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Elucidating the Etiology and Temporal Progress of Rust on Physic Nut Genotypes and Their Relationship with Environmental Conditions in Ecuador

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Abstract: Physic nut (*Jatropha curcas* L.) has emerged as a promising fruit crop in Ecuador, but the recent identification of rust poses a potential threat to its productive development. This study focused on elucidating the morphological aspects of the basidiomycete and assessing rust intensity across different canopy levels of physic nut hybrids and genotypes under field and semi-controlled conditions in Manabí, Ecuador. For the first time, this study confirms that *Phakopsora arthuriana* should be responsible for rust on physic nut in Ecuador based on the characteristics of the fungal structures. Rust incidence was 100% across all canopy layers, with the lower and middle canopies exhibiting higher severity and lesion numbers than the upper canopy. Using the Weibull nonlinear distribution model, we epidemiologically modeled disease progression, revealing that hybrid JAT 001100 displayed the highest temporal progress, recording 15% severity and an area under the disease progression curve of 3228.9 units. Promising genotypes CP-041 and CP-052 demonstrated lower rust intensity. Environmental parameters, including dew point, temperature, precipitation, and relative humidity, were correlated with rust severity and lesion numbers. In greenhouse assays, hybrid JAT 001165 showed higher severity, whereas JAT 001103 and JAT 001164 had more lesions than other genotypes. In contrast, promising genotypes CP-041 and CP-052 consistently exhibited lower rust intensity in both field and greenhouse environments. This study demonstrated that *P. arthuriana* could be epidemiologically modeled with the Weibull model, providing crucial insights into the dynamic interplay between rust infection and physic nut hybrids and genotypes under diverse conditions in the Manabí region of Ecuador.

Keywords: epidemiological parameters; *Jatropha curcas* L.; nonlinear Weibull distribution model; *Phakopsora arthuriana*; rust intensity

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1. Introduction

Physic nut (*Jatropha curcas* L.), a tropical plant native to Mexico and Central America, is notable for its seeds, which contain approximately 36% oil [1]. The agricultural potential of *J. curcas* in tropical regions is affected by several diseases [2,3], including rust caused by *Phakopsora* species. This basidiomycete was first identified in Puerto Rico in 1915 as *Uredo jatrophicola* Arthur [4] and was definitively reclassified as *P. arthuriana*, with reports in the United States of America [5], Brazil, the West Indies [6], Mexico [7], and Thailand [8]. Physic nut leaf rust causes necrotic lesions with a chlorotic halo on the upper surface and a reddish coloration with eruptions (uredia) that form uredospores on the lower epidermis. These lesions lead to increased colonization and reproduction of the pathogen, which causes severe defoliation and drastically reduces the photosynthetically active rate of the plants [9,10].

In Ecuador, the National Institute of Agricultural Research (INIAP) began researching physic nut in 2007, aiming to preserve the genetic diversity and select genotypes with high productive and agroindustrial potential for the Ecuadorian coast. In late 2011, the Ecuadorian government launched an initiative to generate electricity for Floreana Island, one of the Galapagos Islands [11]. In 2021, characteristic rust symptoms caused by *Phakopsora* sp. were observed in physic nut hybrids and promising genotypes at the Technical University of Manabí (UTM). To the best of our knowledge, this disease has been minimally studied in Ecuador; thus, its etiology is poorly understood and its temporal progression within the crop remains unexplored.

Rust intensity can escalate under both intensive and extensive monoculture practices [9,12,13] and is influenced significantly by environmental factors [14–16]. The incidence of the disease ranges from 30 to 70% [7,9]. To date, no alternative hosts for physic nut rust have been identified, and a comprehensive description of its life cycle, which includes five stages, remains incomplete, with only the uredinial and telial stages documented in *J. curcas* [9]. Although rust infections can diminish the leaf area index, the yield, and some yield components in certain short-cycle crops [13,17], the impact of *P. arthuriana* on physic nut is transient and heavily dependent on its epidemiology and the prevailing environmental conditions.

The modeling of rust's temporal progress requires distinct approaches for perennial crops compared with annuals [18]. Given the perennial nature of physic nut, the pathogen finds ample opportunity for survival, spread, infection, colonization, and reproduction across all seasons. In contrast, the progression of rust in annual plants is typically analyzed using Exponential, Logistic, and Gompertz nonlinear models [17,19,20]. These models, however, are less suitable for perennials due to the disease's variable or non-uniform behavior over time. The Weibull model, known for its flexibility, is more adept at capturing the temporal dynamics of diseases in perennial plants [21]. This model's effectiveness was demonstrated by García-López et al. [22], who employed it to examine the temporal patterns of incidence and severity of malformation disease (*Fusarium* spp.) in mango (*Mangifera indica*) cultivars. Its adaptability allows for a more accurate representation of diverse disease progression curves, unlike more rigid models [23].

The Weibull model is characterized by the following three parameters: the location parameter ('a'), indicating the time of disease onset; the scale parameter ('b'), which is inversely related to the rate of disease increase; and the shape parameter ('c'), which determines the curve's asymmetry and the inflection point's position [24,25]. Its widespread use in life testing, even with small sample sizes, stems from the dramatic variations in the density function based on the 'c' value [26]. The simplicity, flexibility, and precision of the Weibull distribution facilitate fitting diverse disease progression curves, making it an invaluable tool for modeling plant disease epidemics.

Based on the described antecedents, our research questions were as follows: (1) What is the fungal pathogen that causes rust on *J. curcas*? (2) How do physic nut genotypes respond to rust? (3) What is the temporal progress of the disease on *J. curcas* under field conditions? and (4) What is the correlation of the disease with some of the environmental conditions? Thus, the objective of this work was to characterize morphologically and to evaluate the intensity and etiology of the physic nut rust present in Ecuador under both semi-controlled and field conditions and analyze its temporal progress in the lower, middle, and upper canopy of adult plants of six genotypes of physic nut. In addition, we studied the correlation between environmental conditions and the disease under field conditions.

2. Materials and Methods

Research under semi-controlled (net house) and field conditions was conducted at the experimental site "La Teodomira" of the Faculty of Agricultural Engineering (FIAG) of UTM, located in the municipality of Santa Ana, province of Manabí, Ecuador (01°09′51″ S; 80°23′24″ W), at an altitude of 60 masl. This area is classified as having a tropical savanna climate (Aw), with clay loam soil and flat topography with slight undulations. The average dew point is 20.6 °C, with temperatures averaging between 22.1 °C and 26.7 °C (Supplementary Figure S1). Furthermore, the area receives on average 81.8 daylight hours, with a relative humidity of 83.0% and an accumulated precipitation of 485.3 mm.

2.1. Morphological Characterization of the Causal Agent of Rust

Symptomatic leaves from established plants under field conditions and artificially inoculated seedlings were used for the morphological characterization of the rust's causal agent. The rust populations, designated as FiagR1 (field conditions) and FiagR2 (semi-controlled conditions), collected in 2022 were analyzed both macroscopically and microscopically. Uredia on the leaves were scraped with a needle to primarily obtain uredospores, while leaf tissues were histologically sectioned using a classic edge blade to observe all potential pathogen structures. Samples were prepared on wet mounts with lactophenol and examined using a light optical microscope (CX22LED, Olympus, China). The dimensions of each structure were measured across 30 uredia and telia and 100 uredospores and teliospores using micrographs captured with a 10 Mpx camera (Better Scientific, Germany) attached to the microscope and analyzed with ImageJ version 1.52v software.

2.2. Artificial Inoculation of Seedlings and Evaluation of Rust under Semi-Controlled Conditions

Seedling management and plant inoculation

Ten physic nut seeds from each of the six genotypes, previously established in the field, were planted in a sandy loam substrate. This substrate had been sterilized before use and the seeds were placed in 3 L volume polyethylene bags. These seedlings were then kept in a greenhouse, where the average temperature was maintained at 24.1 ± 2.5 °C and the relative humidity was kept above 90%. The seedlings were watered thrice weekly for 30 days. The inoculum, derived from a single fungal population, was prepared using symptomatic leaves that produced a large number of uredospores. These leaves were collected from adult plants cultivated at the Faculty of Agronomic Engineering. In the laboratory, the leaves were chopped into approximately 1 cm pieces and then blended into a homogeneous mixture with a sterile distilled water solution containing 0.1% Tween 20. The uredospore suspension was then extracted by filtering the mixture twice through a double layer of cheesecloth. The concentration of the suspension was adjusted to 1×10^6 uredospores mL^{-1} using a Neubauer counting chamber.

The seedlings, with their leaves fully expanded (between 20 and 23 days after sowing), from each physic nut genotype (hybrids JAT 001100, JAT 001103, JAT 001164, and JAT 001165 and the two promising genotypes CP-041 and CP-052) were inoculated using a modified version of the spray method described by [27]. Five seedlings of each *Jatropha* genotype were inoculated with the uredospore suspension using an airbrush attached to a compressor (1/5 HP, 110V, Truper, Mexico), ensuring all leaves were sprayed to the runoff point. Seedlings that were only sprayed with sterile distilled water served as controls and were kept in the same greenhouse but in a separate growth chamber from the inoculated seedlings to prevent the spread of and contamination by uredospores.

Rust assessment

At 20 days after inoculation, disease intensity was assessed. Disease incidence (%) was calculated by counting the number of leaves with or without lesions (pustules). Rust severity was visually estimated by determining the percentage (%) of leaf area covered by rust pustules. Additionally, the number of lesions (pustules) per cm^2 was quantified. Each leaf was longitudinally divided using the central midrib as a dividing line (left and right side), the area was defined, and, with a cork borer (Ø 10 mm), the presence of lesions on both parts of the leaf was quantified [27] with the assistance of a binocular stereoscopic microscope (model SMZ-168 TLED, Motic, Hong Kong, China).

2.3. Rust Evaluation in Adult Plants Established under Field Conditions

Plant management

Adult physic nut plants of four imported hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165 from JatroSolutions GmbH, Stuttgart, Germany) and two promising genotypes (CP-041 and CP-052) were established at the experimental site "La Teodomira" in September 2020 (Supplementary Table S1). Plants of each genotype were transplanted with 2 m between plants and 4 m between rows, covering a total area of 5376 m^2 (96 m $\times$ 56 m), under a completely randomized block experimental design. This setup was distributed across 24 plots, each consisting of 4 rows of 6 plants (24 plants per plot) and organized into four blocks.

Plants were fertilized with a source of urea (CH_4N_2O) at 16 g per plant, phosphorus pentoxide (P_2O_5) at 5 g per plant, and potassium oxide (K_2O) at 25 g per plant following a soil analysis conducted before transplantation (Supplementary Table S2). A drip irrigation system was employed only during the initial months post-transplantation (September–December 2020); thereafter, no irrigation was provided. Weed control was conducted regularly using a motorized mower.

Rust assessment

Three leaves from four randomly selected physic nut plants were collected from the two central rows of each plot (four plants), representing the lower, middle, and upper canopy of each plant (one leaf per canopy level). The plant tissues were placed in pre-labeled bags and transported to the phytopathology laboratory for rust evaluation. Disease intensity was assessed monthly over a nine-month period (from 29 November 2021 to 26 August 2022). The rust evaluation was not conducted beyond nine months due to the leaf drop and intense defoliation observed across all physic nut genotypes, particularly in the lower and middle canopy, starting on 12 September 2022. All monthly disease assessments consistently focused on the four designated plants. The incidence, severity (percentage), and number of rust lesions per cm^2 on leaves of adult physic nut plants were evaluated using the same methods applied to seedlings established under semi-controlled conditions.

2.4. Statistical Analysis

Disease intensity datasets obtained in physic nut plants over time for each genotype were compiled into the area under the disease progress curve (AUDPC), calculated according to [24]. After verifying the homogeneity of the variance and the normality of the residuals for the datasets obtained under field and semi-controlled conditions using the Bartlett and Shapiro–Wilk tests, respectively, the data were analyzed by Analysis of Variance (ANOVA). Subsequently, means were separated using either the Scott–Knott or the Kruskal–Wallis test ($p \leq 0.05$).

For the estimation of the maximum likelihood parameters of the three-parameter Weibull distribution, we used Function (1):

$$L_{(k,\lambda,\eta)} = \left(\frac{k}{\lambda}\right) * \left(\frac{x-\eta}{\lambda}\right)^{k-1} * e^{(-(x-\eta)/\lambda)^k} \quad (1)$$

where k is the shape parameter (c), λ is the scale parameter (b), η is the threshold parameter (a), and x represents the observed data. The shape parameter determines the shape of the distribution, the scale parameter determines the dispersion of the distribution, and the threshold parameter represents the minimum value at which the distribution is defined [25].

To obtain the maximum likelihood estimates (MLEs) of a, b, and c, we used the R package "weibullness" (https://www.r-project.org/, accessed on 15 June 2023). First was calculated the likelihood of the sample data for one set of parameter values (a, b, and c), and then this process for different sets of parameter values was repeated. The Mean Squared Errors (MSEs) were then used to make inferences about the population from which the sample was drawn, and their validity was confirmed by checking that the model met the regularity conditions for maximum likelihood estimation.

The cumulative distribution function (CDF) of the three-parameter Weibull distribution is as described in Function (2):

$$F_{(x)=1-e^{(-(x-\eta)/\lambda)^k}} \tag{2}$$

where x is the random variable, k is the shape parameter, λ is the scale parameter, and η is the threshold parameter. The CDF gives the probability that a random variable will take a value less than or equal to x. It can be useful to provide insight into the probability of failure or the probability of a variable being in a certain range. Using the MLEs obtained from the likelihood function, the CDF can be used to make predictions about the probability of certain events occurring in the population and to estimate the reliability of a system or a product [28].

Pearson correlations were obtained to examine the relationship between rust severity (%) and the number of lesions per square centimeter (cm^2) under field conditions. These correlations were obtained in order to assess the relationship between the disease variables and environmental parameters, including dew point (Dew), maximum temperature (Tmax), mean temperature (Tmed), minimum temperature (Tmin), and precipitation (Prec). Statistical significance levels were established at $p \leq 0.001$, $p \leq 0.01$, and $p \leq 0.05$. Also, the disease severity was correlated with two epidemiological parameters, namely a (the location parameter or the initial disease amount) and b (the scale parameter or the disease progress rate), using the same levels of statistical significance. All these statistical analyses were performed with Rstudio.

3. Results

3.1. Morphological Characterization of the Causal Agent of Rust

We observed only uredia, uredospores, telia, and teliospores on the underside of leaves of all physic nut genotypes established under field conditions, but only uredia and uredospores on the leaf surface of seedlings established under semi-controlled conditions. In both cases, in the FiagR1 population, we observed uredia that were subepidermal, were erumpent, and had peripheral, incurved, and dorsally thick-walled paraphyses surmounting peridial tissue and uredospores that were singly borne, had an echinulate wall, were yellowish or nearly colorless (hyaline) in color, and had scattered pores. Uredia and uredospores analyzed on the underside of leaves of adult plants and seedlings had a similar mean length (109.9 ± 10.8 µm and 14.2 ± 1.8 µm, respectively) and width (140.9 ± 18.3 µm and 18.5 ± 2.1 µm, respectively) (see Table 1). We also found telia that were subepidermal and not erumpent, consisting of crusts of laterally adherent teliospores three or more cells deep, as well as sessile teliospores that were either catenate or irregularly arranged, unicellular, and whose wall was usually brown or brownish (see Supplementary Figure S2). Finally, telia and teliospores observed on the leaves of adult plants showed average length (161.18 ± 9.68 µm and 13.73 ± 1.68 µm, respectively) and width (126.9 ± 7.5 µm and 18.16 ± 1.72 µm, respectively) (see Table 1). The morphological structures observed were similar to those described for *Phakopsora arthuriana*.

3.2. Experiment under Semi-Controlled Conditions

Artificial inoculation of physic nut seedlings allowed for the evaluation of the response of hybrids and genotypes to rust (Figure 1A), with pustules found on the underside of all seedling leaves (Figure 1B–E). The severity of the disease was about three times higher only in the hybrid JAT 001165 (8%) compared with the average found in the other genotypes (3% on average) (Figure 1B,D,F). On the other hand, a higher number of lesions cm^2 was found in leaves of the hybrids JAT 001103, JAT 001164, and JAT 001165 (five lesions on average) compared with the average found in the hybrid JAT 001100 and genotypes CP-041 and CP-052 (two lesions on media) (Figure 1G).

Table 1. Morphological characteristics, including the length and width of uredia, uredospores, telia, and teliospores, were analyzed in two populations of *Phakopsora* sp. These populations were sourced from pustules on the leaves of adult plants (FiagR1) and seedlings (FiagR2) of physic nut (*Jatropha curcas*) hybrids and promising genotypes cultivated in Lodana, Manabí, Ecuador. SD, standard deviation.

Fungal Structures	**Length (µm)**		**Width (µm)**	
	Range	**Mean ± SD**	**Range**	**Mean ± SD**
FiagR1 population collected from adult plant leaves				
Uredia	94.9–179.7	129.6 ± 23.3	126.1–206.5	160.6 ± 23.0
Uredospores	10.1–17.6	14.0 ± 1.8	14.2–22.4	18.1 ± 1.9
Telia	144.10–180.95	161.18 ± 9.68	117.31–137.90	126.9 ± 7.5
Teliospores	11.27–16.27	13.73 ± 1.68	15.01–20.85	18.16 ± 1.72
FiagR2 population collected from seedling leaves				
Uredia	94.0–128.6	109.9 ± 10.8	115.1–185.5	140.9 ± 18.3
Uredospores	10.4–17.8	14.2 ± 1.8	14.9–23.5	18.5 ± 2.1

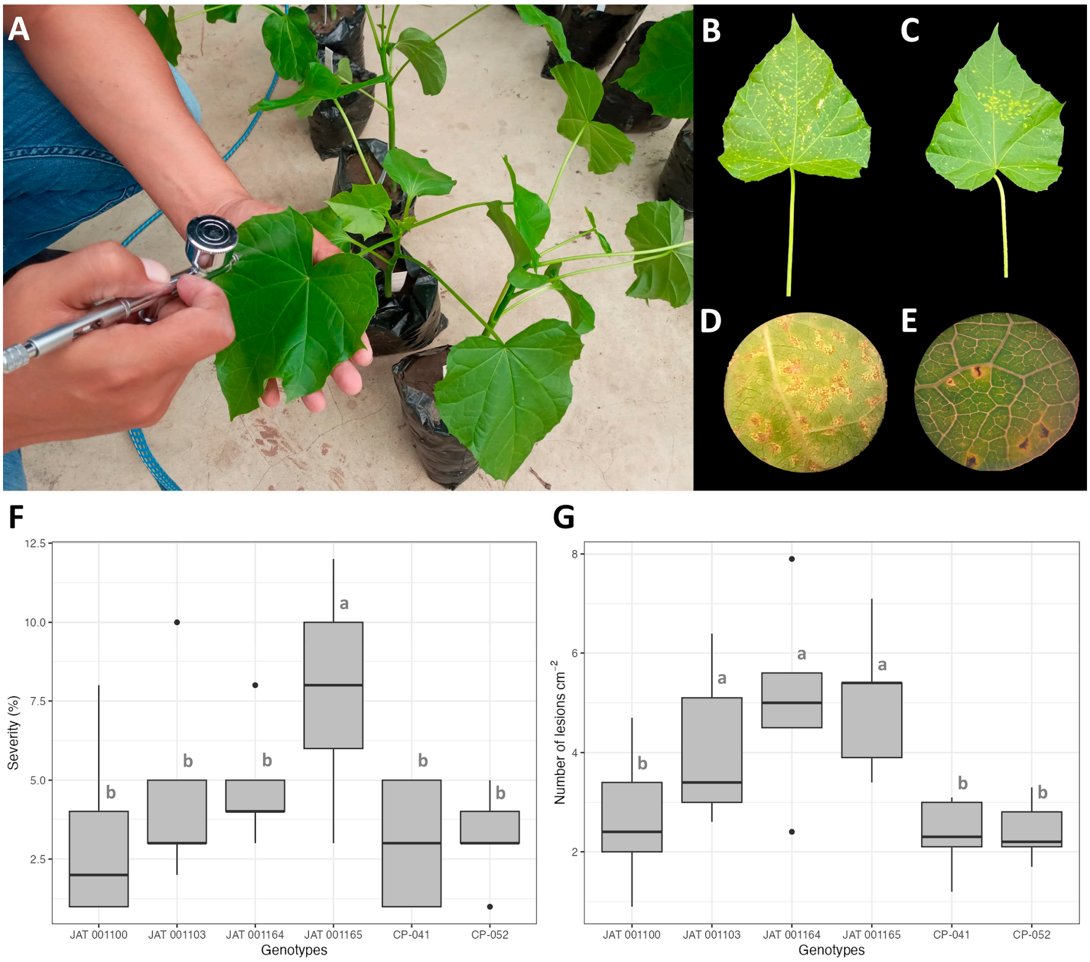

Figure 1. Rust disease on physic nut (*Jatropha curcas*) leaves of hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) established under semi-controlled conditions in Lodana, Manabí, Ecuador. (**A**) Artificial inoculation of seedlings.

(**B**–**E**) Symptomatic leaf showing higher (**B**–**D**) and lower (**C**–**E**) lesion numbers for the hybrid JAT 001165 and the genotype CP-041, respectively. (**F**,**G**) Boxplot for the severity (%) and number of lesions per cm^2 in leaves of physic nut genotypes. Identical letters on the boxes indicate no significant difference (Kruskal-Wallis test, $p \leq 0.05$). Black dots represent outliers. The error bars represent the standard deviations for each genotype.

3.3. Experiment under Field Conditions

Rust was present on all the plants evaluated of the six genotypes of physic nut in almost all of the months of evaluation, representing an incidence of 100%. Likewise, the temporal progress of rust was different and irregular among canopies and genotypes of physic nut, with the disease increasing or decreasing in some months of the year (Supplementary Figure S3; Figure 2).

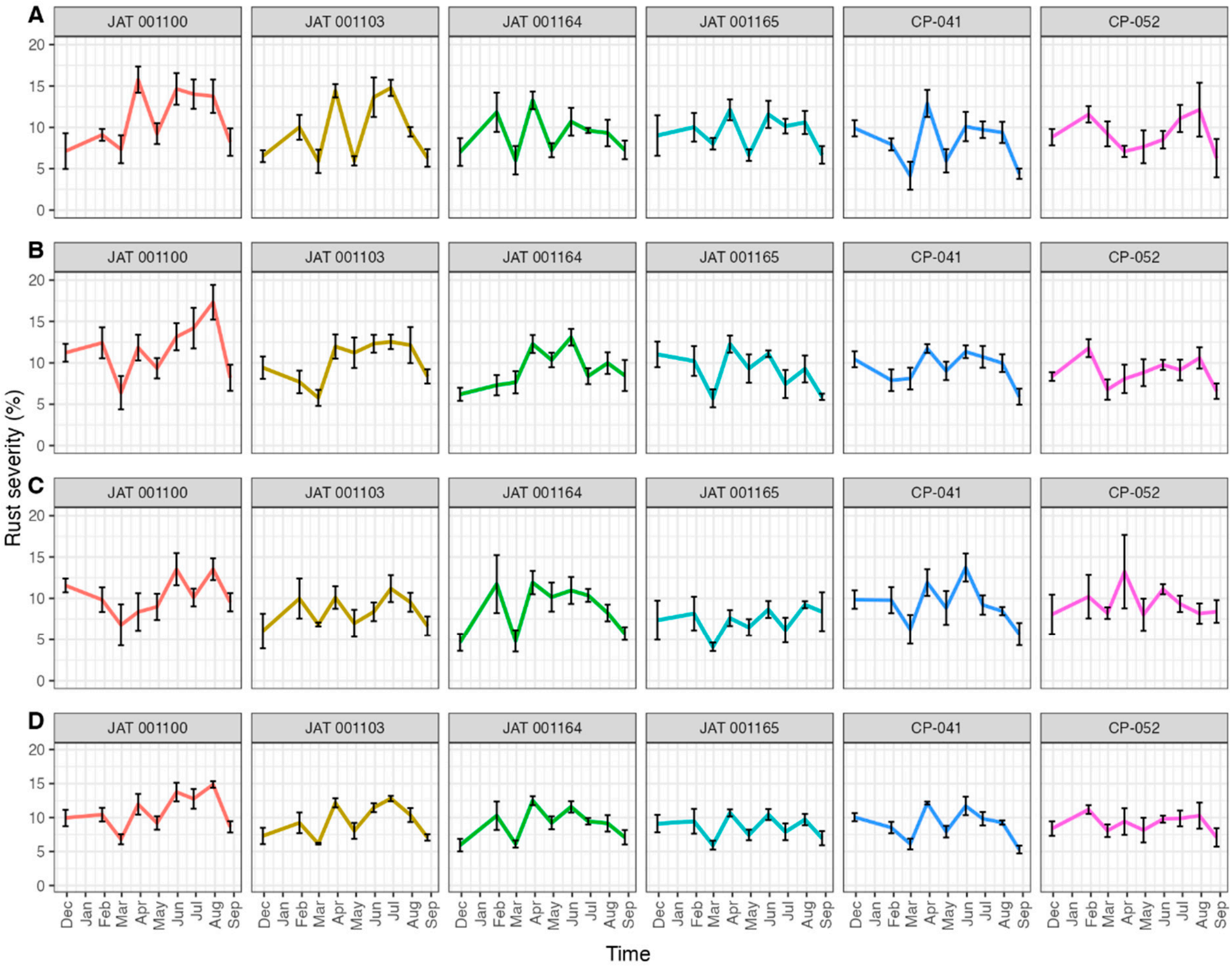

Figure 2. Temporal progress of the rust severity (%) on physic nut (*Jatropha curcas*) leaves of the lower (**A**), middle (**B**), and upper (**C**) canopy and their averages (**D**) in hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) established under field conditions in Lodana, Manabí, Ecuador. The error bars represent the standard deviations from the mean for each time evaluated between December 2021 and September 2022.

In the lower canopy (Figure 2A) of the physic nut plants, rust started with a severity ranging from 6 (the hybrid JAT 001103) to 10% (the genotype CP-041). Although its progress was uneven in all genotypes, disease severity was the highest in hybrids JAT 001103 and JAT 001100 with 14 and 16%, respectively. The disease started to decrease in September in most genotypes, except in the hybrid JAT 001103, where rust started to decrease in August 2022.

In the middle canopy (Figure 2B) of the physic nut plants, the rust severity was 9% (genotype CP-052) and 11% (JAT 001100 and JAT 001165). In hybrids JAT 001100, JAT 001103, and JAT 001165 and genotype CP-052, the disease severity decreased in March 2022. From that month on, the rust severity increased in the JAT 001164 (13%) and JAT 001100 (17%) hybrids in June and August 2022, respectively, while the disease progress was practically similar in the remaining genotypes. Finally, rust reached the minimum severity levels in September in almost all genotypes (6% on average), except for the hybrid JAT 001164, which showed a similar level to that observed in August.

In the upper canopy (Figure 2C), a significant variation was observed among plants within each genotype (refer to Figure 2C for the standard deviation across the evaluated months). Rust in this canopy initiated in December 2021, and its severity ranged from 4 to 11% in the JAT 001164 and JAT 001100 hybrids, respectively. Although the disease progression was nearly linear in almost all genotypes, a notable increase occurred in the hybrid JAT 001100 and the genotype CP-041 between March and June 2022. At the experiment's conclusion, the rust severity diminished only in hybrids JAT 001103 and JAT 001164 and the genotype CP-041, settling at values between 6 and 10%.

When all plant canopies were averaged (Figure 2D), a temporary increase in the rust severity was noted only in plants of the hybrid JAT 001100, reaching an average of 15% in July 2022, which incidentally was the highest severity observed compared with the other hybrids and promising genotypes. Although the disease declined in all genotypes at the evaluation's end, this decrease was markedly progressive from July 2022 in hybrids JAT 001103 and JAT 001164 and in the genotype CP-041.

Both the lower and middle canopy of the hybrid JAT 001100 exhibited nine lesions per cm^2 in May and June 2022, respectively, representing the highest value recorded in the entire experiment. Regarding both severity (%) and the number of rust lesions per cm^2 in relation to the AUDPC on leaves of physic nut genotypes, significant differences were detected exclusively in the average canopy and also in the middle canopy for disease severity (Table 2). The lowest (4086.4 units) and highest (6437.5 units) AUDPC values for severity were recorded in plants of the JAT 001165 (upper canopy) and JAT 001100 (middle canopy) hybrids, respectively. Similarly, the lowest (2429.8 units) and highest (3438.8 units) AUDPC values for the number of lesions per cm^2 were observed in plants of the JAT 001165 (upper canopy) and JAT 001100 (lower canopy) hybrids, respectively.

Table 2. Area under the disease progress curve (AUDPC) for the rust severity (%) and number of lesions per cm^2 on physic nut (*Jatropha curcas*) leaves of the lower (A), middle (B), and upper (C) canopy and their averages (D) in hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) established under field conditions in Lodana, Manabí, Ecuador.

Genotypes	**Rust Severity (%)**				**Number of Lesions per cm^{-2}**			
	Lower	**Middle**	**Upper**	**Mean**	**Lower**	**Middle**	**Upper**	**Mean**
JAT 001100	6046.6 ^{ns}	6437.5 a *	5623.7 ^{ns}	6035.9 a	3438.8 ^{ns}	3331.7	2916.2	3228.9 a
JAT 001103	5413.8	5556.8 b	4746.4	5239.0 b	3102.8	3212.7	2686.6	3000.7 a
JAT 001164	5179.8	5081.8 b	5004.8	5088.8 b	2985.0	2710.2	2614.2	2769.8 b
JAT 001165	5283.6	5176.3 b	4086.4	4848.8 b	2961.7	2844.4	2429.8	2745.3 b
CP-041	4689.6	5260.8 b	5243.8	5064.7 b	2694.7	2938.8	2847.9	2827.1 b
CP-052	5209.0	5064.6 b	5226.2	5166.6 b	3051.7	2777.6	2707.5	2845.6 b
Mean	5303.7 a	5429.6 a	4988.5 b		3039.1 a	2969.2 a	2700.4 b	
CV	9.0	11.2	12.4	7.5	8.3	10.3	8.2	6.8
p-value	0.0292	0.0449	0.0494	0.0118	0.0222	0.0642	0.0841	0.0283

^{ns}, not significant. * Means followed by the same letters in the column do not differ significantly (Scott–Knott test, $p \leq 0.01$).

The severity of rust in relation to the AUDPC (Table 2) was 16% and 19% higher in the hybrid JAT 001100 (averaging 6236.71 units), both in the canopy average and in the upper canopy, respectively, compared with that of the other genotypes (averaging 5154.81 units). A similar trend was observed in the number of lesions per cm^2 for the AUDPC (Table 2), where hybrids JAT 001100 (3228.89 units) and JAT 001103 (3000.7 units) exhibited a 10% higher average compared with that of the other genotypes (averaging 2797.1 units). Finally, both the severity (%) and the number of rust lesions per cm^2 were on average 9% lower on leaves of the upper canopy compared with those of the lower and middle canopy (Table 2).

Weibull Analysis

The analysis of the Weibull distribution for rust severity is shown in Figure 3, showcasing results observed under field conditions. The x and y axes in each panel represent the rust severity and the cumulative probability of the distribution, respectively. The results demonstrate that the fitted curve (blue line, maximum likelihood estimation) closely aligns with the observed data (red dots, empirical data) for most canopies and genotypes. The coefficient of correlation (r) across each genotype in the three canopies and their average ranged from 0.17 to 0.73 (Table 3). Nearly all of the curves were significant (p-values ranging from $p \leq 0.001$ to $p \leq 0.05$), with exceptions in certain cases such as in the hybrid JAT 001165 in the lower ($p \leq 0.0906$) and upper ($p \leq 0.2240$) canopy, in the hybrid JAT 001100 in the upper canopy ($p \leq 0.1078$), and in the genotype CP-052 across all canopies and their average (average p-value of ≤ 0.3921) (Table 3). These findings signify a good fit between the Weibull distribution and the observed data.

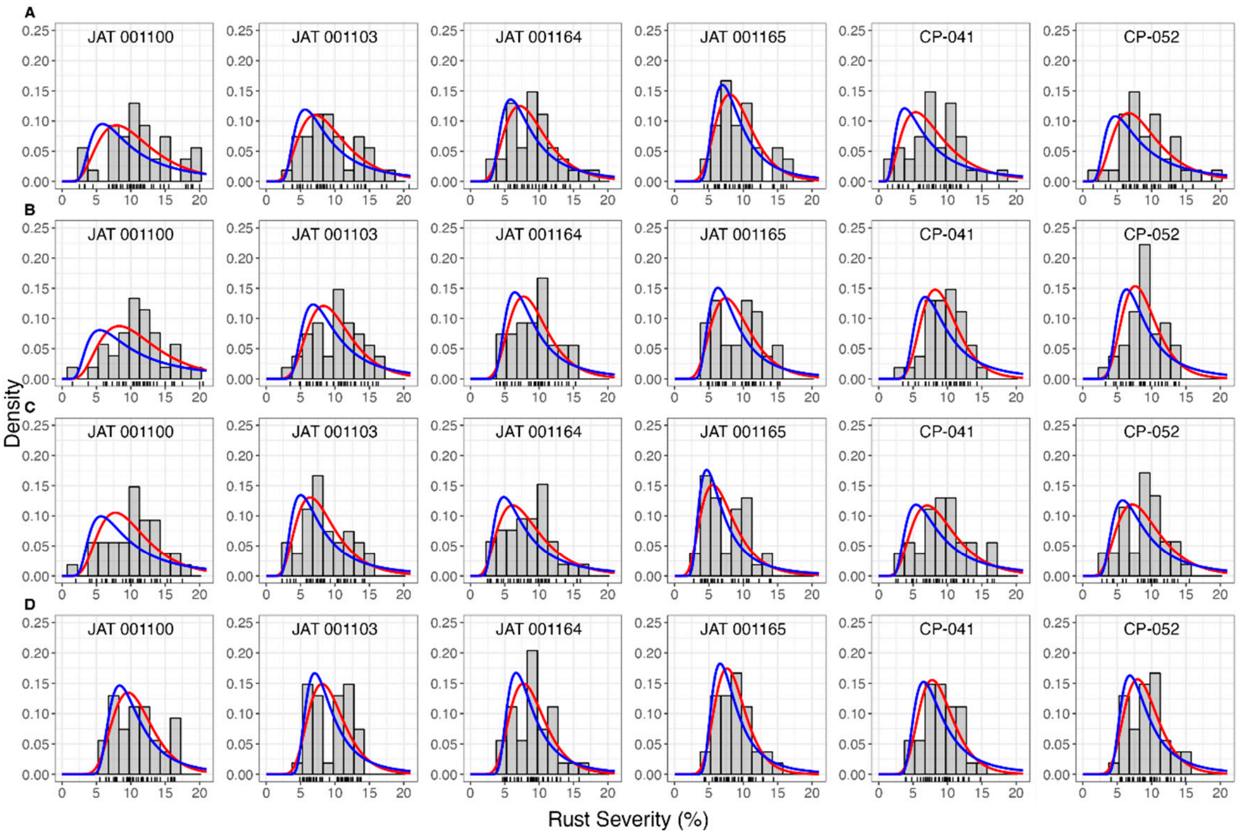

Figure 3. Maximum likelihood estimates of the Weibull distribution of the rust severity (%) on physic nut (*Jatropha curcas*) leaves of the lower (**A**), middle (**B**), and upper (**C**) canopy and their averages (**D**) in hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) established under field conditions in Lodana, Manabí, Ecuador. Each panel shows the data distribution for each genotype, with the red and blue lines representing the data log-normal distribution and the Weibull distribution, respectively, of the maximum likelihood estimation.

Table 3. Parameters estimated by Weibull distribution analysis for the rust severity on physic nut (*Jatropha curcas*) leaves of the lower (A), middle (B), and upper (C) canopy and their averages (D) in hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) established under field conditions in Lodana, Manabí, Ecuador.

Genotypes	a[1]	b[2]	c[3]	r^2 *	*p*-Value **
			Lower canopy		
JAT 001100	0.74	3.23	−1.94	0.55	0.0023
JAT 001103	0.48	2.13	1.28	0.73	0.0001
JAT 001164	0.42	2.26	1.77	0.44	0.0247
JAT 001165	0.34	2.02	3.50	0.36	0.0906
CP-041	0.56	3.02	−1.57	0.60	0.0006
CP-052	0.61	3.15	−1.57	0.28	0.2698
			Middle canopy		
JAT 001100	0.89	3.99	−4.52	0.50	0.0074
JAT 001103	0.49	2.87	1.50	0.47	0.0014
JAT 001164	0.38	2.39	2.59	0.52	0.0050
JAT 001165	0.33	1.89	3.23	0.46	0.0168
CP-041	0.63	5.27	−2.17	0.48	0.0122
CP-052	0.44	3.35	0.95	0.37	0.0877
			Upper canopy		
JAT 001100	0.64	4.53	−3.95	0.35	0.1078
JAT 001103	0.36	2.69	0.48	0.29	0.2240
JAT 001164	0.33	1.88	1.47	0.48	0.0121
JAT 001165	0.23	1.73	2.20	0.23	0.4213
CP-041	0.42	3.05	−0.52	0.45	0.0192
CP-052	0.36	2.00	1.58	0.17	0.6877
			Mean canopy		
JAT 001100	0.56	2.10	4.68	0.61	0.0004
JAT 001103	0.42	1.69	4.61	0.67	0.0001
JAT 001164	0.40	1.52	4.46	0.57	0.0014
JAT 001165	0.40	2.47	3.10	0.41	0.0465
CP-041	0.49	3.51	0.87	0.71	0.0001
CP-052	0.72	2.57	2.82	0.21	0.5231

a[1], location parameter (amount of initial disease); b[2], scale parameter (disease progress rate); c[3], shape parameter (dy/dt vs. t); * r^2, determination coefficient; ** *p*-value, probability value. Provides the exact probability of making a Type I error, also known as the observed level of significance.

As a result of the nonlinear Weibull analysis (Table 3), the parameters 'a' (initial disease amount) and 'b' (disease progress rate) of rust severity were obtained. In almost all canopies of physic nut plants, the hybrids JAT 001165 and JAT 001100 obtained lower and higher mean values of both epidemiological parameters, respectively. Only the promising genotype CP-041 showed a higher disease progress rate in the middle canopy (5.27 units). In the canopy measurement, the hybrids JAT 001164 and JAT 001165 (0.40 units) obtained a lower value compared with the promising genotype CP-052 (0.72 units), which obtained the higher average initial disease amount. Something similar was observed in the same canopies with the disease progress rate, where the hybrid JAT 001164 (1.52 units) and the promising genotype CP-041 (3.51 units) had the lowest and highest mean, respectively.

When we correlated the epidemiological parameters with the intensity of the rust (Table 4), r values above 0.850 and *p*-values ≤ 0.031 were observed only for the initial disease amount in the middle and upper canopy of the physic nut plants.

Table 4. Correlation between epidemiological parameters a (the location parameter or amount of initial disease) and b (the scale parameter or disease progress rate) with the rust severity (%) and the number of lesions per cm^2 on physic nut (*Jatropha curcas*) leaves of the lower, middle, and upper canopy and their averages in hybrids and promising genotypes established under field conditions in Lodana, Manabí, Ecuador.

Severity (%)			**Number of Lesions per cm^2**	
Canopy	**r ***	***p*-Value ****	**r**	***p*-Value**
Location parameter (initial disease amount)				
Lower	0.470	0.342	0.452	0.368
Middle	0.860	0.028	0.882	0.020
Upper	0.885	0.019	0.853	0.031
Mean	0.291	0.576	0.340	0.509
Scale parameter (disease progress rate)				
Lower	0.150	0.770	0.130	0.806
Middle	0.280	0.588	0.303	0.560
Upper	0.741	0.092	0.699	0.122
Mean	0.230	0.653	−0.230	0.662

* r, correlation coefficient; ** *p*-value, probability value ($p \leq 0.05$). Provides the exact probability of making a Type I error, also known as the observed level of significance.

3.4. Correlation between Rust Disease and Environmental Conditions

Correlation analysis between the rust severity at different canopy levels of physic nut plants and meteorological variables revealed varying degrees of correlation (Supplementary Figure S4 and Figure 4). No significant correlation was observed in the lower canopy (Supplementary Figure S4A) and in the average of the strata (Figure 4A). In the middle canopy (Supplementary Figure S4C), the hybrid JAT 001103 showed a strong positive correlation with relative humidity (r = 0.72), while hybrids JAT 001164 (r = 0.71) and JAT 001165 (r = 0.65) showed significant positive correlations with dew point. In the upper canopy (Supplementary Figure S4E), only the promising genotype CP-041 exhibited a significant positive correlation with dew point (r = 0.64).

The correlation analysis between the number of lesions per cm^2 and the meteorological variables (Figure 3) showed only significant negative correlations in the middle (Supplementary Figure S4D) and upper (Supplementary Figure S4F) canopies, but none in the lower canopy (Supplementary Figure S4B) and in the average of the strata (Figure 4B). In the middle canopy (Supplementary Figure S4D), the hybrids JAT 001100 and JAT 001103 showed strong negative correlations with minimum temperature (average r = −0.75) and mean temperature (average r = −0.66). Within the same canopy, the genotype CP-041 displayed a significant negative correlation with dew point (r = −0.77), precipitation (r = −0.75), and minimum temperature (r = −0.69), while CP-052 also showed a significant negative correlation with dew point (r = −0.70) and precipitation (r = 0.68).

In the upper canopy (Supplementary Figure S4F), all hybrids and the genotype CP-041 showed strong negative correlations with minimum temperature (average r = −0.74). Hybrids JAT 001100 and JAT 001164 showed negative correlations with mean temperature (average r = −0.68), while JAT 001100 and JAT 001103 displayed negative correlations with dew point (average r = −0.77). Furthermore, the hybrid JAT 001103 and the genotype CP-052 showed a negative correlation with precipitation (average r = −0.77).

When rust disease was correlated with environmental conditions in the average of the canopies (Supplementary Figure S4G,H), only negative correlations were obtained in the variable number of lesions per cm^2 (Supplementary Figure S4H). Significant negative correlations were found between the hybrids JAT 001100, JAT 001103, and JAT 001165 and minimum temperature (average r = −0.71). Similarly, hybrids JAT 001100 and JAT 001103 exhibited significant negative correlations with maximum temperature (r = −0.67) and dew point (r = −0.69), respectively. Also, significant negative correlations were observed between the genotype CP-052 and dew point (r = −0.75) and precipitation (r = −0.76).

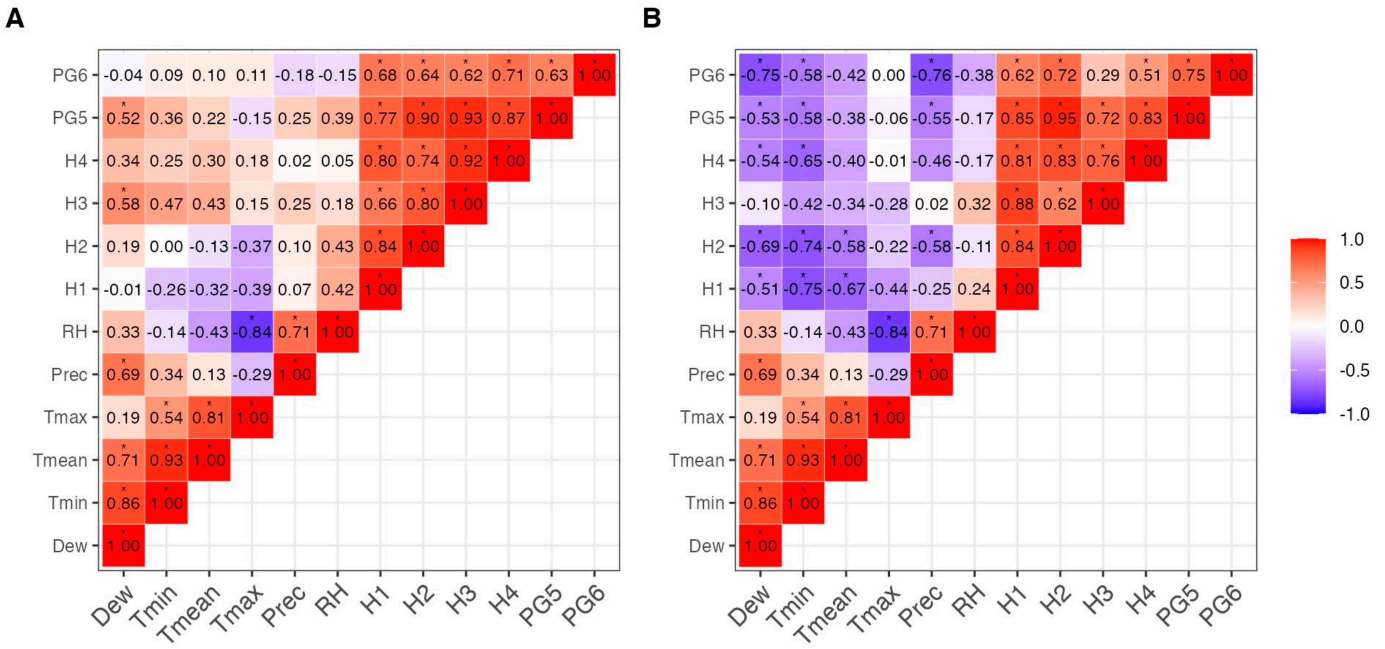

Figure 4. Correlation heatmap illustrates the relationship between meteorological variables and rust severity (%) (**A**) as well as the number of lesions per square centimeter (**B**) on the leaves of physic nut (Jatropha curcas) hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) in Lodana, Manabí, Ecuador under field conditions. Each panel displays the Pearson correlation coefficients (r) and significance levels (* for $p \leq 0.05$) for each genotype and meteorological variable in the disease analysis. The color scale ranges from −1 to 1, indicating negative (blue) to positive (red) correlations. A darker hue represents a stronger magnitude of correlation, with 1 and −1 being the strongest positive and negative correlation, respectively. White indicates no correlation.

Overall, there were significant correlations between the environmental parameters and the intensity of rust in the physic nut genotypes across each of the plant canopies (Supplementary Figure S4A–F) as well as their average (Supplementary Figure S4G,H). This relationship was particularly evident in the average of the canopies. Notably, maximum temperature showed no significant correlation with any of the genotypes.

4. Discussion

Physic nut is an oleaginous plant with high oil content, making it ideal for industrial use, especially in biodiesel production. Nevertheless, few studies have been carried out on rust in this crop species worldwide [7,9,29]. In this study, the rust pathogen associated with this problem in Ecuador was morphologically characterized and the rust intensity on six physic nut genotypes was evaluated under field and semi-controlled conditions on adult plants and seedlings, respectively. We also epidemiologically modeled the disease using the Weibull nonlinear model in adult plants and correlated some climatic parameters with the disease and the epidemiological parameters of the nonlinear model with the disease intensity.

Although the species *Uromyces amapaensis* and *P. jatrophicola* have been reported to cause rust on *Jatropha* spp. (Euphorbiaceae), only the latter has been described on diseased leaves of physic nut (*J. curcas*) plants [7,9,29]. The shape, pigmentation, and size (length and width) of the uredia, uredospores, telia, and teliospores observed by us in physic nut plants and seedlings are similar to those obtained by Díaz-Braga et al. [9], Nolasco-Gúzman et al. [7], and Haituk et al. [8], who describe *P. arthuriana* as the causal agent of rust in physic nut plants. Although it would be interesting in the future to conduct a molecular characterization of physic nut rust populations in Ecuador, the morphological characterization and the pathogenic characterization conducted in this research allow us to indicate for the first time that the basidiomycete that causes physic nut rust in Ecuador is *P. arthuriana*.

Seedling responses of hybrids and physic nut genotypes to rust under semi-controlled conditions differed from those observed under field conditions. For example, in greenhouse assays, the hybrid JAT 001165 exhibited higher severity, and this material, along with hybrids JAT 001103 and JAT 001164, displayed a higher number of lesions per cm^2 compared with the other genotypes. However, hybrids JAT 001100 and JAT 001103 showed a higher disease intensity under field conditions. Conversely, the promising genotypes CP-041 and CP-052 exhibited higher disease intensity under both environmental conditions. Nevertheless, all of the physic nut genotypes were susceptible to rust. Only two reports demonstrate the response of physic nut to rust under field conditions [30] and with detached leaves [9]. In the former, a maximum severity of 13% was recorded, while, in the latter, an average of 15.5 ± 2.3 lesions per leaf, 181.2 ± 19.5 pustules per leaf, and 12.6 ± 2.4 pustules per lesion were observed on the leaves of the abaxial side. Neither of these two studies mentions the specific genotype of physic nut used. Therefore, we cannot directly compare the response of our genotypes to rust with those of the other authors.

Under field conditions, rust lesions were observed on the leaves of all physic nut genotypes across the three canopy levels, reaching an incidence of 100%. Interestingly, these plants were just a little over a year old when we began to evaluate them, so the time it took for them to become diseased was relatively short. The incidence of rust observed in our genotypes is higher than the maximum found by Díaz-Braga et al. [9] and Nolasco-Gúzman et al. [7], at 45% and 70%, respectively, and it could even be the highest incidence of the disease reported in physic nut plants worldwide.

The rust's temporal progress and intensity (severity and number of lesions per cm^2) differed between genotypes and canopies. For instance, in the upper canopy, we observed a higher variation between plants within each genotype and where the disease progress was practically linear in almost all genotypes. Only the hybrid JAT 001100 and the genotype CP-041 experienced an increase in rust intensity between March and June 2022 compared with the rest of the genotypes, while the rust decreased progressively in the hybrids JAT 001103 and JAT 001164 and the genotype CP-041, reaching values between 6 and 10%. Also, the AUDPC for the severity of rust was higher in the middle canopy and in the average of the canopies of the hybrid JAT 001100, and the AUDPC for the number of lesions per cm^2 was higher in the same material and the hybrid JAT 001103 in the average of the canopies, when compared with the rest of the genotypes. In general, hybrids JAT 001100 and JAT 001103 were the physic nut genetic materials most susceptible to the rust caused by *P. arturiana* considering that the occurrence and severity of rust can vary over time and depend on the source of the inoculum, the environmental conditions, and the genetic base of the host [2,30].

The dew point is among the climatic variables most associated with the advancement of the pathogen infection. This factor favors the spread of the disease in plants along with precipitation due to the increase in humidity in the environment. Physic nut is a perennial plant, so the disease would be present in the plant when its leaves are attached. However, the rust infection observed in any plant stratum could also be affected by host defense mechanisms, the temperature (especially the minimum temperature), and the dew point. Due to their being members of a perennial cycle species, when the genotypes are exposed to the climatic conditions of the tropics the disease has enough leaf area to spread when climatic conditions are favorable. Identifying defense mechanisms against rust in physic nut plants will be an exciting challenge for future research.

The intensity and progression of rust were influenced by environmental factors such as dew point, minimum and mean temperature, precipitation, and relative humidity, but not by maximum temperature. In this research, we found positive and (mostly) negative correlations between some meteorological variables and severity (%) and the number of lesions per cm^2 in almost all canopy levels of the physic nut plants, except in the lower canopy. It is known that there is a genotype–environment interaction that affects the intensity of rust in plants [31]. However, a genotype–environment interaction was not observed; instead, the rust intensity was influenced only in some genotypes and canopies. For example, in some physic nut genotypes, the disease was positively induced by dew point (JAT 001164 and JAT 001165) and relative humidity (JAT 001103) in the middle and upper canopy and negatively affected (all genotypes) by dew point, precipitation, and minimum and mean temperature in the middle canopy, upper canopy, and average of the canopies. Our results show that the rust infection in physic nut plants was variable throughout the year and highly dependent on the environmental conditions observed during the evaluation period. These results differ from those expressed empirically by Nolasco-Gúzman et al. [7], who mentioned that a humid and temperate climate with rainfall throughout the year favors the progress of rust in physic nut plants. On the other hand, the infective potential of some rusts like *Uropyxis petalostemonis* on the legume *Dalea candida* decreases sharply at temperatures > 25 °C [32]. Nevertheless, in our field experiment, we found that maximum temperature (between 25.8 and 28.8 °C) did not affect the severity and number of lesions per cm^2 associated with the infection of *P. arturiana* in physic nut.

Under field conditions, we observed negative correlations between the number of lesions per cm^2 of the promising genotypes CP-041 and CP-052 in the lower canopy and between precipitation and the genotypes JAT 001103 and CP-052 in the middle canopy. The probability of pathogen dispersal is higher under a large amount of precipitation in soybean rust [15]. However, under the conditions in which we conducted the experiment, it appears that physic nut rust is favored more by dew point and relative humidity than parameters such as precipitation. In fact, dew point is important for other rusts, such as soybean rust [33].

As we mentioned earlier, we found no significant correlations between meteorological variables and rust severity in the lower canopy and the mean of all canopies and negative correlations with some parameters such as dew point, precipitation, and maximum and minimum temperature. Both pathogens and plants have an optimal environmental condition for their growth and reproduction. An optimal environmental condition is better for the outbreak of a disease, and if more climatic factors deviate from this "disease optimum", a lower intensity of rust will occur on the plant [34]. Interestingly, for physic nut, negative correlations were found only when the environmental conditions were correlated with the number of lesions per cm^2, but not with rust severity. In more-studied rusts, such as soybean rust (*P. pachyrhizi*), the disease severity increases when increasing the number of lesions [27]. In several diseases, the presence of a small number of lesions would be associated with few sites (anatomical features or host resistance), pathogen characteristics (a low number of infectious units or low infection efficiency), or microenvironmental constraints [35]. Although microenvironmental constraints are related to our result, further studies are needed to understand how environmental factors negatively affect the number of physic nut leaf lesions.

The Weibull distribution analysis conducted in this research showed that most of the disease and environmental data fit this model of distribution well, suggesting that this model can be used to model rust in the physic nut crop or in another perennial crop. Almost all of the observed data were close to the fitted distribution. In addition, the estimated parameters, such as the initial disease amount and disease progress rate, agreed with the disease intensity data. For instance, high mean values were found for both epidemiological components in the lower and middle canopy of the hybrid JAT 001100, perhaps explaining why this material had the highest disease severity and number of lesions per cm^2. Coincidentally, in our study, the disease progress rate was significantly correlated with the severity and number of lesions per cm^2 in the middle and upper canopy. The Weibull model also has an additional parameter, the shape parameter (c), which can be used in the analysis of disease progression data. Perhaps the shape of the disease progression curve is indicative of a currently undefined type of host resistance [21,24].

The Weibull model can effectively describe the progress of rust in red raspberry (*Rubus idaeus* L.); however, despite its flexibility, the model seems to have limitations in describing epidemics when the severity values are less than 5% [23]. In contrast, the rust severity observed in the physic nut cultivars exceeded this threshold. On the other hand, not all disease progression curves are well or easily described by a growth curve model, especially in perennial crops [36]. Alternative methods for quantifying the development of epidemics include the AUDPC and nonlinear models such as the Weibull model. Our results confirm the usefulness of the AUDPC in terms of the severity and number of lesions per cm^2 and the Weibull distribution model in terms of determining disease development in different physic nut cultivars because they integrate factors such as host response and pathogen aggressiveness as described by García-López et al. [22] in a study on a malformation disease caused by *Fusarium* sp. in mango. Although these authors did not correlate the disease or the AUDPC with the epidemiological parameters 'a' and 'b' as we did in this research, they found a relationship between the AUDPC, the final infection of the disease, and the apparent infection rate of the malformation disease in mango cultivars.

This research demonstrated that the Weibull model can effectively model rust and compare rust epidemics among physic nut genotypes. Moreover, the Weibull analysis allows for a better understanding of plant diseases from an epidemiological perspective, which has important implications for the future management of rust in physic nut crops. To the best of our knowledge, this is the first report on the modeling of the temporal progress of rust in physic nut. This is particularly important considering that physic nut could contribute to the sustainable production of food and bioenergy, the rehabilitation of degraded lands, and the reduction of atmospheric carbon dioxide in Ecuador. Therefore, the evaluation of rust on physic nut genotypes under both field and greenhouse conditions, along with adequate epidemiological modeling of the disease, is crucial for the development of improved cultivars in the field.

5. Conclusions

According to the morphological and pathogenic characterization of the pathogen causing rust in physic nut plants, the species *Phakopsora arthuriana* is the causal agent associated with this disease in the province of Manabí, Ecuador. This rust caused visible symptoms to occur on leaves from the lower, middle, and upper canopies of physic nut hybrids and genotypes evaluated under field conditions. The rust severity between the canopies was higher in the lower and middle canopies of physic nut plants, with the hybrid JAT 001100 being the most susceptible cultivar assessed among the six genotypes, whereas the promising genotypes CP-041 and CP-052 showed the lowest incidence of rust compared with the other assessed genotypes under field and semi-controlled conditions. In general, the temporal progress of rust was adequately modeled with the nonlinear and flexible Weibull model in most of the canopies and physic nut genotypes. Only the amount of initial disease was positively correlated with the number of lesions per cm^2 in the middle and upper canopies of plants, while the intensity was positively or negatively influenced by environmental components only in the middle canopy, the upper canopy, and the mean of all canopies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy14040712/s1, Figure S1. Climatic conditions (temperature, precipitation, and dew point) from the La Teodomira experimental campus where was established the experiment of the six physical nuts genotypes, between October-2021 and September-2022. Santa Ana, Manabí, Ecuador. Figure S2. Uredia (A), uredospores (B), telia, and teliospores (C) of *Phakopsora* sp. observed on physical nut (*Jatropha curcas*) leaves of hybrids and promisors genotypes established under field conditions in Lodana, Manabí, Ecuador. Figure S3. Rust symptoms on physical nut (*Jatropha curcas*) leaves of hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promisors genotypes (CP-041 and CP-052) established under field conditions in Lodana, Manabí, Ecuador. (A) adult plants. (B,C) asymptomatic (B) and symptomatic (C) leaves. Table S1. Productive and oil characteristics of the physic nut hybrids and genotypes promising evaluated in our research. Characteristics of hybrids were provided by JatroSolutions, and those of promising genotypes by Mejía et al. (2015). Table S2. Physical characteristics (soil type and pH: hydrogen ionic potential) and chemical (OM: organic matter, N: Nitrogen, P: Phosphorus, K, Potassium, Ca: Calcium, Mg: Magnesium, H: Hydrogen, Mn: Manganese, Co: Cobalt, and Z: Zinc) from the La Teodomira experimental campus where was established the experiment of the six physical nuts genotypes. Santa Ana, Manabi, Ecuador. Figure S4. Correlation heat maps between meteorological variables and rust severity (%) (A,C,E) and number of lesions cm^2 (B,D,F) on physical nut (*Jatropha curcas*) leaves of the lower (A,B), middle (C,D), and upper (E,F) canopy in hybrids (JAT 001100, JAT 001103, JAT 001164, and JAT 001165) and promising genotypes (CP-041 and CP-052) established under field conditions in Lodana, Manabí, Ecuador. The color scale ranges from −1 to 1, indicating negative (blue) to positive (red) correlations. A darker hue represents a stronger magnitude of correlation, with 1 or −1 being the strongest positive or negative correlation, respectively. White indicates no correlation.

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