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Two novel *Peronospora* species are associated with recent reports of downy mildew on sages

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ABSTRACT

Recently, downy mildew of *Salvia* species became economically relevant globally, but the taxonomy of the causal agent remains still obscure. The objective of this study was to characterize and distinguish the different *Peronospora* species associated with downy mildew on sages, based on morphological and molecular data. For this purpose we compared *Peronospora* specimens on *Salvia officinalis* and *Salvia plebeia* with *Peronospora swinglei*, including the type specimen on *Salvia reflexa*. We observed that three *Peronospora* species are associated with downy mildew on sages, and the recent outbreak of the disease on *S. officinalis* and *S. plebeia* is associated with two undescribed species, contrasting the view that either *P. swinglei* or *Peronospora lamii* is the causal agent of the downy mildew disease as claimed previously by several studies. In the study presented here, we provide the formal descriptions and illustrations for the two newly introduced taxa, *Peronospora salviae-plebeiae* and *Peronospora salviae-officinalis*. The three species of *Peronospora* investigated seem to be restricted to specific species of *Salvia*: *P. swinglei* to *S. reflexa*, *P. salviae-plebeiae* to *S. plebeia*, and *P. salviae-officinalis* to *S. officinalis*. Speciation may be allopatric and closely linked to the geographic distributions of their host plants.

Introduction

Salvia (sages) is an economically important genus in the mint family *Lamiaceae*, which includes several other genera of aromatic herbs, like basil (*Ocimum*) and thyme (*Thymus*). Recently, the outbreak of downy mildew disease has been recorded from different sage-growing areas of the world (Holcomb 2000; Plenk 2002; Belbahri *et al.* 2005; Liberato *et al.* 2006; Shin & Choi 2006; Humphreys-Jones *et al.* 2008), and the pathogen is quickly spreading to new regions. However, the taxonomic status of the causal agent remains obscure, which resulted in identification of the causal agent as either *Peronospora swinglei* or *Peronospora lamii*. Most morphological studies have previously reported the causal agent of sage downy mildew as *P. swinglei* (Kochman & Majewski 1970; Ul'yanishchev *et al.* 1985; Vanev *et al.* 1993; Stanevicienė 1995; Müller 1999; Shin & Choi 2006), presumably based on a host-genus based species concept, while other studies identified it as *P. lamii* (McMillan & Graves 1994; Gamliel & Yarden 1998; Minuto *et al.* 1999; Holcomb 2000; Byrne 2001; Plenk 2002; Hill *et al.* 2004), according to a broad species concept, as advocated by Yerkes & Shaw (1959), which leads to the perception that *P. lamii* infects a broad range of *Lamiaceae*. However, recent phylogenetic approaches (Voglmayr 2003; Belbahri *et al.*

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Table 1 – *Peronospora* specimens investigated in this study.

Species	Host	Geographical origin/herbarium number or source	GenBank no. *cox2*/ITS
P. belbahrii	*Ocimum basilicum*	Argentina, La Plata, 2008 (KUS-F 23241)	–/EU622314
	O. basilicum	Germany, Baden-Württemberg, 2005 (HOH: HUH 770) – TYPUS	FJ394345/FJ394336
	O. basilicum	Italy, –, 2005 (UASWS 0037)	–/AY919301
	O. basilicum	Switzerland, Geneva, 2003 (UASWS 0007)	–/AY831719
P. belbahrii s.l.	*Solenostemon scutellarioides*	USA, Michigan, 2007 (HOH: HUH 945)	FJ394344/FJ394333
	S. scutellarioides	USA, Michigan, 2007 (HOH: HUH 946)	FJ394243/FJ394334
	S. scutellarioides	USA, Michigan, 2007 (HOH: HUH 947)	FJ394340/FJ394337
	S. scutellarioides	USA, Michigan, 2007 (HOH: HUH 948)	FJ394341/FJ394338
P. elsholtziae	*Elsholtzia splendens*	Korea, Chuncheon, 2003 (KUS-F 19838)	FJ527435/FJ527442
P. lamii	*Lamium amplexicaule*	Korea, Kimhae, 2002 (KUS-F 19412)	FJ527436/DQ643902
	L. purpureum	Austria, Lower Austria, 1999 (WU 22907)	–/AY198261
	L. purpureum	Czech Republic, –, 1926 (BRNM 07849/39)	–/–
	L. purpureum	Germany, Baden-Württemberg, 2000 (MG 1867)	DQ365725/–
P. perillae	*Perilla frutescens*	Korea, Hwaseong, 2007 (KUS-F 23102)	FJ527437/EU513600
P. stigmaticola	*Mentha longifolia*	Austria, Styria, 2000 (WU 22930)	–/AY198295
P. swinglei	*Salvia reflexa*	USA, Kansas, – (FH 00079723) – TYPUS	FJ943339/–
	S. reflexa	USA, Kansas, 1898 (BPI 791079)	–/–
	S. reflexa	USA, Kansas, 1895 (BPI 791080)	–/–
	S. reflexa	USA, –, 1889 (BPI 791081)	–/–
	S. reflexa	USA, Kansas, 1895 (BPI 791082)	–/–
	S. reflexa	USA, Kansas, 1887 (BPI 791083)	–/–
	S. reflexa	USA, Kansas, 1898 (BPI 791084)	–/–
	S. reflexa	USA, Kansas, 1898 (BPI 791085)	–/–
	S. reflexa	USA, Kansas, 1898 (BPI 791086)	–/–
P. sp. 1	*S. plebeia*	Korea, Namyangju, 2003 (BPI 877766; KUS-F 19967)	FJ527438/FJ527443
	S. plebeia	Korea, Namyangju, 2003 (BPI 877767; KUS-F 20025)	FJ527439/FJ527444
	S. plebeia	Korea, Jinju, 2004 (BPI 877768; KUS-F 20206)	FJ527440/FJ527445
	S. plebeia	Korea, Jinju, 2004 (BPI 877769; KUS-F 20408)	FJ527441/FJ527446
	S. plebeia	Korea, Bongwha, 2007 (KUS-F 23050)	–/–
	S. plebeia	Korea, Hongcheon, 2008 (KUS-F 23371)	–/–
P. sp. 2	*S. officinalis*	Germany, Baden-Württemberg, 2007 (HOH: HUH 961)	FJ943342/FJ943346
	S. officinalis	Germany, Baden-Württemberg, 2008 (HOH: HUH 992)	–/–
	S. officinalis	New Zealand, –, 2003 (UASWS 0010)	–/AY831722

2005; Thines *et al.* 2009b) have revealed that the mint family is indeed parasitized by several distinct species of *Peronospora*, and that the narrow species concept of Gäumann (1918, 1923) is phylogenetically more appropriate than the previously widely accepted concept of Yerkes & Shaw (1959). *P. lamii* should therefore be restricted to *Lamium* spp., possibly even only to *Lamium purpureum*. For the findings outlined above, the name *P. lamii* is unlikely to be tenable for the downy mildew on sages as well as several other *Lamiaceae*. However, the nomenclature of sage downy mildew has not yet been standardized in the literature, being named *P. lamii* in most studies like the other pathogens of various *Lamiaceae*.

Recently, Belbahri *et al.* (2005) and Thines *et al.* (2009b) demonstrated that the newly occurring downy mildew agent on *Salvia officinalis* is distinct from *P. swinglei* and also from *P. lamii*. Also in a monographic study of the downy mildews of Korea (Shin & Choi 2006), the size and shape of conidia of *Peronospora* from *Salvia plebeia* are somewhat distinct from those of *P. lamii*, but also different from the type specimen of *P. swinglei* from *Salvia reflexa*. However, in the absence of sequence data Shin & Choi (2006) identified the pathogen as *P. swinglei*. In the light of a previous study (Thines *et al.* 2009b), which has proven that ITS rDNA and *cox2* mtDNA sequence data are useful to resolve closely related species within *Peronospora* parasitic to *Lamiaceae*, a molecular and morphological comparison was performed to identify and characterize the causal agents of sage downy mildew.

Materials and methods

Fungal specimens

Eighteen specimens of *Peronospora* on *Salvia* (six on *Salvia plebeia*, three on *Salvia officinalis*, and nine on *Salvia reflexa*) were phylogenetically or morphologically analyzed in this study. For comparison, eight sequences for *cox2* mtDNA and 16 for ITS rDNA of *Peronospora* spp. were obtained from GenBank. Information about the specimens and sequences is shown in Table 1. Herbaria abbreviations are given according to Holmgren & Holmgren (1998).

Morphological analysis

Herbarium specimens were moistened with 70 % alcohol and oomycetes were transferred to 60 % lactic acid on a slide. The