PRIMARY RESEARCH PAPER | *Philippine Journal of Systematic Biology*
DOI 10.26757/pjsb202317002

Peronosclerospora philippinensis (Philippine corn downy mildew): predicting plant disease emergence and distribution

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Abstract

Peronosclerospora philippinensis, or the Philippine corn downy mildew, is an obligate biotrophic pathogen of the Phylum Oomycota. The organism is tagged as the most destructive pathogen of maize worldwide, and recently, there have been a few reports on the re-occurrence of the pathogen from the past decade. Disease control and mitigation through chemical agents have been the current practice; however, it appears that the pathogen is influenced by environmental factors that drive re-emergence. Presented herein is an attempt to predict the potential geographical distribution of *P. philippinensis* in the Philippines. Two changing climate scenarios were generated, and data suggested a probable expansion of the pathogen to the Southern Tagalog region and some areas in the Visayas region, particularly on Negros Island. Further, the mean diurnal range for the current climate, and precipitation in the driest month for the predicted scenarios appeared as the most contributory bioclimatic variables affecting distribution. Generated data suggest a call for a proactive response to the potential disease breakthrough of the Philippine corn downy mildew.

Keywords: corn, downy mildew, Oomycota, species distribution, species modeling

Introduction

Peronosclerospora philippinensis (Weston) C.G.Shaw is a biotrophic species of the graminicolous downy mildew group of the Phylum Oomycota (Dogma 1969, Exconde 1982). The asexual stage, i.e., conidiophores and conidia, occurs only in a corn host, and no report to date of its gametangia in any species of Poaceae. Logic then dictates that corn plants are either the accidental or intermediate host of *P. philippinensis*. The primary infection mechanism of the organism is believed where the airborne conidia attach to a susceptible corn host. The conidia will germinate and produce a germ tube that will penetrate the stomata and form a haustorium – a structure used during the infection process. Upon successful infection, the pathogen will acquire nutrients from the host until enough nutrients are absorbed to support sporulation, i.e., the formation of new conidia. Once viable conidia are formed, a germ tube is believed to germinate for roughly 1 h, followed by infection for 2-3 h. It is proposed that germination and infection are optimal between 21° to 26°C and that conidiophores and sporangia cannot withstand and are short-lived during sunny conditions (Weston 1920, Dalmacio & Raymundo 1972).

The earliest annotation of this pathogen was by Baker (1916); however, the most comprehensive documentation of the disease was presented by Weston (1920). For the last decades, disease occurrence has been reported in many parts of the Philippines, especially in Northern Luzon and various areas in Mindanao, despite deployed cropping techniques to mitigate the spread of the disease. Being the most virulent of the downy mildew family, *P. philippinensis* severely caused economic loss to corn production, with approximately 40 – 60% disease crop yield observed every time an incidence occurs (USDA, 2006).

In the Philippines, research mainly dealt with disease mitigation and control (Dalmacio & Exconde 1969, Exconde 1970, Dalmacio & Raymundo 1972, Exconde & Raymundo 1974). Compounds tested against *P. philippinensis*, e.g., zinc manganese ethylene bisdithiocarbamate, triphenyltin hydroxide, ferric dimethyldithiocarbamate, 2,3-dichloro-1,4-naphthoquinone, dimethylamino phenyl-diazonium sulfonate, were found effective, albeit only for some generations of harvest (Exconde 1982). However, fungicides like Apron 35 SD (formerly Ridomil, with Mefenoxam as its active ingredient), Metalaxyl, and Fentin hydroxide were effective as a seed-dressing protectant on corn and offered better protection results against *P. philippinensis*. However, recent unpublished explorations inferred that this pathogen is present in supposedly downy mildew-resistant corn plants. Despite this, the records for the disease are merely anecdotal.

For fungi and fungal allied pathogens targeting plants, bioclimatic variables are directly linked with species incidence and species distribution, as regions where the affected plants grow, are highly dependent on the climatic conditions that allow its endemicity (Molloy et al. 2014). Additionally, disease progression caused by pathogens is linked to the overall climate within those regions, as the amount of rainfall and temperature and the changes that occur over the years affect both pathogen sporulation and susceptibility of the affected plants (Swinfield et al. 2012). Analysis of current climate conditions and prediction of changes in bioclimatic variables through maximum entropy modeling have been utilized in

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Date Submitted: 08 August 2022
Date Accepted: 28 November 2023
Date Published: 26 December 2023

many fungal studies (Ascomycetes, Shrestha & Bawa 2014, Gearman & Blinnikov, 2019) and fungal-like (Myxomycetes, Almadrones-Reyes & Dagamac 2018, Dagamac et al. 2021, Limbo-Dizon et al. 2022) to help predict suitable habitats that will aid in understanding the general ecology of those fungi. In addition, the distribution of the disease and risk maps for many plant pathogens in the country are still missing. It is, therefore, the goal of this study to present a predictive model using bioclimatic envelopes for the distribution of *P. philippinensis* and its corresponding factors affecting such distribution.

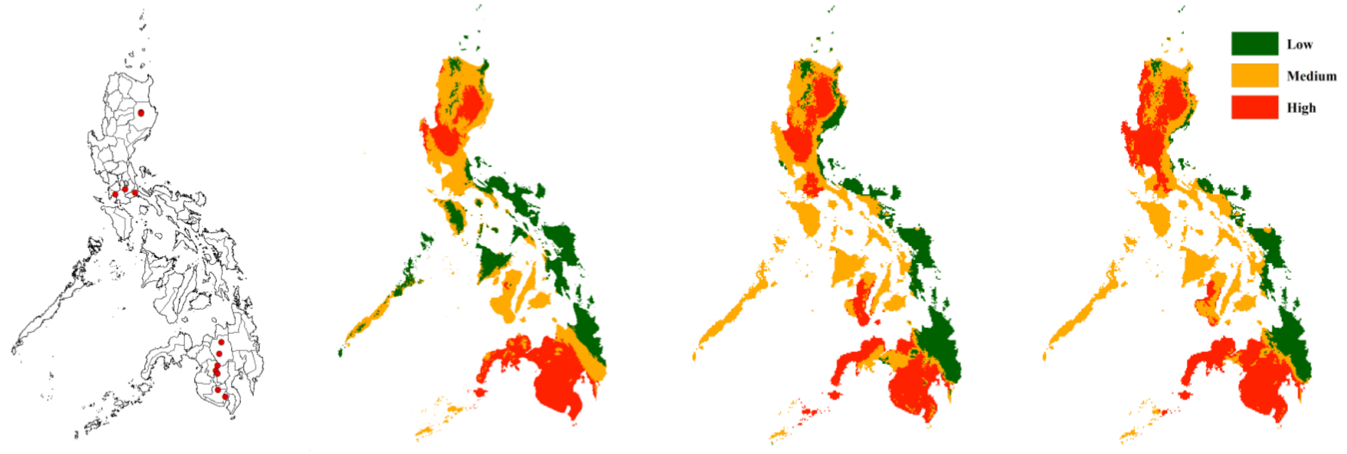
Materials and Methods

Data gathering

Geographical coordinates of the pathogen occurrence were retrieved on three different platforms. First, grey literature of anecdotal reports and scientific research citing the appearance of the disease in corn. For older records with no geographical information initially recorded, the geographic centroid was estimated by triangulating the closest known locality wherein the agricultural land for corn is most likely planted. Second, is the electronic database that reports actual coordinates, and lastly, the personal recordings or anecdotes of people that have been able to survey the occurrence of the disease in the Philippines. Initial data verification was performed to confirm the accuracy of all 12 geographic coordinates used in this correlative modeling study. Coordinates were converted into a CSV file and overlaid on a Philippine map using ArcGIS 10.3. For the environmental layers, the current climatic conditions of 19 bioclimatic variables data were collected from the worldclim database (https://www.worldclim.org) with a raster resolution of 1 km. To predict the future potential distribution of *P. philippinensis* in the Philippines, the future climate projection data were downloaded at the GCM downscaled data portal (http://www.ccafs-climate.org/). The global climate model (GCM), CICRO model representing simulations from the fifth assessment of the Intergovernmental Panel for Climate Change (CMIP5) were patterned from Almadrones-Reyes & Dagamac (2018), hence selecting future climatic conditions of the year 2080 with two different storylines of future climate as representative for this study. The A2 storyline follows an increasing population with a higher carbon emission rate, leading to a predicted global mean temperature of 3.4°C. The B1 storyline assumes a modification in the material production that causes technology to advance more efficiently, hence, predicting an increase by only 1.8°C to the global mean. These two future scenarios were downloaded as an ESRI file and were then converted to ASCII format to fit the requirements of the MaxEnt (maximum entropy species modeling) software.

Model performance and calibration

The software MaxEnt Version 3.4.4 k, was used to map the potential geographic distribution of the 12 coordinates identified for the incidence in the Philippines. The selection of MaxEnt is based on the known advantages of the software it utilizes: present-background data, effective at low numbers of occurrence data, and robust production of models due to the estimation of the probability distribution of species occurrence based on the current presence points and randomly generated background points of environmental conditions by finding the maximum entropy distribution of the species. To optimize model complexity that will improve the predictive ability of the model runs to avoid issues of overfitting, ENMeval was used (Muscarella et al. 2014). For this approach, the fine-tuned setting generated from the ENMeval analysis (method = jackknife, kfold=10) suggested the adjustment of a regularization multiplier (RM) and feature type (FT) for each model runs as follows: *Current Climate* (2.5 [RM] / LQH [FT]); *A2 storyline* (4 [RM]/ LQH [FT]); *B1 storyline* (4 [RM] / LQHPT [FT]). The settings and the model were employed at convergence threshold (10–5), maximum iterations (5000), and the maximum number of background points (10000) to run the model. A Jackknife test was also used to estimate the relative importance of each of the selected variables to the model development. The model performance was tested using



***Peronosclerospora philippinensis* local distribution**

Current Climate

A2 Climate Scenario

B1 Climate Scenario

Figure 1. Species distribution models for the localized distribution of *Peronosclerospora philippinensis* and the predictive suitable habitat areas under the current and two climate storylines (A2 and B1 scenarios) generated by maximum entropy algorithm. The maps were presented on a heat map based on the calculated probability of occurrence. Dark green indicates low suitability (0 – <0.33), yellow-orange indicates moderate suitability (0.34 – <0.66), red indicates high suitability (0.67 – <0.99).

Table 1. List of environmental variables in the Philippines used for the three different climate scenarios and the value of their percent contribution.

Environmental Variables	Current Climate	A2 Climate Scenario	B1 Climate Scenario
Bio1 Annual Mean Temperature	0	0	0
Bio2 Mean Diurnal Range	83.1	32.8	47
Bio3 Isothermality	0	0	0
Bio4 Temperature Seasonality	0	0	0
Bio5 Max Temperature of Warmest Month	6.6	2.4	5.7
Bio6 Max Temperature of Coldest Month	0	0	0
Bio7 Temperature Annual Change	0	0	0
Bio8 Mean Temperature of Wettest Quarter	0	0	0
Bio9 Mean Temperature of Driest Quarter	0	0	0
Bio10 Mean Temperature of Warmest Quarter	0	0	0
Bio11 Mean Temperature of Coldest Quarter	0	0	0
Bio12 Annual Precipitation	0	0	0
Bio13 Precipitation of Wettest Month	0.1	2	0
Bio14 Precipitation of Driest Month	0	62.8	47.3
Bio15 Precipitation Seasonality	0	0	0
Bio16 Precipitation of Wettest Quarter	0	0	0
Bio17 Precipitation of Driest Quarter	4.3	0	0
Bio18 Precipitation of Warmest Quarter	0	0	0
Bio19 Precipitation of Coldest Quarter	5.8	0	0

the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC). AUC values in the model output range from 0 to 1 (unsuitable to highly suitable). When AUC shows values below 0.5, it can be interpreted as a random prediction. Response curves were used to study the relationships between bioclimatic variables and the predicted probability of the presence of *P. philippinensis*. The output file generated from MaxEnt was then exported as ASCII file format. To get a detailed visualization, the ASCII output file format from MaxEnt was imported into ArcMap 10.4 software. The map was then divided in the ArcMap software using defined intervals as a classification method into four different categories.

Results

Under the current climate (Fig. 1), the species can be found infecting some regions on the island of Luzon, specifically in the Ilocos region (Region I), Cagayan Valley (Region II), and the Cordillera Administrative Region. High incidence is also expected in significant portions of Mindanao that include Northern Mindanao (Region X), Southern Mindanao (Region XI), and Bangsamoro Autonomous Region of Muslim Mindanao (BARMM). Considering the predictive models using climate scenarios, the A2 and B1 climate scenarios showed the expansion of *P. philippinensis* to some sections of Region IV (Southern Tagalog Region), specifically in Cavite, Laguna, and small parts of the Visayas island groups, wherein high suitability of proliferation has been predicted to occur specifically on the island of Negros.

Several major bioclimatic variables putatively influence the species' predicted local distribution in the Philippines. For the percent contribution (Table 1), the mean diurnal range (BIO2) contributed 83.1% for the current climate, whereas precipitation in the driest month (BIO14) contributed 62.8% and 47.3% for both A2 and B1 climate scenarios, respectively. In terms of permutation importance, the model calculated that the mean diurnal range (BIO2) was the highest for the current climate at 82.6% and the B1 climate scenario at 56.6%. In contrast, for the A2 climate scenario, precipitation of the driestt month (BIO14) still has the highest with 57.1%. The Area Under the Curve (AUC) values obtained from maximum entropy-based results for the three climatic scenarios were 0.817 for the current climate, 0.849 for the A2 climate scenario, and 0.842 for the B1 climate scenario, indicating strong predictive model efficiency.

Discussion

A survey of literature about the occurrence of *P. philippinensis* is undeniably a challenging task. Incomplete anecdotal reports of the appearance of the pathogen in a particular area, the accuracy of the exact coordinates on occurrence reports, and the ground-truthing steps are often factors that affect occurrence studies. Historical outbreaks of Philippine downy mildew disease have led to the selection and isolation of several downy mildew-resistant inbred lines of corn, wherein varietal hybridization of local and introduced germplasm has led to the development of lines which presented only 1% to 25% infected plants, indicating high resistance. In contrast, susceptible lines have been classified to exhibit over 75% infection. Notable downy mildew-resistant varieties developed from these lines are Philippine DMR 1 and 2 and MIT Sel-2, which have been extensively distributed and produced by the national government (Exconde 1974, Aday 1975).

Although this stratagem has been effective, there is currently still a report of the disease that appears and affects the yield of maize in the Philippines, as shown in the current distribution of the pathogen based on the model (Fig. 1). Nevertheless, the predictive model also suggested regions in the Philippines where *P. philippinensis* could exist under different climate scenarios. Due to regional variation of rainfall and specialized climate conditions, climate zoning in the Philippines has been traditionally based on the Modified Coronas Classification (MCC) system, a rain-gauge network that categorizes variation in average monthly rainfall into four distinct climate zones (Basconcillo et al. 2016). Based on yearly rainfall distribution from the years 1951 to 2010, regions with Type I and III climate zones are indicative of having both wet and dry seasons, while Type II and Type IV climate zones have only a single year-long wet season, varying in minimum monthly rainfall (Corporal-Lodangco & Leslie 2017). Species incidence and distribution in the regions in Northern Luzon coincided with MCC system rainfall data, with the Ilocos Region located in the Type I climate zone, while the western portions and major land areas of both the Cagayan Valley and Cordillera Administrative Regions were within the Type III climate zone. Additionally, areas where the specific incidence of the pathogen on the island of Mindanao in Northern Mindanao, Southern Mindanao, and the Bangsamoro Autonomous Region of Muslim Mindanao can be observed to specifically occur in Type III climate zones. The predicted proliferation of the pathogen on the island of Negros corresponded with the island's climate, which is also a Type III climate zone.

Since Type I and Type III climate zones have the variability between wet and dry seasons, this contributes to higher levels of humidity and longer rainy seasons. Both humidity and rainfall are factors that have been observed to increase pathogen sporulation in similar tropical oomycete species such as *Phytophthora palmivora*. Disease proliferation is linked with the sporulation of *P. palmivora*, starting from the soil by infecting through the roots with the assistance of rain splash and erosion and then eventually spreading to the upper canopy of the hosts through insects and the wind, both of which have been linked with high humidity in tropical regions (Derevnina et al. 2016).

Diurnal temperature range, which pertains to the difference between the daily maximum and minimum temperature range, is another environmental factor shown to affect species incidence and predicted proliferation of *P. philippinensis*. The current geographic incidence of Philippine downy mildew indicated in Fig. 1 has been observed to occur specifically in regions with higher annual mean diurnal temperature range, specifically around 9° – 10°C, as indicated in recorded climate observations by the Climate Research Unit of the University of East Anglia for the years 1961 to 2010 (Osborn et al. 2016). However, in the predicted scenarios, a subsequent increase in the pathogen distribution is observed under decreasing diurnal temperatures caused by climate change. Further, Rohr & Cohen (2020) inferred that increased climate variability and a decrease in the diurnal temperature range are hallmarks of climate change. This scenario is supported by other fungal pathogen diseases from the recent review of Nnadi & Carter (2021) that directly associates climate variability and change in the mean temperature, e.g., *Batrachochytrium dendrobatidis* (Raffel et al. 2013), and *Puccinia striiformis* (de Vallaviele-Pope et al. 2018).

As indicated by the predicted scenarios, an increase in night-time temperature is a possible contributor to a larger distribution of *P. philippinensis* in the surrounding land areas within the affected region. Specific night-time temperatures of 21° – 26°C with high humidity are ideal conditions for conidia production of Philippine corn downy mildew and which is proliferated through the mechanical action of the wind and rain. The decrease in the diurnal temperature range observed in both scenarios caused by increased warming of temperature during the night could aid in species proliferation. Higher global temperatures and subsequent climate change in the area is also a factor for increased conidia dispersal through wind and longevity of the spores due to accompanying moisture, leading to the possible localized spread of the pathogen (Fredriksen & Renfro 1977, USDA, 2006).

In a study conducted by Romero et al. (2022), the primary drivers for global outbreaks of emerging plant diseases caused by fungal and oomycete pathogens are humidity and high temperature, wherein high humidity has been associated as a key factor in at least 36.4% of cases during the years 2014 and 2019. Analysis of climate variables within regions has shown concurrent results with the occurrence and proliferation of plant pathogens, wherein temperature and humidity have been the main determinants utilized in predictive studies.

Variable weather conditions have been shown to affect the proliferation and growth of other plants affected by phytopathogens. In Central and South America, the incidence of Coffee Leaf Rust outbreaks during the years 2008 to 2013 caused by the fungus, *Hemileia vastatrix*, was reported to occur coincident with periods of lower diurnal thermal amplitude which lowered the latency period of the disease (Avelino et al. 2015). Harvell et al. (2002) suggested that increased sporulation of fungi targeting foliage was caused by concurrent higher day and night temperatures, suggesting a lower diurnal temperature range within that period. Similarly, European fungal outbreaks of wheat stem rust caused by *Puccinia graminis* f. sp. *tritici* have been on the rise, wherein the previously rare disease was found in several countries such as Germany in 2013 (Olivera Firpo et al. 2017) and regions such as Sicily in 2016 (Bhattacharya 2017).

Dramatic climate change has been an ongoing experience in this age of the Anthropocene, with predicted rates of global mean temperature increasing unprecedentedly over the last 1000 years (Santini & Gherladini 2015). Extreme climate events are becoming more frequent, especially at a local scale which severely affect the natural ecosystem, including the relationship between plants and pathogens (Tang et al. 2021). Adaptive responses of plant pathogens are described to exploit existing phenotypic plasticity (De Fine Licht 2018), move to areas with more favorable climates (Garett et al. 2014), and evolve new features or attributes (Chakraborty 2013). However, responses to climate change also influence species distribution and interaction.

Conclusion

The study highlights the possible areas in the Philippines where *P. philippinensis* could proliferate and perpetuate based on the predicted models. Climate variability and diurnal temperature range are important ecological factors contributing to the persistence of this highly destructive pathogen. Further, field surveys and proper reporting of disease occurrence are equally important in developing disease prevention management plans and, likewise, in understanding the biology of *P. philippinensis*.

Acknowledgements

RMB and NHAD are funded by an internal grant from the Research Center for the Natural and Applied Sciences, University of Santo Tomas. NHAD received the Department of

Science and Technology-Philippine Council for Agricultural, Aquatic Resources Research and Development (DOST-PCAARRD) Balik Scientist grant.

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