

Peronosclerospora australiensis sp. nov. and *Peronosclerospora sarga* sp. nov., two newly recognised downy mildews in northern Australia, and their biosecurity implications

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Abstract Morphological examination, supported by unnamed phylogenetic lineages found previously from DNA sequence analysis, revealed the presence of two new downy mildews on native *Sorghum* spp. in northern Australia. These species are formally described and illustrated as *Peronosclerospora australiensis* sp. nov. and *Peronosclerospora sarga* sp. nov. One of these species, *P. australiensis*, was also found on cultivated maize. Oospores of *P. australiensis* were present on shredded leaves of the native *Sorghum* spp., and conidia and conidiophores were found on maize leaves with chlorotic streaks. We review earlier reports of downy mildew on maize and native *Sorghum*

species in northern Australia and show that many of these records represent *P. australiensis*. The biosecurity implications of the absence of some downy mildews on grasses from Australia as well as the detection of new cryptic species are discussed.

Keywords Quarantine · *Sarga* · *Sorghum timorense* · *Sorghum plumosum* · Taxonomy · *Zea mays*

Introduction

The downy mildews (Peronosporaceae, Oomycetes) are important pathogens of cultivated tropical and sub-tropical grasses, especially maize (*Zea mays*), sorghum (*Sorghum bicolor*) and sugarcane (*Saccharum officinarum*). *Peronosclerospora* (S. Ito) Hara was established first as a subgenus (Ito 1913) to accommodate graminicolous downy mildews that formed conidia which germinate directly, rather than by sporangia that produce zoospores. It was later raised to the level of genus (Shirai and Hara 1927; Shaw 1978; Shaw and Waterhouse 1980; Kenneth 1981).

Peronosclerospora contains eleven species, viz. *P. dichanthiicola* (Thirum. & Naras.) C.G. Shaw, *P. eriochloae* Ryley & Langdon, *P. heteropogonis* Siradhana, Dange, Rathore & S.D. Singh, *P. maydis* (Racib.) C.G. Shaw, *P. miscanthi* (T. Miyake) C.G. Shaw, *P. noblei* (W. Weston) C.G. Shaw, *P. philippinensis* (W. Weston) C.G. Shaw, *P. sacchari* (T. Miyake) Shirai & Hara, *P. sorghi* (W. Weston & Uppal) C.G. Shaw, *P. spontanea* (W. Weston) C.G. Shaw and *P. westonii* (Sriniv. Naras. & Thirum.) C.G. Shaw. Four of these, *P. eriochloae*, *P. maydis*, *P. noblei* and *P. sacchari*, have been recorded in Australia (Ryley and Langdon 2001). *Peronosclerospora eriochloae* is known to

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occur on *Eriochloa pseudoacrotricha* and maize in subtropical south-eastern Queensland (Ryley and Langdon 2001; Telle et al. 2011). *Peronosclerospora noblei* is endemic to Australia and only known on *Sorghum leiocladum* (Ryley and Langdon 2001), which is distributed within 200 km of the eastern coast of Australia, from northern Victoria to southern Queensland (Spangler 2003). One of these species, *P. sacchari*, was eradicated from Australia with destruction of the last experimental plot of infected sugarcane plants in 1972, having last been found in commercial sugarcane fields in 1959 (Plant Health Australia 2009a).

Peronosclerospora maydis was reported to be widespread across tropical northern regions of Australia and to infect both maize and plume sorghum (*Sorghum plumosum*) (Ramsey and Jones 1988). This species is known to be the cause of the disease called Java downy mildew, one of the most destructive diseases of maize in Indonesia (Semangoen 1970, Thurston 1998). However the identification of Australian specimens as *P. maydis* needs scrutiny because in Australia (i) downy mildew was widespread on annual native sorghum (*Sorghum timorense*) and perennial plume sorghum (*S. plumosum*) but seldom found on maize, while in Indonesia *P. maydis* occurs naturally only on maize (Semangoen 1970), (ii) the downy mildew on maize in Australia was rarely as destructive as Java downy mildew disease in Indonesia, (iii) oospores were commonly produced on native *Sorghum* spp. although oospores of *P. maydis* were not found on maize in Indonesia over several years (Semangoen 1970), and (iv) cultivated sorghum, which is a host of *P. maydis*, growing adjacent to diseased maize was usually unaffected (Ramsey and Jones 1988).

Prior to the advent of molecular techniques, the identification of downy mildews on grasses by morphological methods was difficult as the conidia for several species are similar and oospores are not known, rare or nonexistent for some species, for example *P. maydis*, *P. philippinensis* and *P. spontanea*. Identification of downy mildews is further complicated by the likelihood that taxonomic revision may establish synonymy, especially within the genus *Peronosclerospora* (Spencer and Dick 2002), considering that eight species of *Peronosclerospora* have been reported to infect maize.

Recent molecular phylogenetic analysis has shown there are cryptic species amongst Australian specimens of *Peronosclerospora* (Thines et al. 2008; Telle et al. 2011). Molecular phylogenetic reconstruction based on partial *cox2* (Cytochrome c oxidase subunit II gene) and nrLSU (nuclear ribosomal large subunit) sequences showed two distinct clades of undescribed species of *Peronosclerospora* infecting *Sorghum* species that are native to northern Australia (Telle et al. 2011). In this present study, we have morphologically re-examined those specimens and de-

scribed two distinct novel species. These discoveries require a re-consideration of some past reports of downy mildews on grasses in Australia.

Methods

The herbarium specimens examined are listed under the species description. Lactic acid was used as a mounting medium and slides warmed to allow tissue to regain turgor and expel air bubbles. Microscopic measurements of morphological structures were based on a minimum of 25 observations at $\times 1,000$ magnification under differential interference contrast microscopy with a Leica DM 5500B microscope (Leica, Germany). Measurements were expressed as ranges of observations, means and standard deviations. Images were taken with a Leica DFC 500 camera and Helicon Focus (Helicon Soft Ltd, Ukraine) software was used to create multifocused images. Taxonomic descriptions of novel species were registered in MycoBank (www.mycobank.org).

Results and Taxonomy

Peronosclerospora australiensis R.G. Shivas, Ryley, Telle, Liberato & Thines, sp. nov. (Figs. 1, 2, 3 and 4)

Etymology. Derived from the name of the continent and country where it was discovered.

Oogonia et oosporae in foliis quae dividuntur in massas implexas fibrarum vascularium usque ad 50 cm longarum. Oogonia aureicrocea ad luteo- vel rubrobrunnea, globosa, subglobosa, late ellipsoidea ad irregulariter polyangularia, 55–76 μm diam.; paries (exosporium) 2–15 μm latus, inaequalis, levis, convolutus. Oosporae una per oogonium, subhyalinae ad luteolae, globosae vel late ellipsoideae, 39–55 μm diam., saepe magna vacuola; paries (endosporium) 2.5–4.0 μm latus, aequalis, levis.

Oogonia and oospores in leaves splitting into tangled masses of vascular fibres up to 50 cm long (Figs. 1 and 2). Oogonia golden orange to yellowish or reddish brown, globose, subglobose, broadly ellipsoidal to irregularly polyangular, 55–76 (\bar{x} = 63.0, SD=4.9) μm diam.; wall (exosporium) 2–15 μm wide, uneven, smooth, convoluted. Oospores one per oogonium, sub-hyaline to pale yellow, globose or broadly ellipsoidal, 39–55 (\bar{x} = 47.1, SD=3.8) μm diam., often with a large vacuole; wall (endosporium) 2.5–4.0 (\bar{x} = 3.2, SD=0.4) μm wide, even, smooth (Figs. 3 and 4). Conidiophores and conidia not seen on the type host.

Holotypus: Australia, Western Australia, Parry Creek Road, 500 m north Valentine Spring near Kununurra, alt. c. 45 m, on *Sorghum timorense* (Kunth) Buse (syn. *Sarga timorense* (Kunth) Spangler), 5 May 2005, M.J. Ryley & S. M. Thompson, BRIP 46736, sequences ex-type in GenBank

Figs. 1–6 *Peronosclerospora* spp. on *Sorghum* spp. 1–2. Host symptoms of *P. australiensis* on *S. timorense* (BRIP 46736). 3–4. Oogonia and oospores of *P. australiensis* on *S. timorense* (BRIP 49819, BRIP 46736 respectively). 5. Oogonia and oospores of *P. sargae* on *S. timorense* (BRIP 27691). 6. Oogonia and oospores of *P. noblei* on *S. leiocladum* (BRIP 17462)



HQ261797 (*cox2*), HQ261770 (*nrLSU*), MycoBank MB 519344.

Habitat: In living plants of *Sorghum plumosum*, *S. timorense* and *Zea mays* (Telle et al. 2011)

Other specimens examined on Sorghum timorense: Western Australia: Kununurra, 2 Apr. 2001, *W.P. Weinert*, BRIP 50933; Wyndham, 6 May 2005, *M.J. Ryley & S.M. Thompson*, BRIP 46737, 46738; between Wyndham and Kununurra, 13 Apr. 2007, *A.R. McTaggart, T.S. Marney, S.M. Thompson, M.J. Ryley, M.D.E. Shivas & R.G. Shivas*, BRIP 49816, 49819. Northern Territory: Pine Creek, 17 Mar. 2000, *R.G. Shivas, I.T. Riley, C. & K. Vánky*, BRIP 27784; Groote Eylandt, 19 May 2003, *P.M. Stephens*, BRIP 39880; Tolma Falls, 1 May 2005, *M.J. Ryley & S.M. Thompson*, BRIP 46698; near Batchelor, 2 May 2005, *M.J. Ryley & S.M. Thompson*, BRIP 46735.

Other specimens examined on Zea mays: Northern Territory: Borroloola, May 2005, *P.M. Stephens*, BRIP 46527; Borroloola, 8 Aug. 2005, *P.M. Stephens*, BRIP 46815.

Previous DNA sequence analysis (Telle et al. 2011) showed that *P. australiensis* also infected *S. plumosum* and

maize. *Sorghum timorense* and *S. plumosum* are closely related and difficult to differentiate because both have leaves that senesce during the dry season. They differ primarily in that *S. timorense* is an annual that extends into southern Indonesia, and *S. plumosum* is a tufted perennial that is restricted to Australia (Spangler 2003). A re-examination of *Sorghum* specimens in BRIP infected with *P. australiensis* showed that some specimens identified as *S. plumosum* were better identified as *S. timorense*.

DNA sequence analysis showed that two specimens (BRIP 46815, BRIP 46527) of downy mildew on maize from the Northern Territory were part of a clade that included the type of *P. australiensis* (Telle et al. 2011). These two specimens contained only a few conidia and conidiophores, and lacked oospores. We have provided the following description of the conidia and conidiophores based on BRIP 46815. Conidiophores were dichotomously branched and mostly collapsed. Conidia were produced on the lower leaf surface of maize on chlorotic streaks up to 20 cm long and 5 mm wide. The conidia were globose, subglobose to broadly ellipsoidal, 16–24×16–24 µm and

germinated by a germ tube. We have decided not to formally establish an epitype to describe the conidiophores and conidia, as these structures were in poor condition, and the host matrix might influence the morphology of the asexual structures (Runge and Thines 2011). This description matches closely the descriptions of downy mildew on maize and *S. plumosum* from several specimens across northern Australia attributed by Ramsey and Jones (1988) to *P. maydis*.

Peronosclerospora sargae R.G. Shivas, M.J. Ryley, Telle & Thines, sp. nov. (Fig. 5)

Etymology. Derived from the name of the grass genus *Sarga*, resurrected by Spangler (2003) to accommodate most species formerly placed in subgenera *Parasorghum* and *Stiposorghum*.

De morphologia, similis *Peronosclerosporae noblei*, sed dissimilis specie plantae nutricis, paries oosporae plus crassis et DNA seriebus *cox2* et partialium nrLSU.

Oogonia et oosporae in foliis quae dividuntur in massas implexas fibrarum vascularium usque ad 30 cm longarum. Oogonia luteola ad luteobrunnea, globosa, subglobosa ad late ellipsoidea, interdum irregulariter polyangularia, 30–47 μm diam.; paries (exosporium) 2–8 μm latus, inaequalis, levis. Oosporae una per oogonium, luteolae, globosae, 24–34 μm diam., saepe magna vacuola; paries (endosporium) 1.5–3.0 μm latus, aequalis, levis.

Morphologically similar to *Peronosclerospora noblei*, but differs in its host plant species, oospore wall thickness, and DNA sequences of *cox2* and partial nrLSU genes.

Oogonia and oospores in leaves splitting into tangled masses of vascular fibres up to 30 cm long. Oogonia pale yellow to yellowish brown, globose, subglobose to broadly ellipsoidal, occasionally irregularly polyangular, 30–47 (\bar{x} = 37.9, SD=4.5) μm diam.; wall (exosporium) 2–8 μm wide, uneven, smooth. Oospores one per oogonium, pale yellow, globose, 24–34 (\bar{x} = 29.3, SD=2.5) μm diam., often with a large vacuole; wall (endosporium) 1.5–3.0 (\bar{x} = 2.1, SD=0.4) μm wide, even, smooth (Fig. 5). Conidiophores and conidia not seen.

Holotypus: Australia, Northern Territory, Florence Falls, 13 Mar. 2000, on *Sorghum timorense* (Kunth) Buse (syn. *Sarga timorense* (Kunth) Spangler), R.G. Shivas, I.T. Riley, C. & K. Vánky, BRIP 27691, sequences ex-type in GenBank HQ261809 (*cox2*), HQ261782 (nrLSU), MycoBank MB 519345.

Habitat: Known only from the type specimen.

Discussion

Kenneth (1981) noted that the delineation of species in *Peronosclerospora* was fraught with uncertainty, largely because of the infra-specific morphological variability in asexual structures (conidia and conidiophores). Oospore

morphology is becoming increasingly important in species differentiation of Oomycetes as they appear less variable than asexual stages in some recent studies (Choi et al. 2008, 2011; Ploch et al. 2010). Species classification and identification has been further compounded by uncertainty in linking asexual with sexual stages. Until conidiophores with conidia are found together with oospores on one plant, or molecular methods are applied, then the asexual downy mildews on grasses cannot be confidently identified.

Connecting asexual with sexual stages is difficult because oospores develop at different times in the life cycle of *Peronosclerospora* spp., than do conidiophores and conidia. Most downy mildews on grasses produce conidia on the leaves of their hosts in the early hours of the morning provided temperature and humidity are optimal (Kenneth 1970). The conidia remain on the host for only a few hours before becoming detached or desiccated (Jeger et al. 1998). Consequently infected plants with conidiophores and conidia of *Peronosclerospora* spp. have been less frequently collected than those with oospores, especially in tropical and arid regions. This is particularly apparent with the discovery of cryptic species, which were described and named in this study.

The establishment of *P. australiensis* and *P. sargae*, increases to six the number of downy mildews reported to occur naturally on *Sorghum*. Morphological delineation of the other four species, viz. *P. sorghi*, *P. philippinensis*, *P. noblei* and *P. sacchari*, is often difficult as the description of these species in the literature is often at variance with the original type descriptions. Sometimes this has occurred through misidentifications, for example the original description of the oospores of *P. sacchari* were apparently later attributed by Miyake to *Sclerospora spontanea* (Waterhouse 1964). A stable taxonomy for most groups of plant pathogenic fungi, including the downy mildews, will be best provided by also applying molecular based phylogenetic species recognition criteria (Cai et al. 2011) in addition to morphological delimitation. This approach will need to be based on type specimens, which will require epitypification of many taxa.

Records of downy mildew on maize in Australia are relatively uncommon. Ramsey and Jones (1988) documented several detections of downy mildew on maize (specifically sweet corn) across northern Western Australia, the Northern Territory and Queensland since 1970. Some of these detections resulted in the implementation of precautionary quarantine measures including the destruction of plants. These detections were variously attributed to incursions of either *P. maydis* or *P. sorghi*, but in no case were oospores produced. A direct link between downy mildew on maize and *Sorghum plumosum* was made by Ramsey and Jones (1988) who inoculated maize with conidia from naturally infected *S. plumosum* and then successfully re-inoculated seedlings of *S. plumosum* with conidia from maize.

The identity of downy mildew on maize in south-eastern Queensland in 1995 was only resolved recently when Telle et al. (2011) used DNA sequence analysis to show that the pathogen was *P. eriochloae*, which had not previously been recorded on maize. This extension of the host range of *P. eriochloae* demonstrates the importance of molecular methods in reliably determining the identity of these pathogens. It further demonstrates the ability and potential of downy mildews to jump hosts and infect cultivated, non-native grasses.

Peronosclerospora australiensis has much larger oospores than *P. noblei*, which has oospores that measure 20–(23–29)–34 µm (Weston 1929) and is only known with certainty to infect *Sorghum leiocladum* (Ryley and Langdon 2001). *P. australiensis* also has larger oospores than *P. eriochloae* (27–46 µm) (Ryley and Langdon 2001). Telle et al. (2011) analysed partial *cox2*, and nrLSU sequences to show that BRIP 46736 (designated in this study as the holotype of *P. australiensis*) was included in a monophyletic clade of specimens that infected *S. plumosum*, *S. timorensis* and *Zea mays*.

Peronosclerospora sargae is morphologically different from *P. noblei*. The oospores of *P. noblei* (Fig. 6) were given as 20–(23–29)–34 µm by Weston (1929) and 19–(26.4±2.4)–35 µm by Ryley and Langdon (2001), which are smaller than observed for *P. sargae* (24–(29.3±2.5)–34 µm) in this study. Further, the oospore wall of *P. sargae* is about 2 (x̄ = 2.1, SD=0.4) µm wide, which is greater than found in *P. noblei*, which has oospore walls usually less than 2 µm wide, as represented by specimens BRIP 2103 and BRIP 17462. Weston (1929) reported that *P. noblei* has an oospore walls that ranged from 1–1.5 µm wide. Based on phylogenetic analysis of partial *cox2* and nrLSU sequences, Telle et al. (2011) showed that BRIP 27691 (designated in this study as the holotype of *P. sargae*) is phylogenetically distinct from *P. australiensis*. The asexual stage of *P. sargae* is not known.

It is noteworthy that only one of the eight species of *Peronosclerospora*, including *P. eriochloae*, that infects maize, occurs outside Asia although maize originated in the New World. The exception is *P. sorghi*, which is also not native to the natural range of maize, but occurs in Africa and was introduced to the Americas (Thurston 1998). This indicates that the maize downy mildews originated on unknown grasses in Asia, before subsequently spreading to maize crops. Spencer and Dick (2002) observed that there were two apparent centers of diversity for *Peronosclerospora*, one in subcontinental India (*P. dichanthiicola*, *P. heteropogonis* and *P. westonii*) and the other in eastern Melanesia and Australasia (*P. globosa*¹ Kubicek & R.G. Kenneth, *P. maydis*,

P. miscanthi, *P. noblei*, *P. sacchari* and *P. spontanea*) to which *P. eriochloae*, *P. australiensis* and *P. sargae* can be added, while the remaining species (*P. philippinensis* and *P. sorghi*) have uncertain origins. The uncultivated, original hosts of three of the most devastating maize downy mildews, *P. maydis*, *P. philippinensis* and *P. sorghi*, have not been discovered yet.

Exotic downy mildews have been recognized as amongst the greatest biosecurity threats to the Australian maize, sorghum, and sugarcane industries. In particular, *P. philippinensis*, *P. sacchari* and *P. sorghi*, are listed on the NAQS Target List for Plant Pathogens—May 2009, as having the potential for significant adverse impact on agriculture. Further *P. sacchari* has been given the status of *Emergency Plant Pest* by its inclusion in *Schedule 13*, which lists pests (pathogens and insects) that could have potentially harmful economic consequences should they become established in Australia. *Peronosclerospora philippinensis* and *P. sorghi* were ranked *High* as threats to the Australian grains industry (Plant Health Australia 2009b). Some of the reasons given for this ranking included high entry potential as the pathogens are seed-borne, proximity to Australia, potential alternate weed hosts in northern Australia (for *P. sorghi*), wind-borne spread, and evidence for movement in the last 20 years.

Our results show that *P. australiensis* infects maize, *S. plumosum* and *S. timorensis* in northern Australia. Furthermore, we have shown that on these hosts many specimens of *Peronosclerospora*, including some previously identified as *P. maydis* actually represent *P. australiensis*. *Peronosclerospora maydis* may not be present in northern Australia and consequently it would pose a biosecurity threat to the Australian maize and sorghum industries. There are large gaps in our knowledge about the diversity, host ranges and life cycles of many of the downy mildews in Australia. For example, there are several other Australian downy mildews on native grasses that await detailed study. Some of these occur on *Chionachne*, *Eragrostis*, *Panicum* and *Triodia* (Ryley and Langdon 2001). The development of reliable molecular based diagnostic tests for the downy mildews is a prerequisite for making effective management and biosecurity decisions when detections are made on cultivated crops.

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¹ *nom. nud.*, invalid name according to Art. 36.1 of the International Code of Botanical Nomenclature as published without a Latin diagnosis

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