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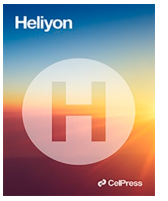

Research article

Climatic drivers for assessment of false smut risk in rice ecosystems: A guide for planning effective management trials

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ABSTRACT

Emergence of false smut (RFS) in rice agroecosystems is causing significant yield losses due to its direct impact on grains. To assess the factors associated with host-pathogen interaction, maximum entropy principle is used to identify bioclimatic variables behind the geo-spatial distribution patterns of RFS. Bioclimatic variables with ecological significance, derived from the monthly temperature and precipitation, such as precipitation in the wettest month, mean temperature of the warmest quarter and precipitation seasonality are linked to the occurrence of the disease. These three variables are identified as the strongest predictors of RFS distribution contributing 47.81 %, 26.63 % and 12.43 % respectively. Seasonal precipitation and its variability have played as a limiting factor for the disease. Temperature plays a crucial role in pathogen growth and development (mycelial growth, sclerotial germination and infection) and exerts influences on disease distribution. Spatial distribution pattern of the disease and its intensity, as well as the number of sclerotia/panicle development, germination and infection suitability, suggest that temperature response and daily precipitation during the booting stage have a significant impact on disease development. Number of favourable days composed of temperature response [$f(T) > 20$] and daily rainfall (>5 mm) is noted to be proportional to the RFS incidence (infected grains/panicle). RFS distribution pattern validated through ground truth data is noted to have a correspondence with rainfall pattern during the wettest month (June–Sep). The rainfall-induced monocyclic infection process at known stage of crop growth is implicated for evaluation of management options as effective fungicides are available.

1. Introduction

Rice is considered as the most significant food crop and plays a critical role in global food security. However, rice agroecosystems are currently facing several challenges due to multiple risks and productivity constraints caused by various biotic and abiotic stresses, climatic uncertainties, and global changes. Moreover, depletion in natural resources due to growing economic pressure poses an additional threat to food security. False smut in rice (RFS) has emerged as a significant biotic threat to rice production, particularly in

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South Asian regions. It has become the most devastating grain disease in the past two decades although it is known since the 1970s in Asian nations [1]. Till recently, a minor disease considered geographically limited but is now established as a major threat in all rice-growing regions [2–5]. False smut incidence is on the rise in hybrid rice in the major rice-growing regions in China and India [6,7], which is a great concern as a significant chunk of the world rice production comes from these regions. False smut can cause a yield loss of 3–70 %, depending on weather conditions and varietal susceptibility [8] and the carcinogenic mycotoxins produced in the grains may cause human and animal health risk on consumption of contaminated grains and straw [9].

The pathogen *Ustilaginoidea virens* has been observed to have both sexual and asexual stages [10,11]. It produces ascospores, conidia, and chlamydospores during rainy days [12,13]. In addition to rice, maize and weeds can also act as alternative hosts [11–14]. Perpetuation of the pathogen in soil or alternative grasses is likely a reality; however, it is still unclear whether the infection is air or soil-borne. How the pathogen's life cycle is coupled with the disease cycle is yet to resolve [1]. Attempts to induce infection through inoculation or spraying conidia and chlamydospores on spikelet's have been unsuccessful as infection does not occur after heading [6, 15,16]. Injection of spores into the sheath during the booting stage has been found to efficiently induce disease symptoms [15,17]. The fungus has been detected (ITS based primer) in panicles at the booting stage, as well as in whole panicles before rice heading [18]. At seedling stage, the pathogen can attack the roots and lead to asymptomatic colonization throughout the entire plant, as detected by molecular techniques and histological observation [19,20]. The sclerotia that exist on or under the soil surface can germinate and form fruiting bodies, which then produce ascospores that contribute to the primary infection process [21].

In order to dispel uncertainties in pathogenesis and better understand the relationship between bioclimatic parameters and disease development it is important to underscore the epidemic features [22]. There is evidence to suggest that temperature plays a role in sclerotial induction or formation, germination, and symptoms development, indicating a seasonal association of the disease [1,9,10]. In fact, low temperature exposure after inoculation has been found to have a strong stimulatory effect on disease development [10]. To this end, RFS risk assessment in relation to environmental parameters can help in predicting disease outbreaks and develop management strategies. A robust assessment framework is required to identify epidemic factors from known geospatial patterns, which can provide valuable insights on habitat suitability, risk mapping, and disease prediction in time and space [23–25]. Modeling RFS risk in terms of timing, abundance, and seasonal patterns of disease development may improve understanding of the relationship between environmental factors and disease cycle in order to reflect important insights of infection dynamics of the disease [22,26].

As host-pathogen interaction is not very clear at working level therefore requisite data on cause-effect relationship is still lagging. Limited data on host-pathogen interaction is a hindrance to evaluate resistance and develop management strategies. Machine learning algorithms are used to generate cause-effect relationship data associated with host-pathogen interactions [28–30]. The Maxent model - maximum entropy algorithm, is a widely used tool for analyzing and identifying geospatial patterns in relation to species distributions, habitat suitability, and disease epidemiology [24,27]. The modelling principle suggests that, given incomplete information, the best probability distribution is the one with the highest entropy subject to known constraints [24]. In the context of RFS distribution, constraints can be derived from the known occurrences of the disease for observed environmental variables (e.g., temperature, precipitation) at locations where the disease is known to occur. In the maximum entropy framework, $P(x)$, the probability that the RFS will be found in the location x is determined by maximizing $H(P)$:

$$H(P) = -\int P(x).logP(x)dx$$

subject to the constraints that match the empirical expectations of the bioclimatic variables. If the bioclimatic variables (x) denoted by the feature function $f_i\ (x)$ (relationship between variables and disease presence) then the expectation of $f_i\ (x)$ over the predicted distribution $P(x)$ should match its empirical average over the locations where the false smut presence is observed:

$$\int P(x)f_i(x)dx = \frac{1}{N}\sum_{j=i} f_i(x_j)$$

where, x_i are the observed disease presence locations and N is the total number of observations; $f_i(x)$ are the feature functions (classes). The probability distribution $P(x)$ is modelled through an exponential distribution:

$$P(x) = \frac{1}{Z(x)} exp\left(\sum_i \lambda_i f_i(x)\right)$$

Where, λ_i are the weight parameters (Lagrange multipliers) for each function; $Z(x)$ is the normalized factor that ensures the probabilities sum to 1:

$$Z(x) = \sum_i exp\left(\sum_i \lambda_i f_i(x)\right)$$

Maximum entropy principle serves as a criterion for learning probability models, where the model's quality is assessed based on the magnitude of entropy, higher entropy indicates a better model [24]. For estimation of potential distribution of black rot in cacao *(Phytophthora megakarya)* in central and west Africa based on its occurrence and environmental factors Maxent model has been used [28]. Maximum entropy principle is used for prediction of suitable habitats for anthracnose disease *(Colletotrichum acutatum)* in fruits and vegetables [29] and bacterial canker *(Pseudomonas syringae* pv. *actinidiae)* in kiwifruit [30] under current and future climates based on their occurrence records and environmental factors.

Consequently, Maxent model has the potential in identifying environmental parameters involved in host-pathogen interaction and finding simple criteria for false smut prediction to be implicated for evaluation of management strategies. The current paper is aimed to understand the false smut epidemic risk which is crucial for implementing effective disease management strategies. The major objectives were: (1) To predict the environmental suitability for false smut development and distribution; (2) To assess the factors regulating epidemic process.

2. Materials and methods

The study aimed to identify the most important bioclimatic parameters associated with false smut occurrence through the training of the Maxent algorithm. This algorithm utilizes the principle of maximum entropy to optimize a set of functions involving bioclimatic variables of the habitat and disease presence data. Maxent outputs as raster maps are used to predict RFS risk by using spatial analyst tools. Through reverse modeling approach bioclimatic variables being referred causally to explain disease development at plant scale and to link the infection process with the disease cycle.

2.1. Assessment of RFS to identification of bioclimatic variable features associated with disease distribution

2.1.1. Disease occurrence data

Through ground truth survey presence of false smut was noted at 160 locations across all agro-climatic zones where rice is grown during June-July-Aug-Sep-Oct (Fig. 1). Using Spthin package duplicate records were eliminated and finally 141 locations were considered. For RFS observation in a field, 3–5 points were chosen along the arms of an imagined Z shape. For each point, 10 panicles (one sq. m) were randomly selected and the number of spikelets or smut balls, as well as the number of sclerotia, were counted. For each location, a composite index for at least 7–10 sites was calculated as the ratio of the sum of the number of infected spikelets (as well as sclerotia) divided by the total number of panicles.

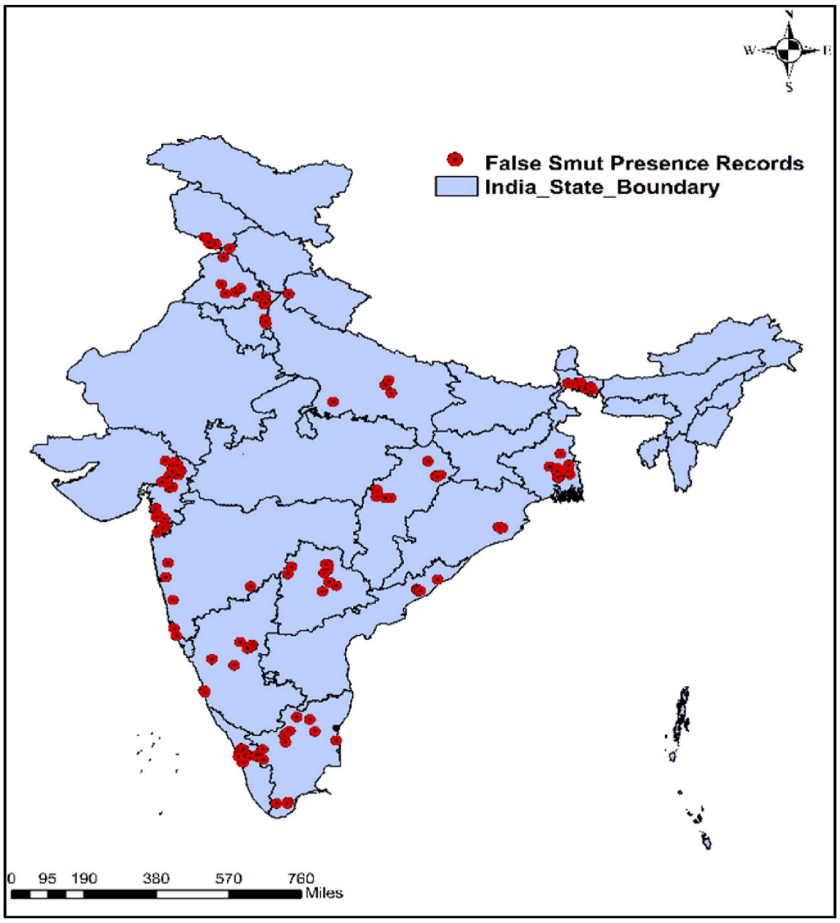

Fig. 1. Ground truth information on false smut occurrence in rice agro-ecosystems.

2.1.2. Environmental or bioclimatic data

A total of 19 bioclimatic variables were retrieved from the WorldClim global climate database (https://worldclim.org/data/cmip6/cmip6_clim2.5m.html) at a spatial resolution of 2.5 arc-min, or approximately 4.6 km at the equator. In order to investigate the bioclimatic determinants and predict the distribution of rice false smut disease, data sets encompassing the period 1970–2000 were collected. To make the data compatible with Maxent software, it was transformed to ASCI format. 'ENMTools' [31] package in R program was used to analyze the cross-correlations among the bioclimatic variables. To determine each variable's initial contribution %, all variables were included in a Maxent baseline model ran prior to selection of the bioclimatic variables. When two variables having a correlation more than 0.8, the most significant variable based on its contribution to the model was kept in the analysis. If the percentage of contribution was more than 1.0, the other variables were taken into account [32]. Seven bioclimatic variables Bio_2 (mean diurnal range), Bio_4 (temperature seasonality), Bio_10 (mean temperature of warmest quarter), Bio_13 (precipitation of wettest month), Bio_15 (precipitation seasonality), Bio_17 (precipitation of driest quarter), and Bio_19 (precipitation of coldest quarter) were ultimately selected to train the Maxent model.

2.1.3. Training of Maxent model for known distribution of false smut

2.1.3.1. Configuration of the Maxent model. The Maxent model, also known as the maximum entropy algorithm, version 3.4.4, was utilized to predict RFS using disease presence data. The original bioclimatic variables dataset was transformed into feature functions or classes (FCs), including linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) [33,34]. The RFS occurrence data was randomly divided into two sets containing 75 % and 25 % of the data for training and testing the model, respectively. The FCs and regularization multipliers (RMs) parameters were adjusted to overcome the overfitting issue of the model [34]. The 'EVMeval' package in R statistical software version 4.2.0 was used to test all possible combinations of FCs, taking one, two, three, four and five features at a time. To determine the feature combination RMs was set between 0.5 and 5 with an interval of 0.5 [35,36]. The optimization of FCs and RM was performed by using tenfold random cross-validation of the total occurrence dataset.

The model performance was evaluated based on the area under the receiver operating characteristic curve (AUC-ROC) and the true skill statistic (TSS). The significance of factors influencing RFS was represented by the average values of the area under the curve (AUC). The accuracy of the model was measured using the area under the receiver operating characteristic (ROC) curve [37,38]. The predictive accuracy of the model was assessed using the cross-validation technique. To select the optimum model parameters, Akaike's Information Criterion (AICc) with small sample size correction was used. Further analysis was conducted using the model parameter combination with the smallest AICc (delta. AICc = 0). In order to assess the consistency of the model and quantify the errors, the model was also fitted on the data set using tenfold cross-validation [39]. TSS was calculated using the maximum training sensitivity plus specificity Cloglog threshold. Finally, the Jackknife test was performed to measure the importance of variables in predicting the potential RFS distribution.

For model configuration the parameters used were maximum iterations of 5000, regularization multiplier of 0.5, output format of cloglog, feature combination of Quadratic, Hinge, and Product (QHP), and default values such as random test percentage of 25, convergence threshold of 0.0001, and maximum number of background points of 10,000 were taken into consideration. The final settings for the model were with: maximum iterations of 5000, convergence threshold of 0.0001, maximum number of background points of 10,000, format of the model output as Cloglog, random test percentage of 25, regularization multiplier of 0.5, and feature classes as Quadratic, Hinge, and Product features (QHP).

2.1.4. Geo-spatial mapping of RFS distribution from Maxent output to ArcGIS 10.8

After the training and evaluation, the model was utilized to anticipate the potential distribution of RFS throughout the Indian rice eco-systems. The anticipated RFS risk values from raster output were plotted in ArcMap (ArcGIS 10.8) utilizing spatial analyst tools. The maximum training sensitivity plus specificity Cloglog threshold' was then used to divide the habitat suitability levels into five different categories. These categories were designated as high habitat suitability area (0.80–1), optimum habitat suitability (0.60–0.80), medium habitat suitability (0.40–0.60), poor habitat suitability (0.20–0.40), and unsuitable habitat (0.0–0.20) [40].

2.2. Temperature response on pathogen growth and development leading infection-under controlled and semi controlled conditions

2.2.1. Mycelial growth and conidial production

False smut infected spikelet's developing balls were collected from the experimental field (NRRI Cuttack, India) and the pathogen was isolated in Potato Sucrose Agar (PSA) medium. After establishing a single spore culture, the identity of the pathogen was confirmed based on spore morphology and the amplification of specific bands (631 bp) using the following primers: Forward primer 5' – TCCGTAGGTGAACCTGCGG – 3′ and Reverse primer 5' – TCCTCCGCTTATTGATATGC – 3' [18]. Nucleic acid sequencing was performed and the data was submitted to the NCBI portal as a specimen to the repository. The pathogen was inoculated in Petri plates having potato sucrose agar and exposed to different levels of temperature viz., 15°, 18°, 21°, 24°,26°, 28°, 30°, 32° and 37 °C. Two BODs were used keeping one at fixed temperature (28 °C) and another for exposing in changing temperatures. Ten days after incubation, radial growth (mm) was recorded. Growth was expressed in proportion to fixed temperature and then normalized as (mean-min)/(max-min).

2.2.2. Sclerotial germination

Hard and matured sclerotia were harvested from the false smut congenial location (UBKV- Pundibari WB, India). Sclerotia were treated for 3 min with 1 % sodium hypochlorite followed by 1 min in 70 % ethanol. After a thorough rinsing in sterile distilled water and overnight drying, sclerotia were incubated at 18°, 23°, 25°, 28°, 32°, and 37 °C keeping in Petri plates with moistened filter paper. Number of days needed for germination in 50 % of the sclerotia at each temperature was noted and expressed as incubation period 50 (IP_{50}). Reciprocals of IP_{50} was used as the growth rate in sclerotial germination. For comparison of temperature effect on proportion of germination z-test was performed.

2.3. Artificial inoculation at booting stage for symptom development

2.3.1. Glass house

A susceptible and short duration variety Co 51 was transplanted in pot (Diameter 12inch) filled with puddled soil. Twenty pots having ten seedlings in each pot were kept in the glasshouse during rice season. At booting stage, the plants were inoculated using a standard protocol [41]. The inoculated plants were kept in semi-controlled conditions with a temperature of 28 °C and relative humidity above 85 %. Four intermittent showers per day were given to facilitate symptom development. Daily observations were made on the panicles, and the number of infected grains per panicle were counted. The incubation period 50 (IP_{50}) was calculated, and the reciprocals of IP_{50} were used as a growth rate in symptoms development. To compare the proportions of infected grains per panicle, a z-test was performed.

2.3.2. Field

The same susceptible variety was grown in the field environment having provision of shade net and sprinkler system. During experimental period day temperature was maintained between 21 °C to 29 °C against the ambient 24 °C to 33 °C. Similarly, the average humidity of 80–95 % was maintained as against ambient 70–85 % to facilitate conducive weather for disease development. Sprinkler irrigation four time a day at 2–2.5 h interval was used to keep the temperature and RH inside the shade net. A pocket weather kit (kestrel) was used to monitor temperature and RH conditions. The plants were inoculated at the booting stage during kharif season and repeated for two season (2022–23 and 2023–24). Daily counts of the number of infected grains/panicles were taken, and the incubation period 50 (IP_{50}) was determined. The growth rate in symptoms development was calculated using the reciprocals of IP_{50}.

2.3.3. Influence of shower in symptom development

The variety Co 51 was grown in 20 pots having ten seedlings in each pot and at booting stage inoculation was given following the same method mentioned. Inoculated plants were kept in semi-controlled conditions and two levels of intermittent shower viz., four and six per day were given to facilitate symptoms development. The panicles were closely observed after inoculation and the number of infected grains per panicle was counted daily. The incubation period of 50 (IP_{50}) was calculated, using the reciprocals of IP_{50} as the growth rate in symptoms development. To compare the proportions of infected grains per panicle for number of showers, a z-test was performed.

2.4. Data analysis

To assess the effect of temperature the non-linear beta function (eq. (1)) [42–44] was used for approximation of threshold temperatures in terms of mycelia growth, sclerotia germination and symptom development.

$$f(T) = \left[\frac{T_{upper} - T}{T_{upper} - T_{opt}}\right] * \left[\frac{T - T_{lower}}{T_{opt} - T_{lower}}\right]^{\wedge} \left(\frac{T_{opt} - T_{lower}}{T_{upper} - T_{opt}}\right) \text{ eq.....} \quad (1)$$

If $T_{lower} \leq T \leq T_{upper}$ and 0 otherwise eq. 1where, T_{upper}, T_{lower} and T_{opt}, is the upper, lower and optimum threshold temperatures, respectively, for radial growth and T is the exposure temperature (°C). By fitting temperature response model on normalized fungal growth, parameters T_{upper}, T_{lower} and T_{opt}, was approximated following non-linear iterative Levenberg -Marquardt (L-M) procedure [45, 46]. Goodness-of-fit was evaluated by the magnitude of asymptotic confidence intervals on parameter estimates and by inspection of residual errors. The reciprocals of IP_{50} for sclerotia germination and IP_{50} for symptom development as well as radial growth observations were compared by fitting with the temperature response function.

2.5. Assessment of favourable index and false smut incidence on known locations

Several locations across all the agroclimatic zones like Pundibari (WB), Cuttack NRRI (Odissa), Anakapalli (Andhra Pradesh), IARI (Delhi), Gangavathi (Karnataka), IIRR (Hyderabad), Thiruvarur (TN), Palakkad (Kerala) having variation in false smut incidence (number of infected spikelet/panicle) and sclerotia (number/panicle) were selected. For estimation of favourable days for false smut infection daily maximum-minimum temperature and precipitation data were collected from the local weather observatory. Based on temperature response estimated as daily $f(T) > 20$ on pathogen growth or infection and daily precipitation (>5 mm) was considered as favourable. Considering crop growth period associated with booting stage mean favourable days for the period 1982–2022 were counted during June-July-Aug-Sep-Oct. Number of mean favourable days and false smut incidence (number of infected grains/panicle estimated for the year 2022–2024) was compared for the known locations.

2.6. False smut infection – a monocyclic process

Seedlings transplanted in pots (diameter 12") were raised to booting stage (65 days after transplanting) and ten tillers were inoculated following the standard method. After inoculation daily 4–6 showers were provided keeping the pots in favourable temperature regime (28° ± 2 °C). Six panicles randomly selected at 10 days after inoculation were observed for spikelet infection. Number of infected grains or spikelet/panicle was counted at 2 days' interval. To assess the nature of infection, number of infected grain/panicles over time was fitted in an infection dynamics model (eq. (2)) for estimation of parameters-primary and secondary rate of infection keeping a fixed level of inoculum [47].

$$\frac{dN_i}{dt} = r_p{*}p{*}\left(1 - \frac{N_i}{N + N_i}\right) + r_s{*}N_i{*}\left(1 - \frac{N_i}{N + N_i}\right) \text{ eq.....} \quad (2)$$

where, N = number of spikelet/panicles inoculated at time t; N_i = number of spikelet/panicles infected at time t; r_p and r_s are the primary and secondary rate of infection; and p = level of inoculum. Model parameters r_p and r_s were approximated based on the minimum residual sum of squares.

3. Results

3.1. RFS distribution in rice agro-ecosystems

Presence of false smut incidence was noted in all the rice agroecosystems in India. Agroclimatic zone-wise, eight locations selected for false smut analysis indicated prevalence of relatively higher RFS incidence (infected spikelet/panicle) and sclerotia (number/panicle) in eastern and north eastern zones associated with higher rainfall pattern. Highest false smut incidence about 6.8 spikelet's/panicle was observed in Pundibari (26.41°E, 89.38°N) having annual rainfall about (3000–4000 mm). Relatively low incidence 3.8–4.1 spikelet/panicle was observed in Cuttack (20.40°E, 85.82°N) and Anakapalli (17.68°E, 82.99°N) with rainfall (2000–3000 mm). False smut incidence 2.0–4.1 spikelet/panicle was in Gangavathi (15.40°E, 76.52°N), Hyderabad (17.37°E, 78.49°N), Thiruvarur (10.76°E, 79.62°N) and Palakkad (10.78°E, 76.63°N) with rainfall 1000–3000 mm. Hilly areas and western zone were noted to be very low or free of incidence. It was evident that RFS incidence showed a pattern associated with rainfall during the rice growing period.

3.2. Identification of bioclimatic variables for RFS distribution through Maxent

The most important bioclimatic variables for RFS occurrence were precipitation of wettest month (Bio_13) and mean temperature of warmest quarter (Bio_10) followed by precipitation seasonality (Bio_15) as compared to other variables considered (Fig. 2). The three variables individually contributed about 47.81 %, 26.63 % and 12.43 % respectively and collectively 86.87 %. Therefore, three variables qualified to be the strongest predictor of RFS distribution.

Stability and variability of the variables represented by AUC (Jackknife method) indicated precipitation of wettest month (Bio_13) and mean temperature of warmest quarter (Bio_10) had more predictive power compare to other variables (Fig. 3A). The regularized test gain also supported these meaningful variables (Fig. 3B). The other bioclimatic variables, viz. precipitation of seasonality (Bio_15) and temperature seasonality (Bio_4) were noted to contribute in RFS distribution.

Higher mean test AUC value of 0.98 indicated a high accuracy of Maxent model to predict the potential distribution of false smut (Fig. 4). The probability of RFS presence based on individual response curves for major bioclimatic factors indicated how false smut occurrence was impacted by the three variables (Fig. 5). Response curve for precipitation of the wettest month (Bio_13) noted to be monotonically increasing from 100 mm and no impact beyond 700 mm (Fig. 5A). Typically, unimodal response of mean temperature of the warmest quarter (Bio_10) were between 25 and 35 °C indicated the critical influence of temperature on pathogen growth (Fig. 5 B). Precipitation variation indicated by the factor seasonality of precipitation (Bio_15) had increasing impact on disease occurrence only in the range between 70 and 170 (Fig. 5C).

Based on maximum entropy principle the most probable distribution of RFS appeared to be influenced by the three major

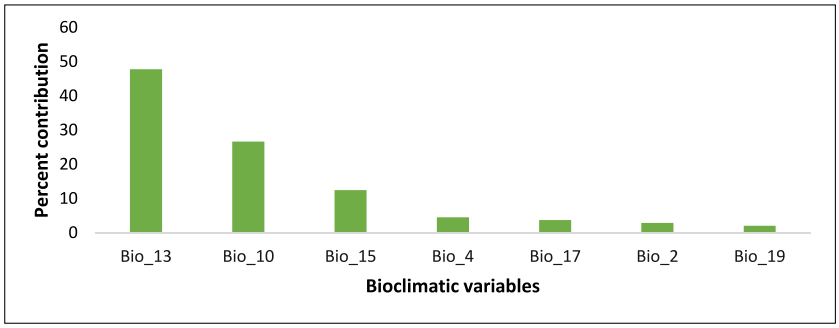

Fig. 2. Relative contribution of different bioclimatic variables to Maxent model for RFS.

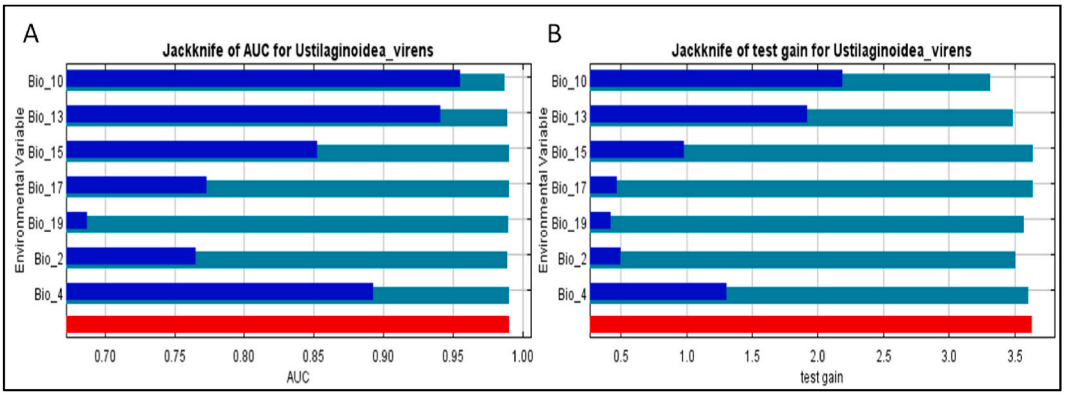

Fig. 3. Relative importance of different predictor variables based on jackknife test in Maxent. A) AUC (area under the receiver operating characteristic -ROC curve) and B) regularized test gain; with all variables (red), with only variables (blue), without variables (cyan).

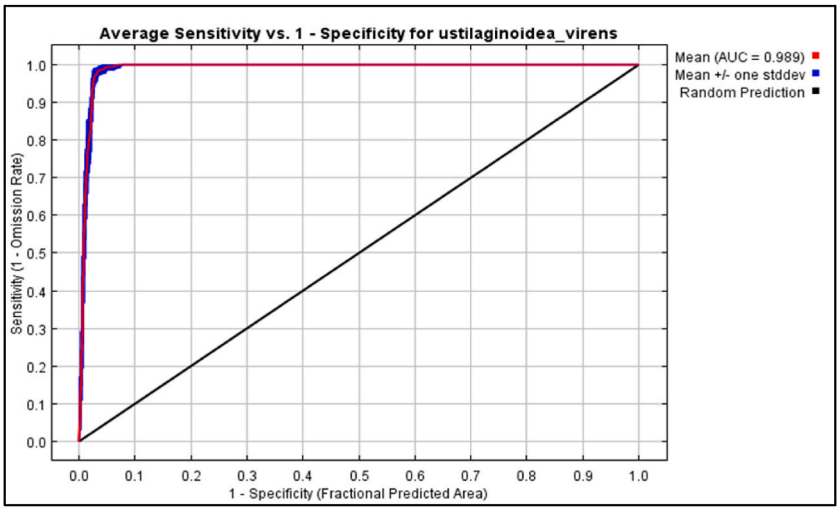

Fig. 4. Model performance in terms of sensitivity and specificity.

bioclimatic variables. RFS suitability based on these variables indicated the disease is more or less distributed across the major rice growing areas except hilly and drier parts having low to scanty rainfall (Fig. 6A). Maximum habitat suitability was noted in major parts of West Bengal, Odisha, Coastal Andhra Pradesh, Telangana, Eastern Madhya Pradesh, Chhattisgarh fringes in coastal Tamil Nadu, Kerala, and Karnataka, eastern and north western part of Gujarat. Major part of Gangetic plains (middle and Western), Madhya Pradesh, Chhattisgarh, and Jharkhand were in moderate level of suitability. Both precipitation and temperature had greater impact on disease occurrence and distribution pattern. It was noted that false smut suitability had a correspondence with the precipitation distribution pattern of the wettest month (Fig. 6 B). Therefore, similarity between false smut distribution and rainfall distribution pattern reflected the possibility of making false smut prediction based on rainfall during the wettest month as temperature profile throughout the country remains more or less favourable for the disease.

It was evident that the effect of precipitation and temperature had characteristically distinct role in RFS distribution. Both amount of seasonal precipitation as well as its variability had importance in disease occurrence indicating it's role as a limiting factor.

3.3. Temperature response on pathogen growth and development leading to infection

The pathogen was identified as *Ustilaginoidea virens* through DNA sequencing (GenBank accession number: PP737593). Mycelial growth in artificial media was noted in the temperature range 15–37 °C with maximum growth at about 28 °C. Parameter estimates (T_{lower}, T_{opt} and T_{upper}) by fitting temperature response function [*f (T)*] were approximated to be 15°, 28°, and 37 °C. Confidence interval (95 %) for the parameter estimates for T_{lower} as 15 °C (2.9–27.1 °C), T_{opt} 28° (26.3–29.7 °C) and T_{upper} 37° (36.1–37.9 °C) were of good fit (R^2 = 0.9653 and adjusted-R^2 = 0.9504). Based on parameter estimates temperature response function was developed (Fig. 7).

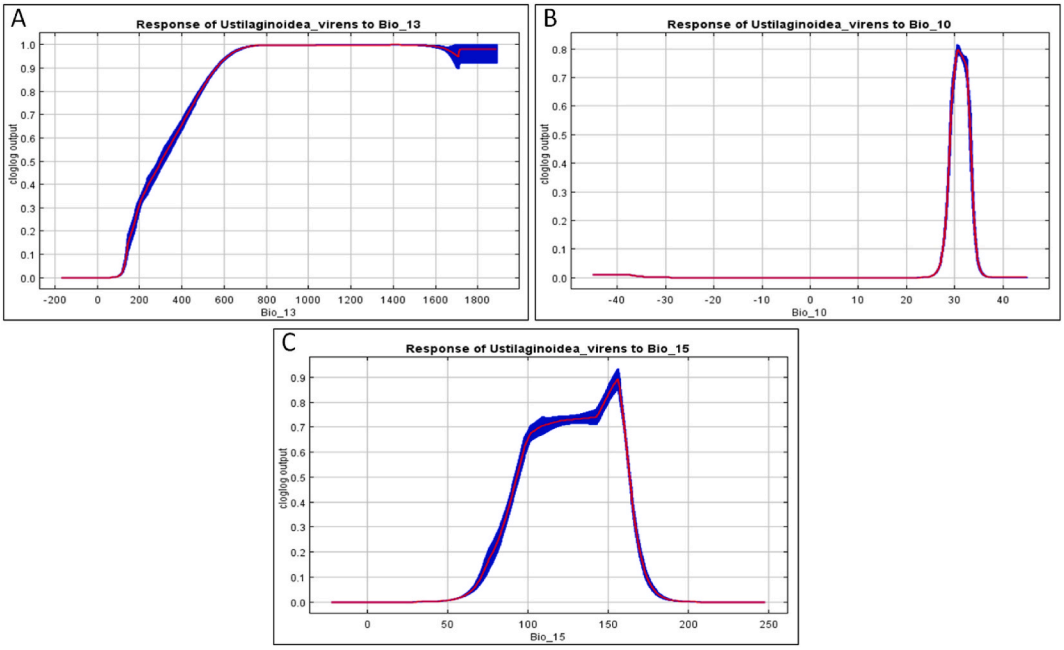

Fig. 5. Response curves for bioclimatic variables affecting RFS distribution, A: Precipitation of the wettest month (Bio_13), B: Mean temperature of warmest quarter (Bio_10) and C: Precipitation seasonality (Bio_15).

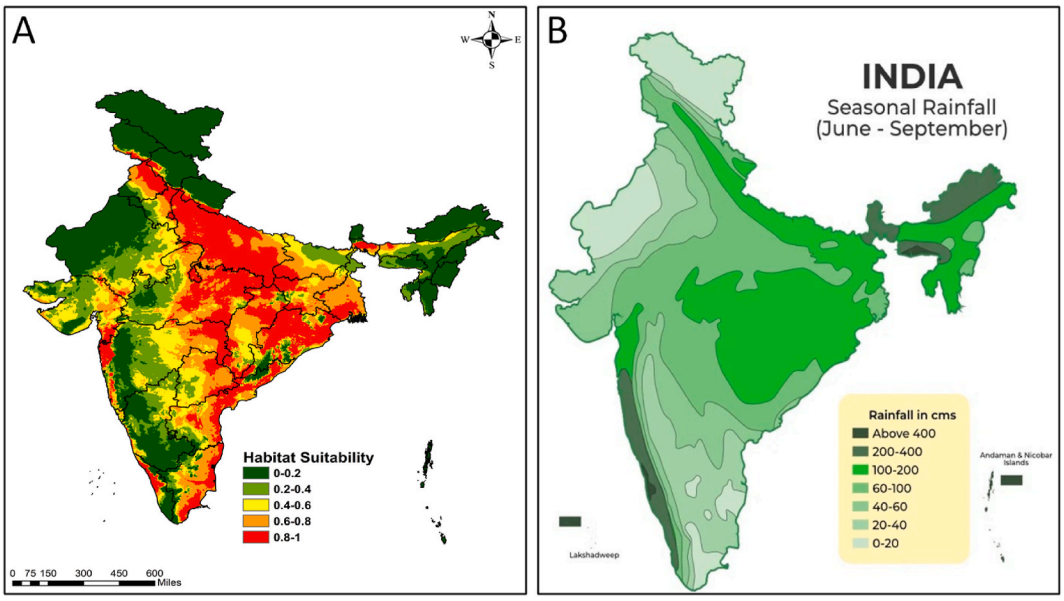

Fig. 6. RFS distribution based on the Maxent model prediction (A) and annual rainfall pattern (B) (image courtesy: https://iasnext.com/rainfall-distribution-indian-geography-upsc).

$$f(T) = [(37 - T)/9]^{*}[(T - 15)/13]^{\hat{1}.444}$$

Incubation period (IP_{50}) for sclerotia germination at 28 °C observed and expressed as growth rate (reciprocal of IP_{50}) noted to fit well with the growth curve derived out of mycelial growth (Fig. 7). From false smut infection experiment, median infection time (50 %) or IP_{50} was noted about 8.9 days at 28 °C in the susceptible genotype Co51. The reciprocal of infection time or IP_{50} (indicator of growth rate) also fitted well with the temperature response function based on radial growth observation (Fig. 7).

It was evident that temperature response function approximated *in vitro* had a good correspondence between pathogen development and infection process observed under semi-controlled conditions. Otherwise, growth rate in terms of mycelial development,

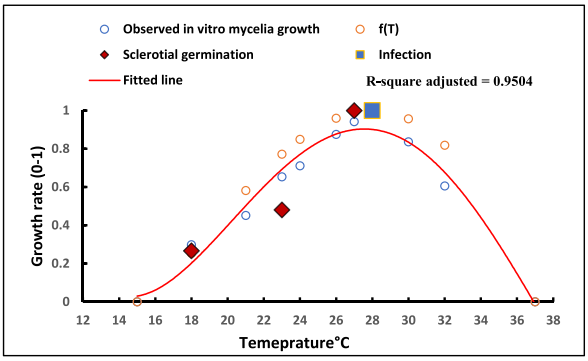

Fig. 7. Graph showing pathogen's cardinal temperatures approximation (radial growth) from non-linear beta model and comparison with sclerotia germination (3 temperature) and infection (optimum temperature).

sclerotial germination as well as infection development were in consonant with respect to temperature. Therefore, temperature response function as a representative growth curve for false smut infection indicated it is a critical factor for disease development.

3.4. *Influence of shower on symptoms development*

Rainfall in the form of shower had significant influence in spikelet infection and smut ball development under semi-controlled conditions. Symptoms development was almost absent when number of showers less than 4. However, the number of shower 4–6 was noted to ensure faster symptoms development with profound effect on both spikelet infection as well as smut ball development.

3.5. *Favourable days for false smut occurrence*

Favourable days in terms of daily temperature response ($f(T) > 20$ and daily precipitation >5 mm) during the wettest month (June-July-Aug-Sep-Oct) and false smut incidence was compared for the known locations (Fig. 8A). Number of favourable days and false smut incidence was noted to be positively correlated ($r = 0.7971$) for the observed locations (Fig. 8 B). Number of favourable days in Pundibari (WB) was estimated 46 where maximum false smut incidence was 6.9 infected spikelet/panicle. Prevalence of relatively lower number of favourable days in NRRI, Cuttack (Odisha), Anakapalli (Andhra Pradesh) and IIRR, Rajendranagar (Hyderabad), Gangavati (Karnataka), Thiruvarur (TN) and Palakkad (Kerala) was corresponded with low disease incidence. Lowest number of favourable days in IARI, Delhi was related with lowest disease incidence. Consecutive occurrence of favourable days was also noted to be associated with consecutively occurring precipitation during the wettest month. It was evident that number of favourable days assumed to be proportional to the false smut incidence. Therefore, false smut infection can be predicted based on the criteria of favourable days where occurrence of rainfall plays an important role.

3.6. *Nature of false smut infection*

Population dynamics model parameters namely primary (r_p) and secondary (r_s) rate of infection estimated fitting population dynamics model ($R^2 = 0.9724$; MSE = 0.0521) were 0.542 and 0.0002–0.002 spikelet/panicle per 3-days, respectively (Fig. 9). The magnitude of primary infection rate at fixed level of inoculum ($p = 2.0$) in comparison to secondary infection rate indicated dominance of primary inoculum in the infection process. Predominance of primary infection in the dynamics of false smut infection indicated the

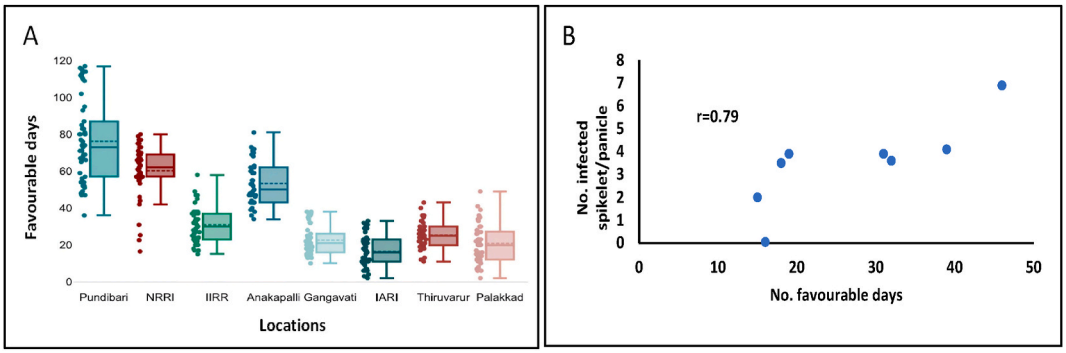

Fig. 8. Distribution of favourable days in eight locations with different false smut incidence (A) and correlation (B).

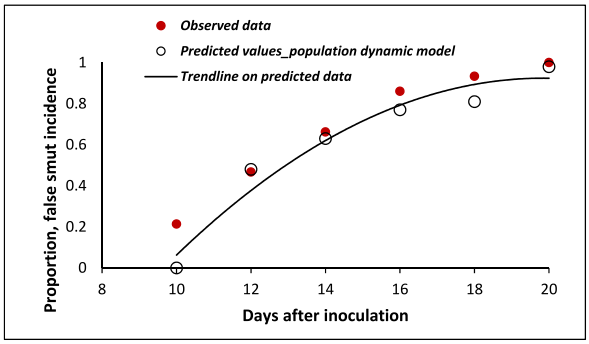

Fig. 9. Data plot from population dynamic model fitting (observed false smut incidence and predicted).

dominant role of primary inoculum that happens after the inoculum contact with the susceptible stage. Therefore, false smut infection is a monocyclic epidemic process where primary inoculum plays important role in disease dynamics.

Based on information generated a disease cycle scheme has been put forward (Fig. 10).

4. Discussion

False smut infection risk in rice is assessed in terms of environmental suitability to shed light on epidemic process involved in disease development hitherto unknown. Major influential factors or bioclimatic variables consistent with disease distribution have been identified. Maximum Entropy principle is used to identify environmental variables associated with the host-pathogen interaction and contributing to RFS distribution. RFS distribution pattern is explained and verified through controlled and semi-controlled observations. Through reverse modeling approach, the most important bioclimatic variables, mainly monthly temperature and rainfall in the wettest month are explained how these factors are associated with disease development. Through analytical insight, infection process in the field has been explained and a simple prediction rule is derived and implicated for evaluation of management options.

An unusual host-pathogen interaction involved in false smut epidemiology is brought to light and the role of precipitation and temperature during the wettest month behind false smut infection has been confirmed.

Both amount of seasonal precipitation as well as its variability is important in disease occurrence indicating rainfall as a limiting factor for the disease. False smut response generated through the Maxent model is shown rainfall has increasing effect on the disease but up to about 700 mm but afterward no effect. In the current study, involvement of rain during booting stage is realized in symptoms development. Importance of precipitation in wettest month (June-July-Aug-Sep) connects three important steps in the infection process namely ascospore release (honey-dewed ostioles), rain-splash spread of ascospores to the tillers and water flowing of spores into the sheath. Assumptions that ascospores enter the booting sheath along with water flowing on the top leaves is consistent with the observation that the disease is much more severe when rice heading stage coincides with rainy and high humidity period [1]. Artificial rain or showers provided under semi-controlled conditions is noted to develop higher disease incidence. RFS is a phenomenon mostly happen in kharif rice (June-Aug-Sep-Oct-Nov) and does not occur in rabi rice period (December-Jan-Feb-Mar) when rainfall is rare. In Indian rice ecosystems, rainfall during booting stage is common and thus the disease is more or less prevalent in all rice growing areas. Role of primary infection from ascospore (overwinter and germination next year) during booting stage made by the previous studies also indirectly support the importance of rainfall in the RFS development [15,16,48–54]. The hypothesis that water flowing from the top (tiller) brings the inoculum into the sheath is noted to be consistent with the observation that the disease is much more severe when rice heading stage coincides with rainy days [1].

Temperature response is reflected to be a critical factor in disease development. Role of temperature is well known for growth and development of the false smut [1,9,10]. Temperature response for the pathogen growth and development (mycelial growth, sclerotial germination and infection) corresponds the climatic features contributed to the disease distribution. Ground truth observation on RFS incidence and number of sclerotia/panicle were comparatively higher in locations having median (75 %) temperature close to optimum threshold (28 °C). Temperature thresholds for mycelial growth, sporulation, sclerotia germination and infection are identical verified through controlled and semi-controlled experiments. Temperature has important role to play especially in inoculum multiplication as well as maintenance of inoculum to be available for infection during susceptible stage. It is reported that low temperature is important to induce sclerotial differentiation and formation. In years with relatively low temperatures in autumn, sclerotia numbers would tend to increase and vice versa [10]. Sclerotia are often formed in later autumn, with relatively lower temperatures and when temperature differences between day and night are large [55,56].

Both precipitation and temperature had greater impact on disease occurrence and distribution pattern. In the current study, RFS incidence (number of infected grains/panicle) is shown to be proportional to the number of favourable days composed of daily temperature effect (response curve) and rainfall. However, similarity between false smut distribution and rainfall distribution pattern reflected the possibility of making false smut prediction based on only rainfall during the wettest month as temperature effect appeared to be redundant.

Epiphytic colonization of *Ustilaginoidea virens* on biotic and abiotic surfaces implies the widespread presence of ascospores to be

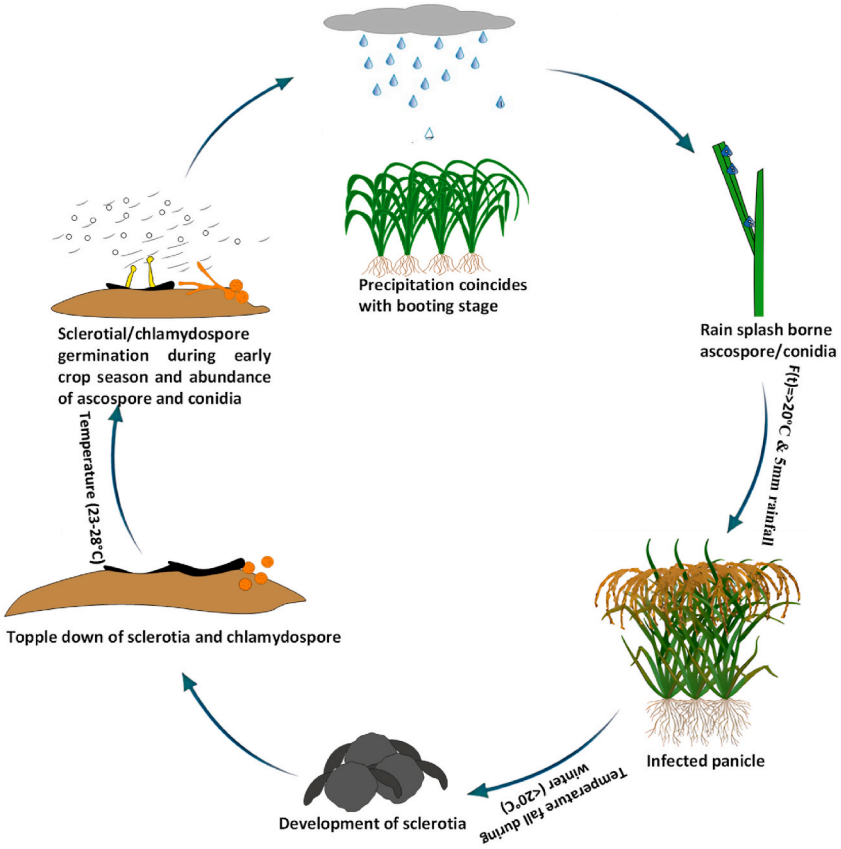

Fig. 10. Graphical representation for rice false smut (RFS) infection.

potential source of primary inoculum for infection [10]. However, release of ascospores from the secreted droplets on the ostioles (stromata) requires some kind of insect vectors or raindrops [57]. It appears role of rainfall gets importance in three connections. Firstly, release of ascospores from honey droplets requires water. Secondly, the released ascospores in water requires rain-splash to be available on the host surface. Thirdly, spore cladded rain droplet is playing role for inoculum delivery inside the gap between leaf sheath and culm. Saturation effect of precipitation above 700 mm as shown in response curves indicates higher magnitude of rainfall works as limiting factor on the disease development. Reasonably high rainfall has the possibility of wasting ascosporic inoculum moving into the water and reduces number of spores in the splash. Moreover, ascospores in moving water incapacitate the contact with the host. An important hypothesis here is that providing irrigation water or standing water level during booting stage may reduce ascosporic concentration available for infection. Moreover, monocyclic progress of spikelet infection is another evidence how primary inoculum (ascospores) plays important role in disease progress.

False smut risk prediction provides an important foresight to link crop health management and possible adaptation strategies in disease control. Temperature and precipitation determine the false smut risk pattern particularly during June to September in most of the rice agro-ecosystems when favourable days (temperature and rainfall) are common in South Asian countries. Fungicidal spray (propiconazole or similar type) is reported to be effective but timing of application is important. The best time of application is the booting stage [58–60]. In Japan spraying simeconazole three weeks before and in China six days before heading gave the better results [61,62]. So, for tactical management, prediction of favourable days is useful during susceptible stage. Exploring management practices targeting inoculum level reduction through irrigation or interrupting inoculum with host contact and fungicidal sprays during the booting stage is to be explored for effective control of the disease.

5. Conclusions

Epidemiologically meaningful bioclimatic variables contributing to false smut disease occurrence and distribution are identified and implicated for evaluation of management strategies. Based on maximum entropy (Maxent) principle, precipitation in the wettest month and mean temperature in the warmest quarter along with precipitation seasonality are identified as the key predictors for RFS distribution, contributing 47.81 %, 26.63 %, and 12.43 % respectively. These predictors are crucial for inoculum development, disease initiation, and progression. Rainfall in the wettest months is critical for driving epidemiological processes like, ascospore release, spread and infection. The monocyclic infection process, where the infection is primarily driven by rainfall events, underscores the

importance of precipitation in the disease cycle. Temperature plays a pivotal role in pathogen development including mycelial growth, sclerotial germination, and infection processes is characterized. Optimal temperatures (around 28 °C) are connected to pathogen growth, infection as well as sclerotia germination during the wettest period, while lower temperatures (<20 °C) in winter months associated with sclerotia formation. Rainfall during the booting stage is the most important determining factor for RFS development, influencing the delivery of inoculum to the developing panicle. In summary, the study highlights the intricate interplay of temperature and rainfall in RFS development and provides a comprehensive understanding of environmental suitability for the disease. This knowledge is instrumental in formulating effective disease management and control strategies like timing of fungicidal applications and/or irrigation practices to reduce inoculum levels, ensuring better crop health and yield stability in rice agroecosystems. The RFS distribution predicted as an inventory for identification of hotspots and likely to facilitate global projection of the disease in terms of climate change.

CRediT authorship contribution statement

Kumar Sathiyaseelan: Methodology, Investigation. **Bappa Das:** Software. **Duraisamy Ladhalakshmi:** Methodology. **Emmadi Venu:** Data curation. **Vimalkumar C:** Validation. **Bishnu Maya Bashyal:** Formal analysis. **Tusar Kanti Bag:** Visualization. **Parimal Sinha:** Writing – original draft, Conceptualization.

Ethics statement

This research fully complies with all applicable ethical guidelines, rules, and regulations. No animal or human subjects were involved in this study. The research did not involve the use of biological materials, human participants, or live animals.

Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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List of abbreviations

RFS	False Smut in Rice
ITS	Internal Transcribed Spacer
FCs	Feature Classes
RMs	Regularization Multipliers
AUC-ROC	Area Under the Receiver Operating Characteristic Curve
AUC	Area Under the Curve
AICc	Akakie's Information Criterion
TSS	True Skill-Statistic
QHP	Quadratic, Hinge, Product
BOD	Biological Oxygen Demand
IP_{50}	Incubation Period 50
MSE	Mean Squared Error

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