarely present	Often present	Absent
Ultimate branchlets			
Shape	Flexuous to curved	Flexuous to curved	Straight to substraight
Length	10–32 (av. 15.5) µm	8–23 (av. 12.3) µm	6–14 (av. 9.5) µm
Base width	2–3 (av. 2.5) µm	2–3.5 (av. 2.6) µm	1.5–3 (av. 2.4) µm
Tips	Obtuse or subtruncate	Obtuse	Conical to obtuse
Conidia			
Shape	Broadly ellipsoidal to ellipsoidal	Broadly ellipsoidal to ellipsoidal	Broadly ellipsoidal
Color	Pale brown to olivaceous	Olivaceous with grayish tint	Pale brownish to yellowish
Length	24.5–35.0 (av. 30.7) µm	24–35 (av. 29.5) µm	22.5–27.5 (av. 25.5) µm
Width	20.5–27.3 (av. 23.8) µm	22–26 (av. 23) µm	18–23.8 (av. 21.7) µm
l/w Ratio	1.18–1.56 (av. 1.31)	1.2–1.5 (av. 1.35)	1.11–1.28 (av. 1.19)
Pedicel	Mostly present as short-conical or cylindrical	Present and short-conical	Mostly absent, a minute protuberance visible

the broadly ellipsoidal to ellipsoidal conidia and its higher l/w ratio. The flexuous to curved ultimate branchlets and the pedicellated conidia allowed separation of the quinoa pathogen from *P. chenopodii* on *C. hybridum* and *Peronospora* sp. on *C. ambrosioides*. The morphological comparison between *Peronospora* sp. from quinoa, *Peronospora variabilis* from *C. album*, and *Peronospora farinosa* s.l. from *Atriplex patula* were performed in more detail (Table 2). The quinoa pathogen was clearly distinguished from *P. farinosa* on *A. patula* by larger size and higher l/w ratio in conidia. However, no morphological difference was found between *Peronospora* isolates from *C. quinoa* and *P. variabilis* from *C. album*. The present characteristics are also in agreement with previous records of the causal agent of quinoa downy mildew by Tewari and Boyetchko [7] and Danielsen and Ames [25] and of *P. variabilis* by Choi et al. [12]. The only significant difference in conidial size is found between the present observations (av. 30.7 × 23.8 µm) and that of Danielsen et al. [9] (av. 22 × 18 µm).

Phylogenetic Analysis

The 66 sequences were adjusted to the length of the complete ITS region (ITS1, 5.8S rDNA, and ITS2). The quinoa downy mildew sequences were consistently 796 bp in length. The phylogenetic relationship was inferred from ML, MP, and MCMC analyses of the ITS alignment. Out of 811 total characters, 97 were parsimony-informative, and parsimony analysis resulted in a most parsimonious tree of 190 steps, with a CI of 0.8174 and an RI of 0.9412. As no difference was found between the tree topologies from the ML, MP, and MCMC analyses, only the ML tree is shown in Fig. 2, with the addition of the support values of MP and MCMC analyses. The final alignment and the trees obtained were deposited in TreeBASE (http://www.treebase.org) and are available under accession no. S2510.

In the ITS tree, the 36 isolates of *Peronospora* sp. originating from *C. quinoa* formed a well-supported clade with the *P. variabilis* sequences from *C. album*, which are supported by strong supporting values of

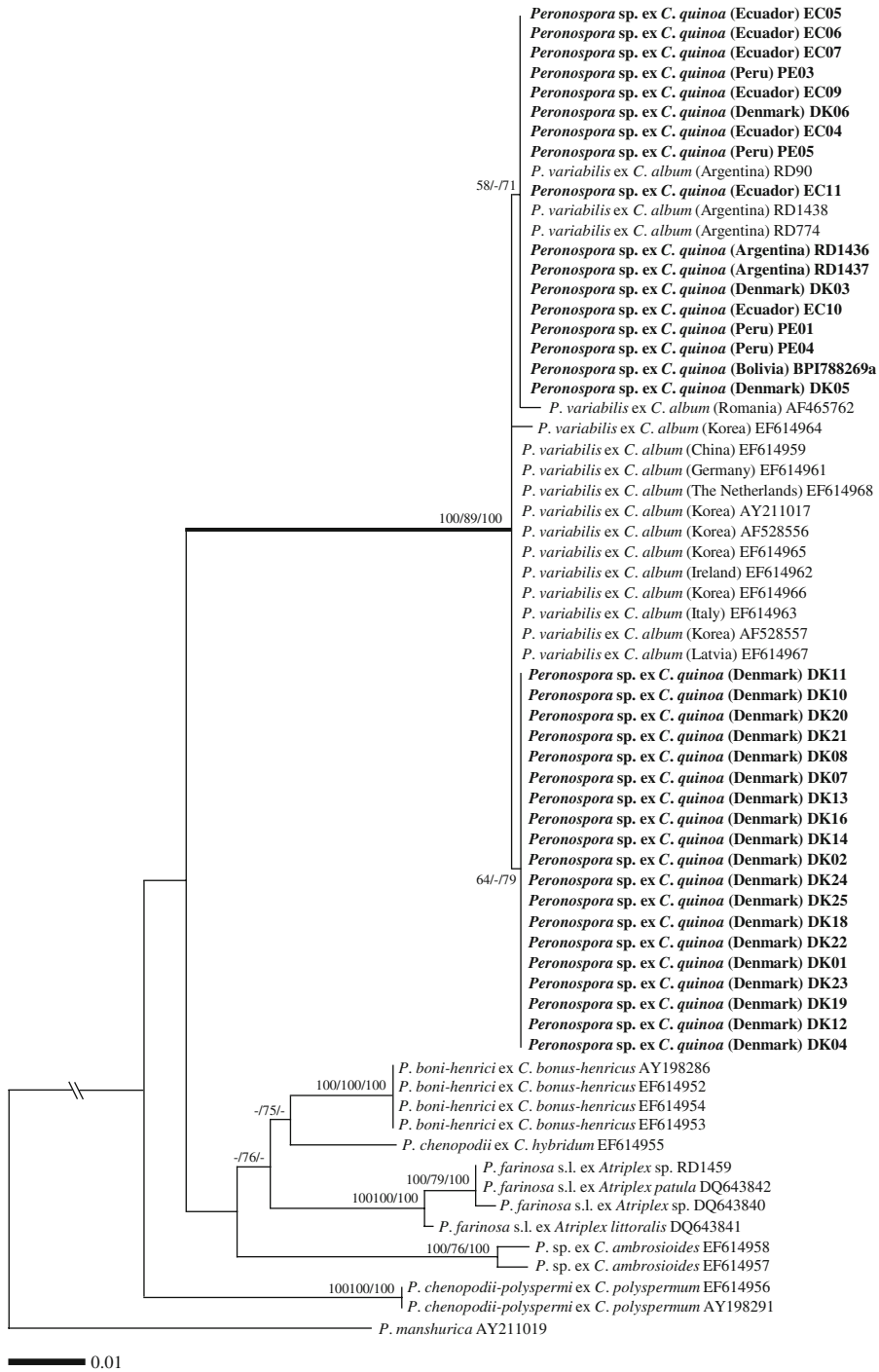

Fig. 2 Phylogenetic tree inferred from ML analysis of the complete ITS region (ITS1, 5.8S rDNA, and ITS2). Supporting values (ML BS/MP BS/MCMC PP) above 50%/50%/70% are given above the branches. The number of nucleotide changes between taxa is represented by branch length and the *scale bar* equals the number of nucleotide substitutions per site. *Peronospora* specimens from the quinoa are shown in *bold*

100%/89%/100% in ML, MP, and MCMC analyses, respectively. The group was distantly related with *P. farinosa* from *Atriplex*, with sequence divergence of 6.5%. The phylogenetic tree revealed that all branches correspond well with the genus or species of host plants they infect; *Peronospora boni-henrici* from *C. bonus-henricus*, *P. chenopodii* from *C. hybridum*, *P. chenopodii-polyspermi* from *C. polyspermum*, *Peronospora* sp. from *C. ambrosioides*, and *P. farinosa* s.l. from *Atriplex* spp. The phylogenetic distances between

Peronospora from quinoa and the four *Peronospora* species parasitic to other *Chenopodium* spp., *viz. P. boni-henrici*, *P. chenopodii*, *P. chenopodii-polyspermi*, and *Peronospora.* sp. on *C. ambrosioides*, were 5.5, 4.8, 6.5, and 6.4%, respectively. The ITS sequences of the *Peronospora* isolates from quinoa were identical to those from *C. album* from Argentina, and only exhibit one base different with *P. variabilis* from *C. album* originated from various countries. The quinoa isolates originating from Argentina, Bolivia, Ecuador, and Peru were uniform in ITS sequences, but two base substitutions were found within the majority of the Danish isolates. Three isolates from Denmark (DK03, DK05, and DK06) clustered within the South American group. No sequence difference was found among *Peronospora* isolates parasitizing different cultivars of quinoa.

Discussion

The international market for quinoa is growing, creating a demand for commercial production in and outside of South America. As the quinoa downy mildew poses a serious threat for the cultivation of the grain, there is an urgent need for clarifying the identity of the causal agent. In the present study, the pathogen on *C. quinoa* was identified as *Peronospora variabilis*, and not *P. farinosa* as claimed by most authors. For about 50 years, *P. farinosa* has been regarded as the pathogen responsible for downy mildew on many Chenopodiaceae, including *Chenopodium* species [26]. The broad species concept has mostly been adopted by plant pathologists, especially by those interested in applied agricultural aspects, having affected the taxonomical opinion on several other groups of downy mildews, such as *Bremia lactucae*, *Hyaloperonospora parasitica*, *Peronospora lamii*, *P. viciae*, and *Plasmopara halstedii*. However, this view should be given up on grounds of significant molecular and morphological diversity and biological specialization toward specific host genera or species [10–14]. It supports that a narrow species concept is more appropriate for the taxonomy of downy mildews. The name *P. farinosa* is improper for the *Peronospora* species infecting quinoa, since the quinoa downy mildew isolates are morphologically and molecularly distinct from those infecting *Atriplex*, from which the name *Botrytis farinosa* (now *P. farinosa*) was firstly described.

Interestingly, the ITS rDNA sequences allowed the separation of quinoa downy mildews into two large groups corresponding to their geographic origins. Isolates originating from South Americas (Argentina, Bolivia, Ecuador, and Peru) were uniform in ITS sequences, but exhibited two nucleotides different from most of the Danish isolates. The presence of two geographically distinct groups among quinoa downy mildew isolates was also found using a PCR fingerprinting technique, UP-PCR [27]. The genetic variation within a downy mildew species has previously been investigated for *Plasmopara halstedii* [28–30], *P. sparsa* [31], and *P. tabacina* [32], but the resulting groups did not correlate with the geographic origins of the isolates. Conversely, it was recently shown that numerous lineages with restricted geographic origins are present even at the species level; for *Plasmopara* spp. parasitic to the *Geraniaceae*, Constantinescu [33] and Voglmayr et al. [34] found that *Pl. pusilla* was restricted to Europe and *Pl. geranii* to North America. Similarly, for *Plasmopara* parasitic to *Cucurbitaceae*, Constantinescu [35] found that *Pl. orientalis* is restricted to Far-East Russia and East Asia and *Pl. australis* to North and South America. The results show that only two transitions exist between quinoa isolates from South America and the majority of the Danish isolates. This indicates that molecular tools with higher resolutions like multigene phylogenetic analysis are required to further unravel the relatedness regarding the diversity and geographic origins. Interestingly, three Denmark isolates were identical to the South American isolates, which could be hinting that the downy mildew was transmitted by the commercial seed trade from the latter region to Europe. The possibility of the seed-borne transmission of quinoa downy mildew has previously been demonstrated [36]. In the present study, the ITS sequences found in all of the quinoa isolates from South America and in the three *C. album* isolates from Argentina were identical, while the *C. album* isolates from Asia and Europe are different, which might speculate that the origin of *P. variabilis* infecting *C. album* in Argentina is from *C. quinoa* and has recently jumped to *C. album*.

Previously, Choi et al. [12] noted that *Peronospora* spp. infect only a specific species of *Chenopodium*, but in the present study *P. variabilis* seems to be

parasitic to at least two species of the genus, *C. album* and *C. quinoa*. The pathogenetic similarity of *Peronospora* from *C. album* and *C. quinoa* is also corroborated by previous cross-inoculation experiments of *Peronospora* isolates on *Chenopodium* species. Aragón and Gutiérrez [37] recorded that isolates from *C. quinoa* var. La Molina 89 infect *C. album*, but not *C. murale*, *C. ambrosioides*, and even *C. quinoa* var. Blanca de Junín. Danielsen et al. [9] pointed out that in Denmark downy mildew-infected *C. album* plants grow close to infected quinoa plants. Our isolates RD1436 (from *C. quinoa*) and RD1438 (from *C. album*) were obtained from a field where *C. album* was growing as a weed near the experimental plots of quinoa. It is therefore tempting to speculate that the cosmopolitan *C. album* might constitute an important inoculum source for the quinoa crop in Argentina and elsewhere.

Correct diagnosis is a fundamental requirement for effective disease management. The clarification of the taxonomic identity of quinoa downy mildew pathogen described in this study allows future control strategies to be more effective and targeted.

Acknowledgments The authors are grateful to the curator of herbarium BPI for allowing access to specimens in their care.

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