Chiang Mai J. Sci. 2024; 51(4): e2024062
https://doi.org/10.12982/CMJS.2024.062
Journal homepage : http://epg.science.cmu.ac.th/ejournal/

Research Article

Maize Downy Mildew (*Peronosclerospora neglecta*) in Cambodia, Lao PDR, and Thailand

Manorat Sudsanguan [a,b], Roger G. Shivas [c], Yu Pei Tan [d], Chanintorn Doungsa-ard [b], Khonesavane Chittarath [e], Chhun Hy Heng [f] and Sarunya Nalumpang [a]*

[a] Division of Plant Pathology, Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand
[b] Plant Protection Research and Development office, Department of Agriculture, Bangkok 10900, Thailand
[c] Centre for Crop Health, University of Southern Queensland, Toowoomba 4350, Australia
[d] Queensland Plant Pathology Herbarium, Department of Agriculture and Fisheries, Dutton Park, Queensland 4102, Australia
[e] Plant Protection Center, Department of Agriculture, Vientiane 01000, Lao PDR
[f] General Directorate of Agriculture, Department of Plant Protection, Phnom Penh 120406, Cambodia

*Author for correspondence; e-mail: sarunya.v@cmu.ac.th

Received: 2 April 2024
Revised: 7 June 2024
Accepted: 13 June 2024

Abstract

Peronosclerospora species cause downy mildew diseases on maize (*Zea mays*) worldwide. Maize leaves with symptoms of downy mildew were collected from field crops in Cambodia, Lao PDR, and Thailand, during surveys between 2018 and 2022. Initial determination of the presence of downy mildew on specimens was determined microscopically by the presence of conidiophores and/or oospores in leaf tissue. Phylogenetic analyses of the cytochrome c oxidase subunit II (*cox2*) gene sequences showed that all specimens were *Peronosclerospora neglecta*. Reference specimens from Thailand were deposited at the Thai Plant Pathology Herbarium, Bangkok, Thailand, while those from Cambodia and Lao PDR were deposited at the Queensland Plant Pathology Herbarium, Australia. *Peronosclerospora neglecta* was widespread in field crops of maize in Cambodia, Lao PDR, and Thailand during the survey period. This is the first time that *P. neglecta* has been reported in Cambodia and Lao PDR.

Keywords: crops surveyed, disease, downy mildew, grasses, phylogeny

1. Introduction

Downy mildew caused by species of *Peronosclerospora* (Peronosporaceae, Peronosporales) are responsible for severe damage to maize (*Zea mays* L.) crops worldwide [1]. Eight species of *Peronosclerospora* have been reported on maize, namely *P. eriochloae*, *P. heteropogonis*, *P. maydis*, *P. neglecta*, *P. philippinensis*, *P. sacchari*, *P. sorghi*, and *P. spontanea* [2–5]. *Peronosclerospora neglecta* on maize was reported as widely distributed from Thailand to eastern Indonesia [2], with the earliest specimen collected in Thailand in 2018 [6]. The first report of *P. neglecta* from Thailand was based on a reassessment of GenBank sequences first identified as *P. maydis* [2,6]. *Peronosclerospora maydis* has generally been considered the cause of downy mildew on maize in Thailand [5,6]. In Cambodia, both *P. sorghi* and *P. maydis*, have been reported on maize [7]. There are no reports in the literature of downy mildew on maize in Lao PDR.

The accurate identification of maize downy mildews in South-East Asia is important, as breeding maize varieties with resistance to downy mildew is an important tool in disease management [2,8]. In the past, the nomenclature of plant pathogenic fungi was based only on morphological characteristics, or sometimes their host associations played an important role in species delimitation, with little consideration for morphology [9]. Definitions of species evolve over time as knowledge of the biology, morphology, and evolutionary relationships of fungi increases [10]. Many of the historical reports of downy mildew on maize in south-east Asia are unverifiable as they were based on morphological traits that are highly variable within a species and overlap between species [11]. Further, it has become increasingly apparent that some downy mildews have multiple hosts [5]. Accurate species identification is important for plant pathology and plant quarantine [12]. Molecular methods have been increasingly used for accurate species identification, as morphology alone is often unreliable [10]. In this study we compared *cox2* gene sequences with ex-type reference barcodes [5] to identify downy mildews collected from maize crops in Cambodia, Laos, and Thailand between 2018 and 2022.

2. Materials and Methods

2.1 Sample Collection and Examination

Leaf specimens of maize with chlorotic streaks symptomatic of downy mildew (Figure 1) were collected from Thailand, Cambodia and Lao PDR between 2018 and 2022. The morphology of conidia and conidiophores were examined under stereo (Carl Zeiss Stemi 2000-C) and compound (Olympus System Microscope Model BX53) microscopes from small pieces (1 mm^2) of leaf tissue excised with a scalpel and mounted in lactoglycerol.

2.2 DNA Extraction, PCR, Sequences and Phylogenetic Analysis

Leaves found to have downy mildew were cut into small pieces and transferred to a microfuge tube for DNA extraction. Genomic DNA was extracted with the PureDireX Genomic DNA Isolation Kit (Blood/Cultured Cell/Fungus) (Bio-Helix Co., Ltd.) in accordance with the methods of Doungsa-ard et al. [13]. A partial

Figure 1. Downy mildew symptoms on maize in Kanchanaburi province.

region of the cytochrome c oxidase subunit II (*cox2*) gene from mitochondrial DNA (mtDNA) was amplified with Taq DNA Polymerase [Green Hot Start PCR Master Mix Direct-Load, 2x (biotechrabbit)]. The *cox2* gene was amplified with the primers COX2-F/COX2-RC4 [14]. The PCR cycling conditions were 95 °C for 4 min, 36 cycles of 95 °C for 40 s, 50 °C for 40 s, 72 °C for 60 s; and final extension of 72 °C for 5 min. The PCR products were purified and sequenced by Macrogen Incorporated (Seoul, Korea). The *cox2* sequences were assembled in contigs with Geneious Prime (Biomatters Ltd., New Zealand) and deposited in GenBank (Table 1). These sequences were aligned with reference sequences retrieved from GenBank with the MAFFT v7.450 standard alignment algorithm in Geneious. Sequences from *Sclerospora graminicola* were used as the outgroup. Maximum likelihood (ML) analysis was performed with RAxML v8.1.15 [15] in Geneious. The resulting tree was evaluated with 1000 bootstrap replications of maximum likelihood bootstrap to test the clade stability.

3. Results and Discussion

3.1 Sample Collection and Disease Symptom

The primary symptoms of infection by *P. neglecta* were chlorotic leaf streaks that developed from the base of the younger leaves and stunted plants. Leaf shredding and the formation of oospores in leaf tissue were not observed. This survey was found that *P. neglecta* was prevalent in sweet corn and waxy corn in Chiang Mai and Kanchanaburi provinces, Thailand. The highest rates of infection were seen on eight-row corn at Klongtakot (Photharam district, Ratchaburi province), Thailand and hybrid sweet corn, hybrid waxy corn, and field corn (grown from self-harvested seed) at Mueang Ka Rung (Ban Rai district, Uthai Thani Province), Thailand. *Peronosclerospora neglecta* was not found in baby corn in this survey. Conidiophores and conidia of *P. neglecta* were produced on both surfaces of the leaf. *Peronosclerospora maydis*, *P. philippinensis*, *P. sorghi*, and *P. spontanea*, have also been reported on maize in Thailand [26]. The conidia of *P. neglecta* range in shape from subglobose to ovoid, and are larger than those of *P. maydis* [28], and smaller than those of *P. sorghi* [5,29], *P. philippinensis* [30] and *P. spontanea* [31]. However, the morphology of downy mildews has little diagnostic value in their identification as environmental factors and varietal host range may influence conidial and other dimensions [21]. The results of this study show that *P. neglecta* is widespread and damaging on maize in Cambodia, Lao PDR, and Thailand. Similarly, *P. neglecta* is widespread on maize in Thailand, with a distribution extending eastwards to Indonesia and northwards to Cambodia and Lao PDR [2,6,26, this study]. This is the first reported of *P. neglecta* in Cambodia and Lao PDR. Reliable and accurate identification of downy mildews is essential for successful disease management as well as to prevent their spread through seed exportation.

3.2 Phylogenetic Analysis

Phylogenetic analysis of the *cox2* gene sequences from Cambodian, Lao and Thai specimens showed that they belonged to a strongly supported clade, which included the ex-type *cox2* gene sequence of *P. neglecta* from Indonesia (Table 1, Figure 2). Five other species of *Peronosclerospora* that had previously been reported on maize in Thailand [6, 16–19], namely *P. maydis*, *P. philippinensis*, *P. sacchari*, *P. sorghi*, and *P. spontanea*, were not found. Reference sequences of *P. spontanea* were not available from type material or bona fide specimens for inclusion in our study, which is significant as a possible occurrence of *P. spontanea* was reported from Thailand [20].

3.3 Taxonomy

Peronosclerospora neglecta Muis, Ryley, Suharjo, Y.P. Tan, Thines & R.G. Shivas, *Mycol. Prog.* 22: 3 (2023) Figure 3.

Description: *Asexual sporulation* of *Peronosclerospora neglecta* was found on 20 maize leaf specimens

Table 1. Specimens included in the phylogenetic analysis. Accession numbers from this study are in bold.

Species	Voucher	Host	Locality	GenBank Accessions No. (*cox2*)	Reference
Baobabopsis marneyi	BRIP 70341[T]	*Enneapogon polyphyllus*	Georgetown, Australia	OK336436	[23]
Eraphthora drenthii	DAR 4201[T]	*Eragrostris cilianensis*	Gunnedah, Australia	HQ413338	[24]
Peronosclerospora aristidae	BRIP 67069[T]	*Aristida hygrometrica*	Mareeba, Australia	OK336438	[23]
P. boughtoniae	BRIP 14388[T]	*Sorghum plumosum*	Lizard Island, Australia	OK336439	[23]
P. eriochloae	BRIP 13693[T]	*Eriochloa pseudoacrotricha*	Upper Pilton, Australia	OK336442	[23]
P. heteropogonis	HOH HUH 898	*Heteropogon contortus*	Udaiur, Rajasthan, India	EU116054	[25]
P. ischaemi	BRP 70369[T]	*Ischaemum fragile*	Croydon, Australia	OK336443	[23]
P. jamesiae	BRIP 65234[T]	*Sorghum intrans*	Wagait Beach, Australia	OK336444	[23]
P. mactaggartii	BRIP 57677[T]	*Sorghum timorense*	Robin Falls, Australia	OK336446	[23]
P. maydis	BRIP 46736[TA]	*S. timorense*	Valentine Springs, Australia	HQ261797	[26]
	KRAM O-5859(J)[T]	*Zea mays*	Java, Indonesia	MW025835	[27]
P. miscanthi	NY	*Miscanthus japonicus*	Luzon, Philippines	HQ261811	[28]
P. neglecta	BO 24212[T]	*Z. mays*	East Java, Indonesia	OK336429	[2]
	TPPH 05625	*Z. mays* var. *ceratina*	Chiang Mai, Thailand	**OR838703**	This study
	TPPH 05672	*Z. mays* var. *rugosa*	Chiang Mai, Thailand	**OR838713**	This study
	TPPH 05676	*Z. mays* var. *indenata*	Chiang Mai, Thailand	**OR838715**	This study
	TPPH 05675	*Z. mays* var. *indenata*	Chonburi, Thailand	**OR838714**	This study
	TPPH 05571	*Z. mays* var. *rugosa*	Kanchanaburi, Thailand	**OR838699**	This study
	TPPH 05574	*Z. mays* var. *rugosa*	Kanchanaburi, Thailand	**OR838700**	This study
	TPPH 05620	*Z. mays* var. *ceratina*	Kanchanaburi, Thailand	**OR838702**	This study
	TPPH 05659	*Z. mays* var. *rugosa*	Kanchanaburi, Thailand	**OR838707**	This study
	TPPH 05703	*Z. mays* var. *ceratina*	Lamphun, Thailand	**OR838716**	This study
	TPPH 06029	*Z. mays* var. *rugosa*	Loei, Thailand	**OR838718**	This study
	TPPH 05669	*Z. mays* var. *rugosa*	Nakhon Pathom, Thailand	**OR838712**	This study
	TPPH 05577	*Z. mays* var. *indenata*	Nakhon Ratchasima, Thailand	**OR838701**	This study
	TPPH 05650	*Z. mays* var. *indenata*	Nakhon Ratchasima, Thailand	**OR838704**	This study
	TPPH 05653	*Z. mays* var. *ceratina*	Ratchaburi, Thailand	**OR838705**	This study
	TPPH 05656	*Z. mays* var. *ceratina*	Ratchaburi, Thailand	**OR838706**	This study
	TPPH 05704	*Z. mays* var. *rugosa*	Saraburi, Thailand	**OR838717**	This study
	TPPH 05661	*Z. mays* var. *indenata*	Uthaithani, Thailand	**OR838708**	This study

Note: Stevens' Philippine Fungi, Island of Luzon, No.811; [T] holotype; [TA] ex-type of *Peronosclerospora australiensis*.

Table 1. (Continued).

Species	Voucher	Host	Locality	GenBank Accessions No. (*cox*2)	Reference
	TPPH 05663	*Z. mays* var. *rugosa*	Uthaithani, Thailand	**OR838709**	This study
	TPPH 05665	*Z. mays* var. *ceratina*	Uthaithani, Thailand	**OR838710**	This study
	TPPH 05668	*Z. mays* var. *ceratina*	Uthaithani, Thailand	**OR838711**	This study
	BRIP 67693	*Z. mays*	Vientiane, Lao PDR	**PP061441**	This study
	BRIP 67695	*Z. mays*	Vientiane, Lao PDR	**PP061442**	This study
	BRIP 70147	*Z. mays*	Champasak, Lao PDR	**PP061447**	This study
	BRIP 70148	*Z. mays*	Champasak, Lao PDR	**PP061448**	This study
	BRIP 69061	*Z. mays*	Kampong Cham, Cambodia	**PP061445**	This study
	BRIP 69045	*Z. mays*	Kandal, Cambodia	**PP061443**	This study
	BRIP 69046	*Z. mays*	Kandal, Cambodia	**PP061444**	This study
	BRIP 69063	*Z. mays*	Preah Vihea, Cambodia	**PP061446**	This study
P. noblei	BPI 187306	*S. leiocladum*	Australia	OK185343	[5]
P. panici	DAR 35733^{T}	*Panicum laevinode*	Narromine, Australia	HQ261814	[23]
P. philippinensis	BPI 187044	*Z. mays*	Los Banos, Philippines	OK185341	[5]
P. sacchari	BRIP 44241	*Saccharum* sp.	Lautem, Timor Leste	HQ261791	[28]
P. sargae	BRIP 27691^{T}	*S. timorense*	Litchfield, Australia	HQ261809	[26]
P. schizachyrii	BRIP 67070^{T}	*Schizachyrium fragile*	Mareeba Wetlands, Australia	OK336452	[23]
P. sehimatis	BRIP 49806^{T}	*Sehima nervosum*	Arnhem Hwy, Australia	OK336453	[23]
P. sorghi	HOH HUH 897	*S. bicolor*	Karnakata, India	EU116055	[28]
Sclerospora graminicola	HOH HUH 894	*Pennisetum glaucum*	India	EU116050	[26]
	FR-0046007	*Cenchrus americanus*	Gujarat, India	HQ261789	[28]

Note: Stevens' Philippine Fungi, Island of Luzon, No.811; ^{T}holotype; ^{TA}ex-type of *Peronosclerospora australiensis*.

from Thailand (in 10 provinces); four from Cambodia; and four from Lao PDR. Typically, *P. neglecta* on maize in Cambodia, Lao PDR, and Thailand produced erect, dichotomously branched *conidiophores*, 180–280 µm long, that emerged from stromata; with oval, thin-walled, smooth and hyaline *conidia*, 16–25 × 10–20 µm that germinated by a germ tube. *Oospores* were not found.

Specimens examined:CAMBODIA, Kampong Cham, on leaves of *Z. mays*, 5 Sep. 2018, S. Thavrith, O. Samoul, R. Vanna, M. Socheat, M.D.E. Shivas, R.G. Shivas (BRIP 69061); Kandal, on leaves of *Z. mays*, 3 Sep. 2018, S. Thavrith, O. Samoul, R. Vanna, M. Socheat, M.D.E. Shivas, R.G. Shivas (BRIP 69045); Kandal, on leaves of *Z. mays*, 3 Sep. 2018, S. Thavrith, O. Samoul, R. Vanna, M. Socheat, M.D.E. Shivas, and R.G. Shivas (BRIP 69046); Preah Vihea, on leaves of *Z. mays*, 5 Sep. 2018, S. Thavrith, O. Samoul, R. Vanna, M. Socheat, M.D.E. Shivas, R.G. Shivas (BRIP 69063); LAO PDR, Champasak, on leaves of *Z. mays*, 27 Jul. 2018, R.G. Shivas, M.D.E. Shivas, K. Chittarhat, Soulin (BRIP 70147); Champasak, on leaves of *Z. mays*, 27 Jul. 2018, R.G. Shivas, M.D.E. Shivas, K. Chittarhat, Soulin (BRIP 70148); Vientiane, *Z. mays*, 9 Jul. 2018, K. Chittarhat, M.D.E. Shivas,

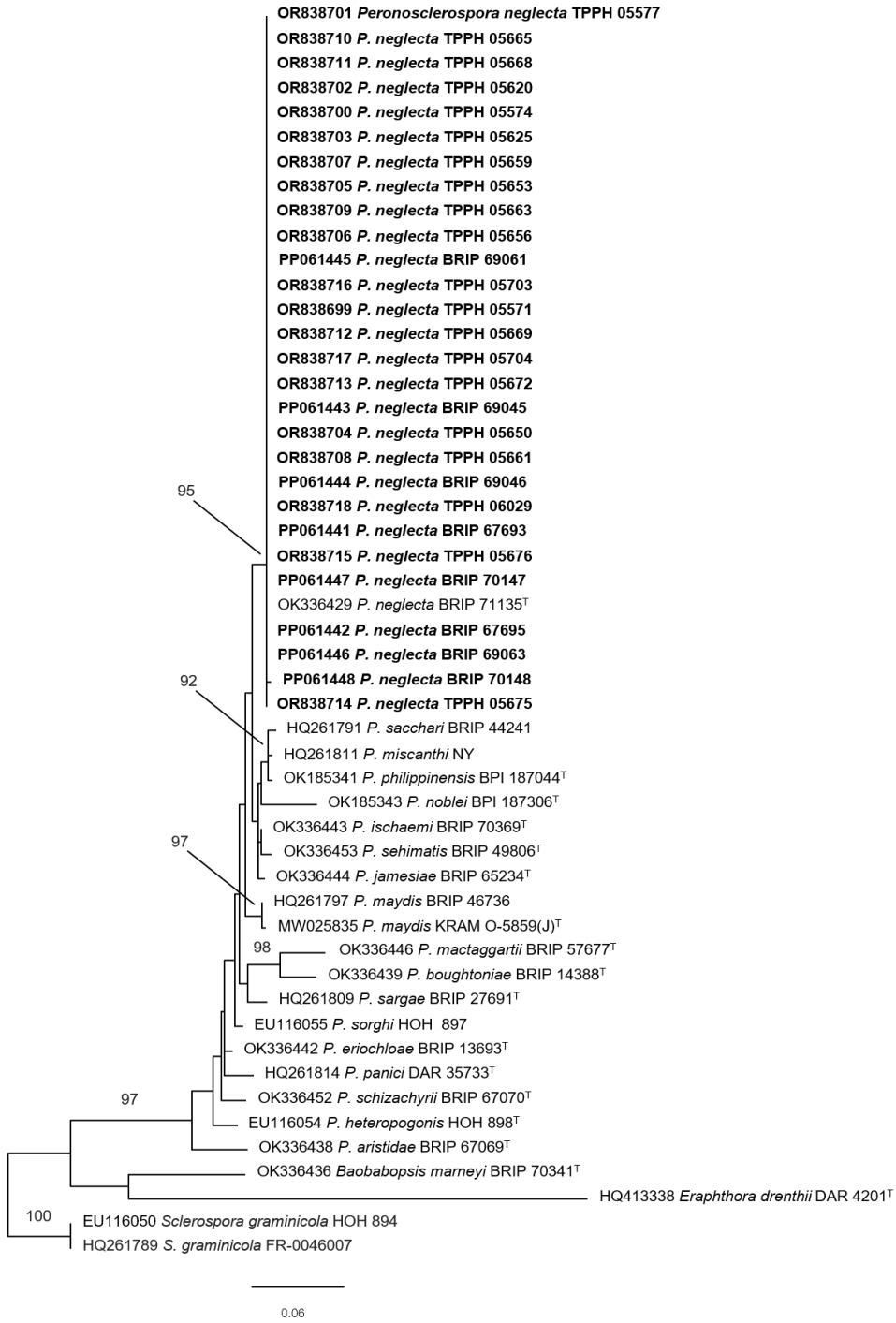

Figure 2. RAxML tree generated by maximum likelihood analysis of *cox2* sequence data. Bootstrap support values for maximum likelihood (ML, left) ≥70%. The tree is rooted to *Sclerospora graminicola* (HOH894) and *S. graminicola* (FR-0046007). The superscript "T" indicates ex-type strains. Specimens from this study are in bold.

Figure 3. *Peronosclerospora neglecta* on maize collected from Ratchaburi Province, Thailand. (A) conidia and conidiophores on maize leaf, (B) conidia and conidiophore. Scale bar B = 40 μm

R.G. Shivas (BRIP 67693); Vientiane, on leaves of *Z. mays*, 9 Jul. 2018, K. Chittarhat, M.D.E. Shivas, R.G. Shivas (BRIP 67695); THAILAND, Chiang Mai, on leaves of *Z. mays* var. *ceratina*, 18°33'00.0"N, 98°52'16.7"E, 288.7 m., 12 Dec. 2021, J. Tongnok, (TPPH 05625); Chiang Mai, on leaves of *Z. mays* var. *rugosa*, 19°04'25.7"N, 98°56'01.3"E, 331.2 m., 24 Jun. 2022, M. Sudsanguan, C. Doungsa-ard, A. Chaiyasen, P. Yoosabai, O. Luenkham (TPPH 05672); Chiang Mai, on leaves of *Z. mays* var. *indenata*, 19°11'54.7"N, 99°10'23.2"E, 398.8 m., 8 Sep. 2022, A. Chaiyasen (TPPH 05676); Chonburi, on leaves of *Z. mays* var. *indenata* 13°13'02.2"N, 101°14'14.3"E, 62.6 m., 5 Oct. 2022, M. Sudsanguan, C. Doungsa-ard, W. Pet-amphai, P. Yoosabai, O. Luenkham (TPPH 05675); Kanchanaburi, on leaves of *Z. mays* var. *rugosa*, 13°57'38.9"N, 99°39'04.7"E, 23.4 m., 25 Mar. 2021, M. Sudsanguan, K. Srimai, P. Maneechoat (TPPH 05571); Kanchanaburi, on leaves of *Z. mays* var. *rugosa*, 13°55'51.2"N, 99°28'35.0"E, 34.0 m., 25 Mar. 2021, M. Sudsanguan, K. Srimai, P. Maneechoat (TPPH 05574); Kanchanaburi, on leaves of *Z. mays* var. *ceratina*, 13°58'24.2"N, 99°27'21.2"E, 38.1 m., 25 Mar. 2021, M. Sudsanguan, K. Srimai, P. Maneechoat (TPPH 05620); Kanchanaburi, on leaves of *Z. mays* var. *rugosa*, 13°56'19.6"N, 99°34'10.6"E, 45.7 m., 30 Mar. 2022, A. Tanutong (TPPH 05659); Lamphun, on leaves of *Z. mays* var. *ceratina*, 18°41'58.6"N, 99°08'55.8"E, 318.4 m., 22 Sep. 2022, J. Tongnok (TPPH 05703); Loei, on leaves of *Z. mays* var. *rugosa*, 17°43'55.6"N, 101°43'33.6"E, 238 m., 5 Feb. 2023, M. Sudsanguan, C. Doungsa-ard, W. Pet-amphai, P. Yoosabai, O. Luenkham, Y.P. Tan, M.D.E. Shivas and R.G. Shivas (TPPH 06029); Nakhon Pathom, on leaves of *Z. mays* var. *rugosa*, 14°00'29.6"N, 99°57'20.8"E, 10.6 m., 13 Sep. 2022, P. Patanavipas, W. Chaersa-ard (TPPH 05669); Nakhon Ratchasima, on leaves of *Z. mays* var. *indenata* 14°38'54.5"N, 101°18'39.1"E, 383.7 m., 11 Aug. 2021, W. Bunkoed (TPPH 05577); Nakhon Ratchasima, on leaves of *Z. mays*

var. *indenata*, 14°38'56.2"N, 101°18'39.2"E, 384.9 m., 29 Jan. 2022, W. Bunkoed (TPPH 05650); Ratchaburi, on leaves of *Z. mays* var. *ceratina*, 13°42'59.7"N, 99°51'09.0"E, 18.9 m., 26 Feb. 2022, M. Sudsanguan, S. Sriwilaiwan, C. Pothikhawet (TPPH 05653); Ratchaburi, on leaves of *Z. mays* var. *ceratina*, 13°42'58.2"N, 99°51'09.5"E, 17.4 m., 26 Feb. 2022, M. Sudsanguan, S. Sriwilaiwan, C. Pothikhawet (TPPH 05656); Saraburi, on leaves of *Z. mays* var. *rugosa*, 14°44'38.4"N, 100°50'16.9"E, 105.1 m., 14 Dec. 2022, P. Trakunsukharat (TPPH 05704); Uthaithani, on leaves of *Z. mays* var. *indenata*, 15°12'51.1"N, 99°42'28.4"E, 93.6 m., 18 Jun. 2022, M. Sudsanguan, C. Doungsa-ard, W. Pet-amphai, P. Athipunyakom, S. Likhitekaraj, P. Yoosabai, O. Luenkham (TPPH 05661); Uthaithani, on leaves of *Z. mays* var. *rugosa*, 15°12'51.0"N, 99° 42'29.6"E, 94.3 m., 18 Jun. 2022, M. Sudsanguan, C. Doungsa-ard, W. Pet-amphai, P. Athipunyakom, S. Likhitekaraj, P. Yoosabai, O. Luenkham (TPPH 05663); Uthaithani, on leaves of *Z. mays* var. *ceratina*, 15°12'48.1"N, 99°42'27.1"E, 96.8 m., 18 Jun. 2022, M. Sudsanguan, C. Doungsa-ard, W. Pet-amphai, P. Athipunyakom, S. Likhitekaraj, P. Yoosabai, O. Luenkham (TPPH 05665); Uthaithani, on leaves of *Z. mays* var. *ceratina*, 15°12'48.0"N, 99°42'28.6"E, 94.4 m., 18 Jun. 2022, M. Sudsanguan, C. Doungsa-ard, W. Pet-amphai, P. Athipunyakom, S. Likhitekaraj, P. Yoosabai, O. Luenkham (TPPH 05668).

Known distribution: Cambodia [This study], Indonesia [2], Lao PDR [This study], and Thailand [6, this study].

4. Conclusions

This study showed that *P. neglecta* was widespread on maize in Thailand and also present on maize in Cambodia and Lao PDR. Accurate identification of maize downy mildew pathogens is important for disease management through breeding resistant maize varieties. The distribution and regional presence of maize downy mildews may also have biosecurity implications for the movement of planting material, especially seed.

Acknowledgements

The authors express appreciation to the Agricultural Research Development Agency (Public Organization), Thailand for financial support of this research. Thanks to staff member in the Plant Protection Department, Vientiane, Lao PDR, as well as staff members in the mycology laboratory, Plant Pathology Research Group, Plant Protection Research and Development Office, Department of Agriculture, Bangkok, Thailand, and also a staff member in the General Directorate of Agriculture in Phnom Penh, Cambodia, for the survey and collected downy mildew samples in the field.

Conflicts of interest

The authors declare no conflicts of interest.

References

[1] Arulselvi S., Selvi B. and Pandiyan M., *Int. J. Curr. Microbiol. Appl. Sci.,* 2018; **7**: 1472-1488. DOI 10.20546/ijcmas.2018.708.168.

[2] Muis A., Ryley M.J., Tan Y.P., Suharjo R., Nonci N., Danaatmadja Y., et al., *Mycol. Prog.*, 2023; **22**: 1-7. DOI 10.1007/s11557-022-01862-5.

[3] Rathore R.S., Trivedi A. and Mathur K., *Proceeding of 8th Asia Regional Maize Workshop,* Bangkok, Thailand, 5-8 August 2002; 366-379.

[4] Muis A., Nonci N. and Pabendon M.B., *AAB Bioflux*, 2016; **8**: 143-155.

[5] Crouch J.A., Davis W.J., Shishkoff N., Castroagudín V.L., Martin F., Michelmore R., et al., *Fungal Syst. Evol.*, 2022; **9**: 43-86. DOI 10.3114/fuse.2022.09.05.

[6] Janruang P. and Unartngam J., *Int. J. Agric. Technol.*, 2018; **14**: 845-860.

[7] Kim H.C., Kyung-Hee K., Kitae S., Jae Y.K. and Byung-Moo L., *Genes*, 2020; **11**: e191. DOI 10.3390/genes11020191.

[8] Kim J.Y., Moon J.-C., Kim H.C., Shin S., Song K., Kim K.-H., et al., *Appl. Plant. Sci.*, 2017; **5**: e1600132. DOI 10.3732/apps.1600132.

[9] Ko T.W.K., McKenzie E.H.C., Bahkali A.H., To-anun C., Chukeatirote E., Promputtha I., et al., *Chiang Mai J. Sci.,* 2011; **38**: 625-637.

[10] Rossman A.Y. and Palm-Hern ndez M.E., *Plant Dis.*, 2008; **92**: 1376-1386.

[11] Widiantini F., Yulia E. and Purnama T., *J. Agric. Eng.*, 2015; **3**: 23-27. DOI 10.18005/JAEB0302002.

[12] Cheewangkoon R., Kodsueb R., Monkhung S., Karunarathna K.V.A., Wongwan T., Withee P., et al., *Chiang Mai J. Sci.*, 2021; **48**: 726-759.

[13] Doungsa-ard C., McTaggart A.R., Geering A.D.W., Dalisay T.U., Ray J. and Shivas R.G., *Australas. Plant Pathol.*, 2015; **44**: 25-30. DOI 10.1007/s13313-014-0301-z.

[14] Choi Y.-G., Beakes G., Glockling S., Kruse J., Nam B., Nigrelli L., et al., *Mol. Ecol. Resour.*, 2015; **15**: 1275-1288. DOI 10.1111/1755-0998.12398.

[15] Stamatakis A., *Bioinformatics*, 2014; **30**: 1312-1313. DOI 10.1093/bioinformatics/btu033.

[16] Pupipat U., *Kasetsart J. (Nat. Sci.)*, 1976; **10**: 106-110.

[17] Pupipat U., Sommart T., Chamsawarng C., Phatak H.C., Kriengyakul V., Choonhawongse K., et al., *Thailand National Corn and Sorghum Program 1976 Annual Report*, Department of Agriculture, Bangkok, Thailand. 1976; 247-256.

[18] Pitakspriwan P. and Giatgong P., *Kasetsart J. (Nat. Sci.)*, 1976; **10**: 118-120.

[19] Doungsa-ard C., Athipunyakorm P. and Seemadua S., *Proceedings of The 13th National Plant Protection Conference,* Rua Rasada Hotel, Trang, 21-23 November 2017, 151-164.

[20] Pupipat U., Renfro B.L., Chamswarng C., Saengwanich W., Saengwanich U., Sommartya T., et al., *Thailand National Corn and Sorghum Program 1975 Annual Report*, Department of Agriculture, Bangkok, Thailand, 1975; 287-292.

[21] Runge F. and Thines M., *Eur. J. Plant Pathol.*, 2011; **129**: 147-156. DOI 10.1007/s10658-010-9650-9.

[22] Ryley M.J., Tan Y.P., Kruse J., Thines M., and Shivas R.G., *Mycol. Prog.*, 2022; **21**: 297–310. DOI 10.1007/s11557-021-01750-4.

[23] Telle S. and Thines M., *Mycol. Prog.*, 2012; **11**: 121-129. DOI 10.1007/s11557-010-0735-9.

[24] Thines M., Göker M., Telle S., Ryley M., Mathur K., Narayana Y.D., et al., *Mycol. Res.*, 2008; **112**: 345–351. DOI 10.1016/j.mycres.2007.10.010.

[25] Shivas R.G., Ryley M.J., Telle S., Liberato J.R. and Thines M., *Australas. Plant Pathol.*, 2012; **41**: 125-130. DOI 10.1007/s13313-011-0097-z.

[26] Suharjo R., Swibawa I.G., Prasetyo J., Fitriana Y., Danaatmadja Y., Budiawan A., et al., *Mycol. Prog.*, 2020; **19**: 1309-1315. DOI 10.1007/s11557-020-01628-x.

[27] Telle S., Shivas R.G., Ryley M.J. and Thines M., *Eur. J. Plant Pathol.*, 2011; **130**: 521-528. DOI 10.1007/s10658-011-9772-8.

[28] Raciborski M., *Ber. Dtsch. Bot. Ges.*, 1897; **15**: 475-478.

[29] Waterhouse G.M., *Commonw. Myco. Inst. Misc. Publ.*, 1964; **17**: 1–30.

[30] Weston W. H., *J. Agric. Res.*, 1920; **19**: 97–122.

[31] Weston W. H., *J. Agric. Res.*, 1921; **20**: 669–684.