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ORIGINAL PAPER

Environmental factors that modulate the release and transport of airborne urediniospores *Hemileia vastatrix* (Berk. & Broome) in coffee crops in Veracruz México

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Abstract The coffee leaf rust, *Hemileia vastatrix*, is the most destructive coffee-growing disease and the most important economically. More aggressive outbreaks of the disease were recently reported worldwide, including in Mexico, where coffee production showed a 40% decrease. This work aimed to determine the environmental conditions that favor release and air transport of the *H. vastatrix* urediniospores in coffee crops in Veracruz. The monitoring of airborne coffee leaf rust urediniospores was performed using three types of aerobiological traps at different heights: Hirst Spore Trap (HST, 1.5 m), Passive Spore Trap (PST 1.5, 3, 6, and 9 m), and Sedimentation Spore Sampler (SSS 1 m) from January 2014 to October 2015, in two plots in Veracruz, Mexico. The airborne urediniospores counts exhibited a bimodal distribution. Low concentrations that increase over time are evident from January to April, decreasing abruptly in May and June, only to rise again in August, reaching the highest record for airborne urediniospores during the mid-summer drought phenomenon. Dispersal of coffee rust urediniospores is mainly influenced by temperature, rain, wind, and humidity in leaves. They can reach heights in the air up to 9 m (above the canopy) in shade coffee crops. The dispersal of pathogens in the atmosphere comprises complex processes interconnected; their knowledge allows better comprehensive management of them.

Keywords *Hemileia vastatrix* · Airborne spores · Meteorology coffee rust · Agricultural pathogens · Mexico

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1 Introduction

The coffee leaf rust, *Hemileia vastatrix* Berk & Br., is the most destructive disease for coffee growing and the most important economically worldwide (Agrios, 2005). It can infect all known cultivated species in the genus *Coffea* (McCook, 2006), including *Coffea Arabica* L., one of the most important agricultural products in the world. This disease causes premature leaf fall, promoting a reduction in photosynthetic capacity and the weakening of diseased trees. In severe infections, it can cause regressive death in branches and even the death of trees (Agrios, 2005; APS, 2011), translating into significant decreases in production (Moreno and Alvarado, 2000). The presence of *H. vastatrix* represents a significant danger for the coffee-growing activity in Mexico, the ninth producer of *C. arabica* worldwide (ICO, 2018), with a planted area of 722,444.32 ha and a production value that surpasses 250 million USD (SIAP, 2019). Although the pathogen has been present in Mexico since 1981, it had not caused any significant reduction in coffee production. However, since 2012, more alggressive outbreaks of the disease were reported worldwide (Avelino et al., 2015; Yamaoka, 2014; Zambolim, 2016), which have caused an unusual behavior of the disease, increasing its incidence and severity, as is the case in Brazil (Zambolim, 2016), Colombia (Cristancho et al., 2012), and other Central American countries (Avelino and Rivas 2013; Avelino et al., 2015), including Mexico. In fact, from 2012 to 2018, coffee production in Mexico showed a 40% decrease, mainly due to the effect of *H. vastatrix* on crops (SIAP, 2018), which are mainly cultivated with high susceptibility varieties such as Typica, Bourbon, Mundo Novo, Caturra, and Garnica (Lopez et al. 2013). According to the International Coffee Organization (ICO, 2018), economic (decapitalization of producers) and agronomic (lack of crop management) factors have also contributed to these losses.

The aggressiveness of the disease is influenced by environmental factors (Avelino and Rivas, 2013). For *H. vastatrix* urediniospores to germinate, the presence of free water is required for at least 6 h in temperatures between 21 and 25 ºC and dark conditions (Agrios, 2005; Nutman et al., 1963; SENASICA, 2016). The appressorium requires a period of 5.3 to 8.5 h to form. The germination is inhibited by light and by the evaporation of water from the leaf since it affects the growth of germ tubes. However, after germinating, the fungus penetrates the leaves through natural openings (stomata) located on the underside of mature leaves (Rayner, 1961). The time from infection to spore production is called the latency period, which fluctuates between 34 and 37 days in the sun and between 31 and 35 days in the shade (Rivillas et al., 2011). The urediniospores of *H. vastatrix* are disseminated in the air after passing through three phases: the phase of separation of the urediniospores upon shedding of the uredium; the release and dispersal phase of leaf spores; and the phase of its deposition in new leaves (Avelino and Rivas, 2013). According to Nutman et al. (1960), the liberation of urediniospores is solely possible in the presence of free water; it is achieved through the splashes caused by rain (Bock, 1962; Nutman et al., 1963). Guzmán and Gómez (1987) discovered that 5 mm of rain was necessary for the water accumulated on the upper face of the leaf to overflow, pass to the lower face, and, therefore, have directly detached the urediniospores from the uredium. Rayner (1961) confirmed that wind or vibrations caused by the impact of drops on the leaves could release the spores. In fact, in recent years, it has been suggested that the wind can carry the urediniospores over long distances, including continental scales (Brown & Hovmøller, 2002; Acosta-Martinez et al., 2015). However, these hypotheses were only supported by Bowden et al. (1971), who measured the fall rate of urediniospores with a cascading impactor, indicating a terminal velocity of 0.6 cm s^{-1}, similar to that of rust spores that are transported over long distances; also, Becker and Kranze (1977) detected urediniospores in the air by monitoring airborne spores in Kenya, at an altitude of 1,500 mamsl, with an annual average temperature of 17.5 °C and annual accumulated precipitation of 1,280 mm. Even though coffee rust continued to spread, reaching the American continent, there had been no studies based on aerobiological sampling to reaffirm these reports for forty years. Recently, Boudrot et al. (2016) carried out a study in Turrialba, Costa Rica (600 mamsl; accumulated precipitation 2996 mm; average temperature. 22.5 °C) to determine the effect of shade trees on the dispersal of urediniospores in the air using Hirst-type spore traps for monitoring. They reported that rainfall is the principal dispersing agent under shade, and gusts of wind promote the dispersal of urediniospores under dry conditions in full sun, whereas they did not affect shaded conditions, probably because the canopy blocks the wind. Gagliardi et al. (2020) made an *H. vastatrix* urediospore sampling using two Spore Watch electronic spore samplers (Burkard), which were placed on the windward and leeward side of a coffee crop in Costa Rica Spore samplers were positioned at the height of 1.5 m, during three days from 11:00 to 17:00 h. No significant differences in captured airborne urediniospores between the windward and leeward positions were found, so they reported an increase in captured airborne urediniospores in plots where high wind speeds were reduced more frequently.

These studies are the only aerobiological work reported recently. To date, there are no studies that have used different types of aerobiological samplers at different heights of the crop, nor in the environmental conditions of coffee crops in Mexico, which are, for the most part, under shade. Therefore, this work aimed was to determine the environmental conditions that favor the release and air transport of *H.*

vastatrix urediniospores using aerobiological methods at different heights in two coffee crops under shade in the state of Veracruz.

2 Materials and methods

2.1 Site description

The aerobiological study was carried out continuously during the period from January 2014 to October 2015 in 2 coffee cultivation plots in the state of Veracruz. The first, a farm with traditional polyculture under the shade, is located in Pacho Viejo municipality of Coatepec, Veracruz (19.477, −96.918), at the height of 1207 mamsl. The second is in a cultivation plot with a specialized shade system, located within the Teocelo Experimental Field of the National Institute of Agricultural and Livestock Forest Research, SAGARPA, in the municipality of Teocelo, Veracruz (19.395; -97.001) at the height of 1277 mamsl. The region's prevailing climate is semi-warm humid, and sub-humid, with an average temperature of 19.2 °C and an average annual rainfall of 1926 mm (INEGI, 2016).

2.2 Monitoring of urediniospores in the air

Monitoring of air urediniospores in the selected sentinel plots was performed using three types of aerobiological traps.

2.2.1 Hirst-type spore trap (HST)

A Hirst-type Spore Trap (Burkard Manufacturing Co Ltd, Rickmansworth, UK) was placed in each plot. HST has a 14 × 2 mm inlet hole, and a drum in which particles are impacted on a cellophane tape (Melinex) impregnated with a mixture of Vaseline and hexane (1:5) (Hirst, 1952). The drum is attached to a clock mechanism that moves 2 mm per hour, allowing the continuous and hourly sampling of particles in the air. It has a vane that keeps the air inlet hole in the direction of the prevailing wind, as well as a vacuum pump, which sucks 10 L of air per minute for seven days (Fig. 1A). The sampled tape was divided into sections equivalent to each sampling day (7 × 24 h). Each fragment was placed on a slide and mounted with glycerine jelly stained with fuchsine, and analyzed under the light microscope. Impacted *H. vastatrix* urediniospores were counted throughout the slide-mounted tape fragment. Particular characteristics searched were reniform urediniospores, 28–36 × 18–28 µm; hyaline wall, strongly warted on the convex face, smooth on the straight or concave face 1 µm thick, urediniospores content were soft orange-colored (Laundon and Waterston, 1964). Therefore, the total number of urediniospores collected per hour, per day, and per month was obtained.

2.2.2 Passive spore trap (PST)

The Passive Spore Trap (Martinez Bracero et al., 2018) is a tubular system that has a slide with an adhesive (Vaseline with hexane 1:5) inside to collect the aero particles by impact. The dimension of the coated area of the slide was 60 × 25 mm. This system has a wind vane that rotates upwind (Fig. 1B). Eight PSTs were placed in Pacho Viejo and ten PSTs in Teocelo. The PST were placed at different heights from ground level (1.5, 3, 6, and 9 m), and the monitoring was continuous and carried out twice per month from January 2014 to September 2015, so the number of counted urediniospores was, every time, and accumulated from 15 days. At the end of the sampling, the slide was removed and transported to the laboratory for fixation with glycerine jelly stained with fuchsine and analyzed under a light microscope. The total number of urediniospores collected biweekly was counted and added together to obtain the monthly total of each trap. Mean values were obtained for every PST height.

2.2.3 Sedimentation spore sampler (SSS)

The Sedimentation Spore Sampler (SSS) is a modified type Durham trap (Durham, 1946). It consists of a plastic surface, on which slides covered by a light layer of Vaseline with hexane (1:5) were placed to impact the aero particles passively. The trap has a metal support that places it one meter above the ground, and they are protected from the rain by a plastic dome cover (Fig. 1C). Four SSSs were placed on May 10, 2014, which were left running for periods of 15 days, coinciding with the sampling of the PSTs. At the end of each sampling, the slides were disassembled and transported to the laboratory for fixation and analysis under a light microscope. The

Fig. 1 **a** Hirst-type spore trap (HST). **b** Passive spore trap (PST). **c** Sediment spore trap (SSS).

total number of urediniospores collected in each one was counted and added to obtain the average monthly total.

2.3 Determination of the incidence of the disease on the Pacho Viejo farm

The incidence of *H. vastatrix* in coffee cultivation in the town of Pacho Viejo was determined; for this purpose, 17 samplings were carried out on the farm (once a month) from March 2014 to September 2015. The method of Montes et al. (2012) was used to determine the incidence percentage. Zig-zag tours were carried out in the plot, and ten trees were randomly selected; ten branches from each were chosen, making 100 branches per lot. The total number of leaves and leaves with rust were counted and recorded for each branch. The incidence percentage was calculated as follows: Incidence % = (Total leaves with rust on 100 branches) × 100/total leaves in 100 branches. Additionally, a Spearman correlation test was realized to find relations between monthly incidence percentages and meteorological variables in Pacho Viejo.

2.4 Record of meteorological variables

Meteorological parameters were measured continuously (during all sampling periods) in both areas of study. Variables such as the average, maximum, and minimum temperature, accumulated precipitation, average and maximum wind speed, relative humidity, and leaf humidity were measured, analyzed, and associated with the number of urediniospores collected in each trap. Since temperature is a fundamental factor for *H. vastatrix* infection in the coffee plants, we analyzed the average temperature recorded with the portable meteorological station installed in Teocelo during 2014 and 2015 and the corresponding data obtained from a high-resolution reanalysis for both years (see below).

2.5 Description of ERA5-land

The European Centre for Medium-Range Weather Forecasts is producing an enhanced global dataset for the land component of the fifth generation of European ReAnalysis (ERA5; Hersbach & Dick, 2016), hereafter referred to as ERA5-Land. ERA5-Land provides important hourly variables of the energy and water cycles at 9 km spatial resolution, describing the evolution of these cycles over land consistently over the production period, which covers from 1950 to the present. Recently, Muñoz-Sabater et al. (2021) showed that ERA5-Land has a comparable performance with ERA5 describing the energy cycle variables, but ERA5-Land has an overall improvement of the water cycle compared to previous reanalyses. As these authors pointed out, although the time resolution is the same in both ERA5-Land and ERA5 (hourly), the increased spatial resolution of 9 km is the main advantage of ERA5-Land compared to ERA5 (31 km). These characteristics make ERA5-Land a valuable dataset to support land and environmental studies.

2.6 Statistical analysis

Normality tests were done to determine the distribution of all urediniospore counts data in each trap type. Because urediniospores counts had a non-normal distribution, a normalization of data (Ln) was done to perform parametric tests for the analysis of the results. ANOVA test ($p<0.05$) with a complementary Tukey´s test was used to compare urediniospores counts between traps and group means significantly different from each other. Pearson correlations ($p<0.05$) and a principal component analysis were performed to determine which environmental variables influence the release and transport of *H. vastatrix* urediniospores. The software used was IBM SPSS ver. 22.

3 Results

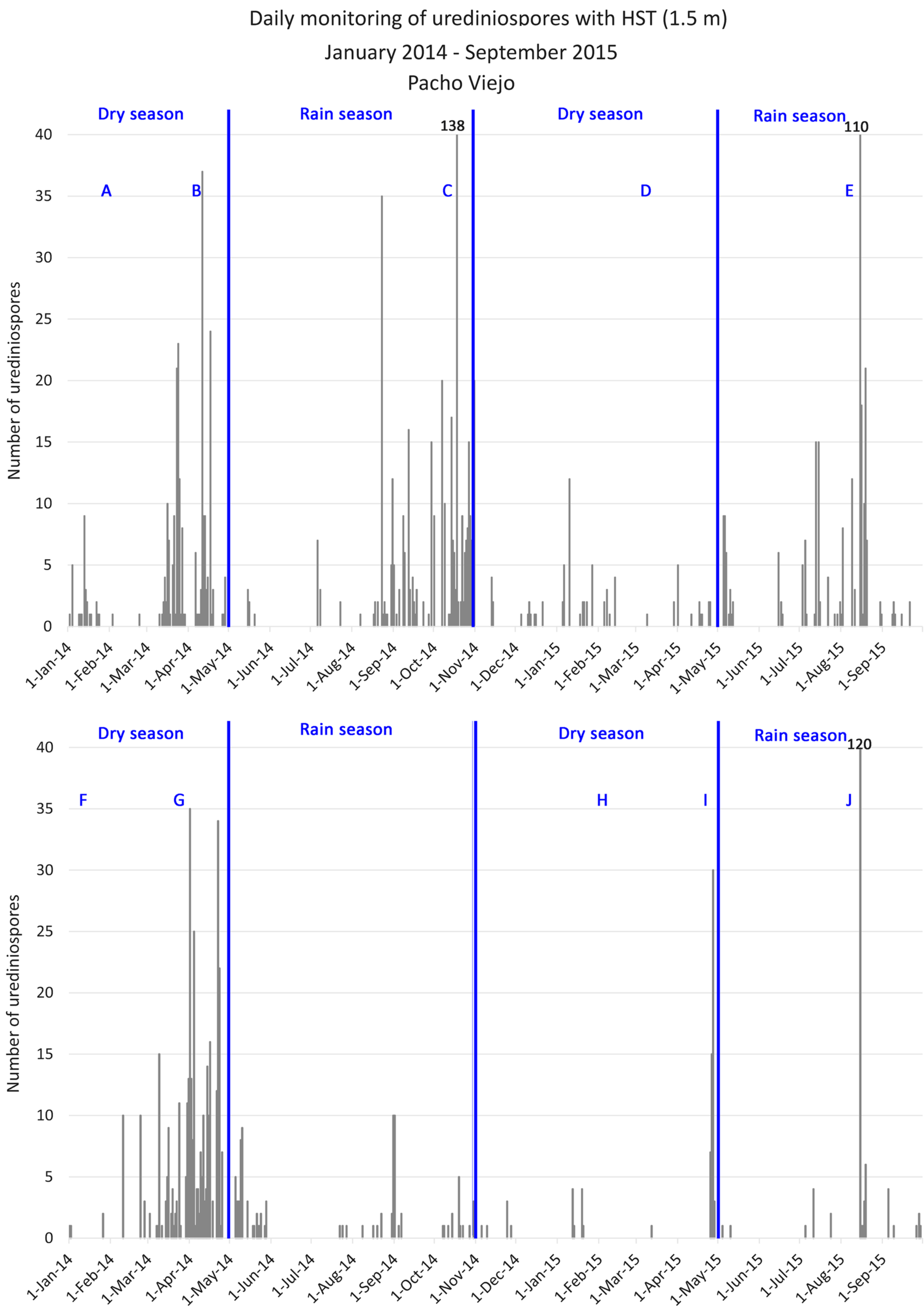
3.1 Daily airborne urediniospore monitoring with an HST sampler (1.5 m)

3.1.1 Pacho Viejo

From January to March 2014, low amounts of urediniospores were recorded in the air with the HST (Fig. 2A). However, an increase was obtained during March and April, reaching 37 urediniospores, collected on April 11, 2014 (Fig. 2B). Between August and October, the highest peaks of urediniospores were observed in the year, reaching a maximum of 138 spores on October 18, 2014 (Fig. 2C). For November and December 2014 and the first half of 2015, very low counts were recorded (Fig. 2D); however, they gradually increased in July and August, even reaching 110 urediniospores on August 15, 2015 (Fig. 2E). Nevertheless, a decrease was observed in September.

3.1.2 Teocelo

From January to February 2014, very low urediniospore counts were recorded (Fig. 2F). However, an increase was recorded from March 2014, reaching 35 urediniospores on April 1, 2014 (Fig. 2G). The number of urediniospores collected was low during the rest of the year (Fig. 2H). In 2015, only some point peaks were recorded: 30 urediniospores on April 27 (Fig. 2I) and 120 urediniospores on August 15, 2015 (Fig. 2J).


Daily monitoring of urediniospores with HST (1.5 m)
January 2014 - September 2015
Pacho Viejo
Dry season
Rain season
Dry season
Rain season
138
110
A
B
C
D
E
Number of urediniospores
1-Jan-14
1-Feb-14
1-Mar-14
1-Apr-14
1-May-14
1-Jun-14
1-Jul-14
1-Aug-14
1-Sep-14
1-Oct-14
1-Nov-14
1-Dec-14
1-Jan-15
1-Feb-15
1-Mar-15
1-Apr-15
1-May-15
1-Jun-15
1-Jul-15
1-Aug-15
1-Sep-15
Dry season
Rain season
Dry season
Rain season
120
F
G
H
I
J
Number of urediniospores

◂**Fig. 2** Daily counts of airborne *H. vastatrix* urediniospores collected in Pacho Viejo and Teocelo from January 1, 2014, to September 30, 2015

3.1.3 Punctual environmental conditions prevailing on selected days with the absence or presence of airborne urediniospores collected with HST (1.5 m) in Pacho Viejo y Teocelo

The punctual hourly records of the environmental conditions on selected days with the absence or presence of urediniospores are shown in Table 1. It was observed that conditions such as the high relative humidity of the environment (90–100%), mean temperatures less than 16 °C, and leaf humidity greater than 12 do not favor the dispersal of spores in the air (Table 1, Pacho Viejo A, D; Teocelo F, H). In contrast, conditions of lower relative humidity $< 80\%$, average temperatures greater than 19 °C, and leaf moisture < 7 favor the release and dispersal of spores in the air (Table 1, Pacho Viejo B, C, E; Teocelo G, I; J).

3.2 Monthly monitoring of airborne *H. vastatrix* urediniospores

3.2.1 Pacho Viejo

In Pacho Viejo, the distribution of airborne urediniospore counts collected with the HST, PST, and SSS during 2014 exhibits a bimodal distribution. Low concentrations which increase with time are evident from January–April, which decreases abruptly in May and June, and then rises again, reaching PST maximum values of urediniospores of 2563 at 1.5 m, 1664 at 3 m, 174 at 6 m, and 521 at 9 m and a SSS maximum value of 29,017 urediniospores. In the case of 1.5 m HST, it was observed that during January–April 2014, collected urediniospores counts were comparable to PST samplers, and then, as in the case of PST samples, the collected number diminished during May and June. The number of HST-collected urediniospores increased from July, reaching maximum values in October (322). Finally, the number of urediniospores collected by PST, SSS, and HST gradually decreased during the year's final months.

In contrast, in 2015, low concentrations of urediniospores were recorded during the first months. However, like the previous year, in August, a maximum of spores was presented in PST and SSS samplers, at the height of 1.5 m, 3,721 urediniospores were recorded, while at 3 m, it was 1,511, at 6 m, it was 338, and at 9 m, it was 300 urediniospores; with SSS, a maximum count of 29,823 were recorded. In this year, the maximum count collected with HST was also in August, with a peak of 194 urediniospores.

During eight months of sampling, a more significant number of urediniospores was presented in the PST traps placed at the height of 9 m than in those registered at 6 m; likewise, in April and November 2014, the PST traps located at the height of 9 m had a more significant number of urediniospores than those registered at 3 and 6 m, at the height of 1.5 m.

ANOVA test was performed to determine differences between all the samplers; there were significant differences only between SSS and the other traps ($p < 0.0001$). (Table 2).

3.2.2 Teocelo

As in the Pacho Viejo locality, a bimodal distribution was observed in urediniospore counts, although the number of urediniospores was notably lower than in Pacho Viejo (Table 3).

During 2014, a small maximum of spores occurred during March and April, decreasing towards May and June. Later, during August, using the PST sampler, a maximum of 92 urediniospores was collected at 1.5 m, 696 at 3 m, 159 at 6 m, and 128 at 9 m. Likewise, with the HST sampler, only 17 airborne urediniospores were collected. Towards the end of the year, a decrease in urediniospores was observed in the air.

In 2015, unlike the previous year, low concentrations of airborne urediniospores were recorded during February and March. Starting in April, an increase in the number of urediniospores was observed in Teocelo, registering between 12 and 50 spores collected with the PST sampler. With the beginning of the rainy season in May, a decrease in spore concentration was observed again. However, as of July, urediniospores increased considerably in the air than those recorded in the previous year. The spores collected with the PST sampler reached 3473 urediniospores at 1.5 m, 3536 at 3 m, 147 at 6 m, and 1808 at 9 m. Likewise, the airborne urediniospores collected with

Table 1 Meteorological conditions prevailing on selected days with the absence or presence of airborne urediniospores collected with HST (1.5 m)

	Pacho Viejo					Teocelo				
	A	B	C	D	E	F	G	H	I	J
Number of urediniospores	0	37	138	0	110	0	35	0	30	120
Date	25 Jan 2014	11 Apr 2014	18 Oct 2014	28 Feb 2015	16 Aug 2015	28 Jan 2014	01 Apr 2014	28 Jan 2015	27 Apr 2015	15 Aug 2015
Mean temperature (°C)	15	19	20	15	21	16	21	12.5	25	21
RH (%)	98	50	86	91	82	90	80	90	50	80
Wind (m/s) [Wind gusts (m/s)]	2	1 [6]	1	0.3	1 [5]	2	1.5	1	1	1.5
Wind direction	NE/NW	S-SW	S-SW	S-SW	N-NW	E	W	W	E	W
Moisture leaf (0 = dry to 15 = wet)	15	0	7	12	-	15	0	14	0–4	1
Collection time	–	00:00–07:00 h 12:00–18:00 h	16:00–17:00 h	–	00:00–02:00 h	–	02:00–09:00	–	00:00–09:00	00:00–10:00

the HST sampler maintained low urediniospore levels (131), similar to those registered in 2014 (17) during August. In September, the number of urediniospores in the air decreased again.

ANOVA test was performed to determine differences between the PST at different heights; There was only a significant difference between the 1.5 m PST and the 6 m PST ($p < 0.05$) (Table 3).

3.3 Comparison of PST urediniospores counts between Pacho Viejo and Teocelo

Teocelo total urediniopores counts were higher than Pacho Viejo, however, the temporal distribution was similar during all the sampling period, showing the maximum peaks in August of both years (Fig. 3).

3.4 Determination of the incidence of coffee rust disease in Pacho Viejo

From April 2014, a gradual increase in the disease incidence was observed, reaching 69.5% in November. Subsequently, coffee rust gradually decreased to a minimum of 14.5% in May 2015. As of July, *H. vastatrix* began to increase in incidence again, from 29.1% in July to 51.2% in September. The highest incidence of fungus was recorded from September to December 2015 (Fig. 4).

There were found positive correlations between incidence and relative humidity and leaf humidity. Negative correlations were found between mean temperature, maximum temperature, and mean wind velocity (Table 4).

3.5 Environmental conditions

3.5.1 Temperature

The average temperature recorded in January and December 2014 and January and February 2015 was below 16 °C, which is below the minimum threshold temperature that *H. vastatrix* requires for development. From March to October, the mean temperature is already within the favorable range for the germination of the fungus, approaching the optimum temperature for its development starting in April. It can be seen that the increase of temperature to one that is optimal for germination and the development of *H.*

Table 2 Monthly averages of airborne urediniospores collected at different heights of ground level with PST sampler, SSS sampler and number of urediniospores accumulated monthly from January 2014 to September 2015 with HST sampler, in Pacho Viejo

	1.5 m PST	3 m PST	6 m PST	9 m PST	Monthly average SSS	Monthly accum. HST
Jan-14	6	21	21	–	–	
Feb-14	22	34	7	–	–	29
Mar-14	110	74	7	43*	–	2
Apr-14	95	77	44	84**	–	110
May-14	1	24	1	0	8	108
Jun-14	0	19	2	2	381	6
Jul-14	373	438	0	370*	5790	0
Aug-14	2563	1664	174	521*	29,017	12
Sep-14	181	109	48	9	1083	63
Oct-14	1049	346	56	215*	9621	71
Nov-14	420	57	57	62**	792	322
Dec-14	0	10	0	0	36	6
Jan-15	34	12	0	11	17	9
Feb-15	0	0	0	0	0	31
Mar-15	0	0	0	0	0	10
Apr-15	5	4	0	0	31	3
May-15	141	2	0	6	231	14
Jun-15	87	6	28	9	879	32
Jul-15	1123	654	122	125*	11,413	9
Aug-15	3721	1511	338	300	29,823	54
Sep-15	543	116	14	53*	4345	194
ANOVA	AB	B	B	B	A	B

*Number of airborne urediniospores collected at a height of 9 m (more spore counts than collected at a height of 6 m)

**Number of airborne urediniospores collected at a height of 9 m (more spore counts than collected at heights of 3 and 6 m)

ANOVA: The ANOVA test was performed with the transformed data (Ln). According with additional Tukey test, count means between traps that do not share a letter are significantly different from each other ($p < 0.0001$)

vastatrix results in a greater count of urediniospores (Fig. 5).

The first months of 2015 were colder than in 2014, with the temperature decreasing from 17 °C to approximately 14.5 °C. That condition resulted in a significant decrease of 2.5 °C in February 2015. This decrease, registered by the meteorological stations, was consistent with the data obtained from the ERA5 reanalysis (Fig. 6, dotted lines). Moreover, based on the reanalysis data, it was possible to determine that the temperature behavior was not local but instead was part of a regional cooling pattern, which covered much of the Mexican southeast during the first months of 2015 (Fig. 7).

3.5.2 Relative humidity

Relative humidity was favorable for the germination and development of the fungus throughout the study period, with an average of 60%.

3.5.3 Accumulated precipitation

In May and June 2014, a decrease was observed in the number of urediniospores collected compared to the previous months at the beginning of the rainy season. The registered rainfall was 507.82 mm in Pacho Viejo and 477.06 mm in Teocelo.

However, in July and August, the amount of rainfall decreased in Pacho Viejo and Teocelo (185.49 and 182 mm, respectively), and it was in this period, the highest concentration of urediniospores was recorded in both locations in 2014. In September of that year, as precipitation increased, a gradual decrease in the concentration of urediniospores collected was observed. For November and December, after the rainy season, the number of urediniospores decreased in both locations. In the first months of 2015, an accumulated rainfall was more significant than in 2014 in Pacho Viejo and Teocelo, especially in March (319.1 mm, 161.5 mm, respectively). The increase in precipitation coincided with a decrease

Table 3 Monthly averages of airborne urediniospores collected at different heights of ground level with PST sampler and number or urediniospores accumulated monthly from January 2014 to September 2015 with HST sampler in Teocelo

	1.5 m PST	3 m PST	6 m PST	9 m PST	Monthly Accum. HST
Jan-14	0	0	0	6*	4
Feb-14	0	0	3	2	23
Mar-14	44	17	14	44**	90
Apr-14	16	23	27	207**	240
May-14	1	7	1	38**	46
Jun-14	0	1	0	0	0
Jul-14	69	44	72	14	3
Aug-14	92	696	159	128	17
Sep-14	196	66	39	37	13
Oct-14	182	416	80	109*	16
Nov-14	121	126	0	20*	6
Dec-14	27	31	32	8	0
Jan-15	65	28	0	25*	10
Feb-15	0	0	0	0	0
Mar-15	5	5	1	2*	1
Apr-15	43	50	6	12*	55
May-15	75	50	0	0	2
Jun-15	193	230	10	10	0
Jul-15	3473	3536	147	1808*	7
Aug-15	2213	3372	200	2469*	131
Sep-15	99	98	0	48	9
ANOVA	A	AB	B	AB	AB

* Number of airborne urediniospores collected at a height of 9 m (more spore counts than collected at a height of 6 m)

** Number of airborne urediniospores collected at a height of 9 m (more spore counts than collected at heights of 3 and 6 m)

ANOVA: The ANOVA test was performed with the transformed data (Ln). According to additional Tukey test, count means between traps that do not share a letter are significantly different from each other ($p < 0.05$)

in urediniospores for the same period, concerning 2014. In May and June 2015, the precipitation values recorded for both locations were lower than in 2014. However, although the accumulated precipitation was high during July, August, and September, airborne urediniospore concentrations remained high. Although a more significant presence of urediniospores was observed in the rainy season, when rainfall is abundant, the air concentration decreases (Fig. 8 a, b).

3.5.4 Wind

In Teocelo, although there was a significant increase in the number of airborne urediniospores collected from 2014 to 2015, the daily wind patterns in July and August of both years were comparable in both magnitude and direction. The wind field is dominated by the zonal component in this location, presenting only slight differences between these years. During the night and early morning, the wind regime shows winds towards the sea (V10), which changes to prevailing winds from the sea in the rest of the day (U10), with maximum values occurring between 1:00 pm and 2:00 pm (Fig. 9).

In 2014 and 2015, similar wind conditions prevailed in July and August. However, the maximum value of spores, caught at the height of 9 m, occurred in August 2015. This value is larger than that recorded in 2014 by a factor of 10. Considering that stronger winds can transport a larger quantity of urediniospores, no wind events in 2015 explain this utterly different behavior. At the height of 9 m, the prevailing winds represent the only physical process that carries urediniospores toward our samplers, so a possible dynamic explanation for the higher concentrations recorded in August 2015 can be the convergence of the wind field. Unfortunately, the complex terrain in Teocelo implies a high spatial resolution wind to explore this possibility. There are no wind products with this characteristic, and it is necessary to use an adequate atmospheric numerical model for this task, which is beyond the scope of this work.

3.6 Correlations with environmental variables

In both localities, it is observed some correlations (Pearson, $p < 0.05$) between the number of collected urediniospores and mean temperature, max temperature, min temperature, wind velocity, and relative humidity (Tables 5 and 6).

3.7 Principal component analysis

Principal Component Analysis showed that in Pacho Viejo was not a clear grouping of meteorological variables and the urediniospores counts. Only in Teocelo, the spore counts obtained with the PST traps were related to the minimum temperature.

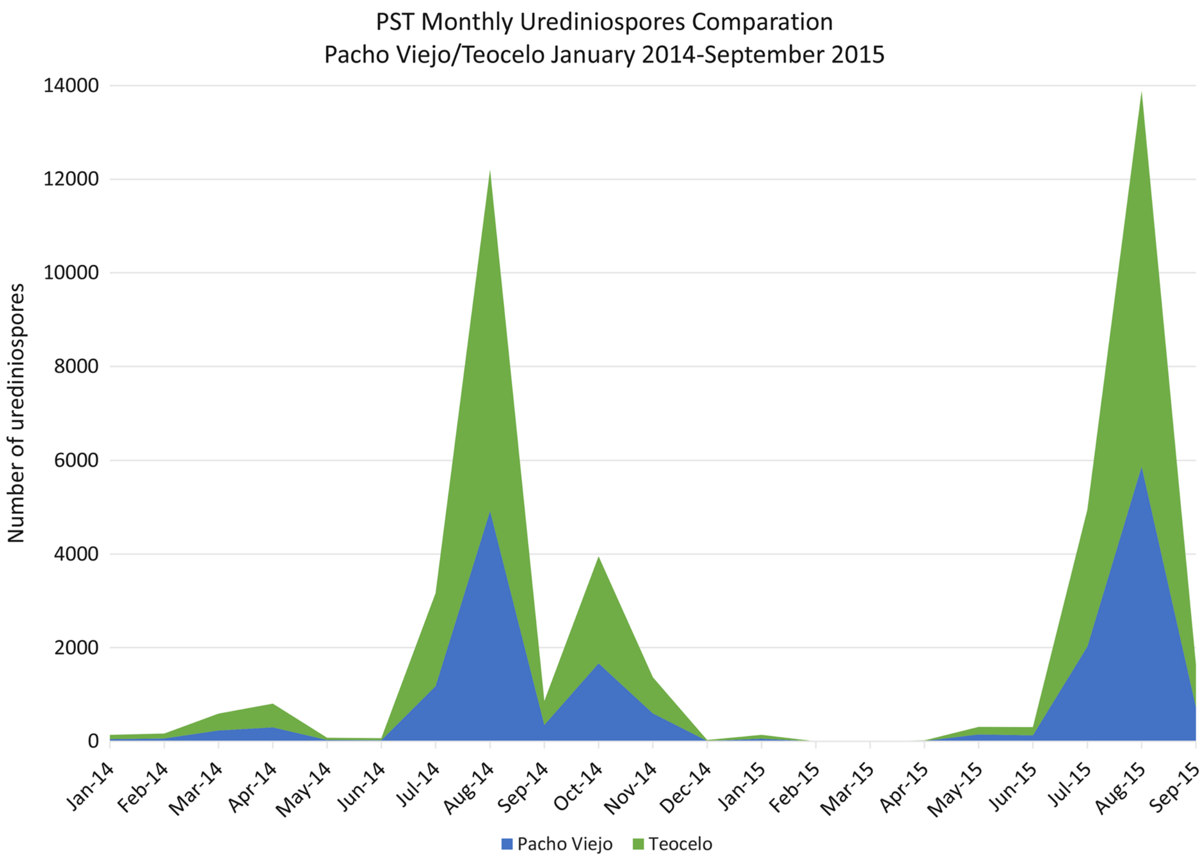


Fig. 3 PST monthly urediniospores comparison of Pacho Viejo and Teocelo from January 2014 to September 2015

4 Discussion

The punctual observations of the daily monitoring of urediniospores with the TEH in both locations, taking into account the days with the highest number of urediniospores collected, showed that the environmental conditions that prevailed during the presence of urediniospores in the air were: 1. Average temperatures between 19 and 23 °C, which coincides with the range of favorable temperatures for the development of the fungus described by Nutman et al. (1963), who determined that the optimal temperature for germination is 21 °C, with an interval between 15.5 and 28.5 °C. 2. Relative humidity less than 85% and wind gusts greater than 3 m/s, as described by Becker (1975) and Boudrot et al. (2016), who collected a greater number of airborne urediniospores in conditions of low relative humidity and the presence of wind gusts greater than 2 m/s which favor the release of urediniospores. 3. The degree of humidity on the leaf surface was less than seven since a higher degree of humidity prevents the release of urediniospores into the air.

Based on environmental conditions recorded during the airborne urediniospore collection periods with PST, SSS, and those accumulated with HST, the relationship of the environmental variables with the development and release of urediniospores was observed. A similar temporal distribution of the presence of airborne urediniospores collected was observed in the three types of traps in both localities, although quantitatively different: SSS obtained a significantly higher collection than PST and HST; as well as Teocelo had higher urediniospores counts than Pacho Viejo.

Low amounts of urediniospores (< 60) were collected from January to February in both years, both in the PST placed at heights of 1.5, 3, 6, and 9 m and in the HST. This is related to the recorded temperatures below 16 °C, which is lower than the minimum

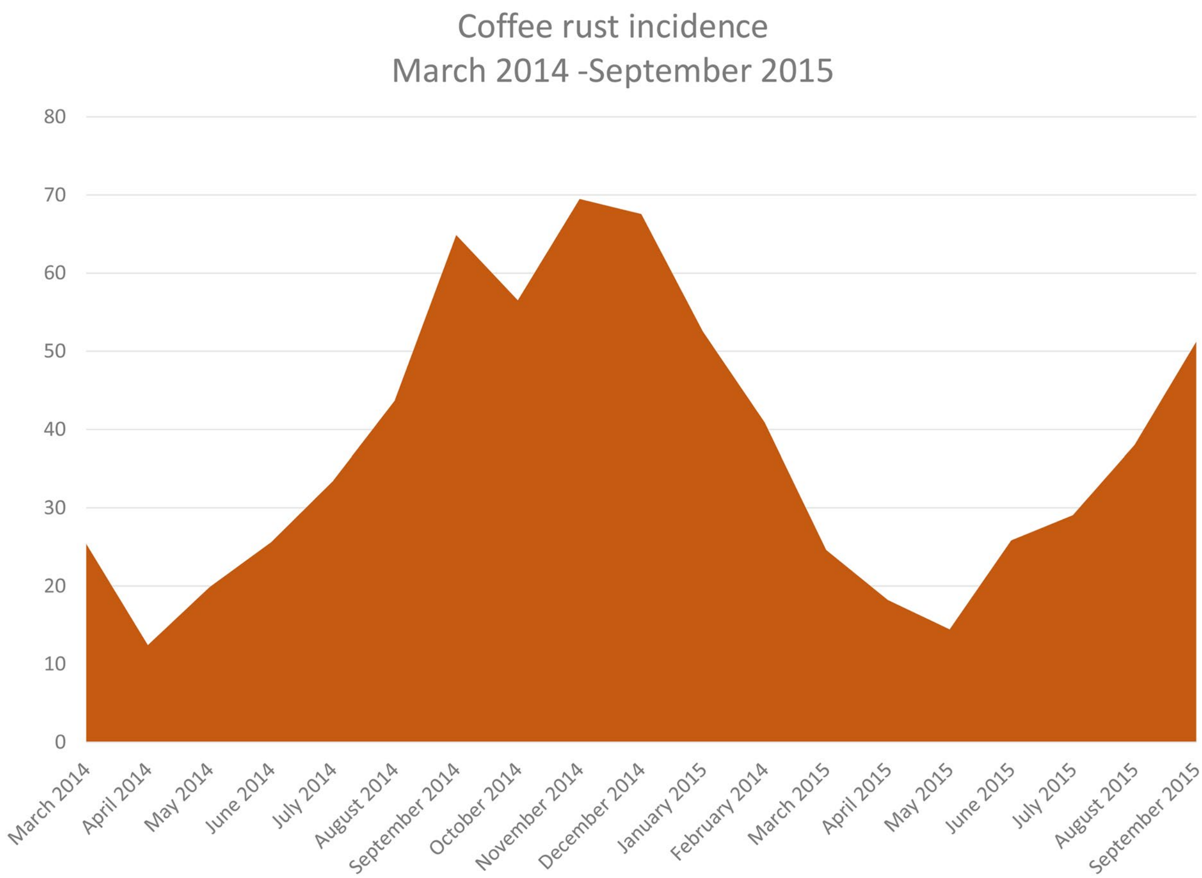


Fig. 4 Coffee rust incidence in Pacho Viejo 2014–2015

Table 4 Spearman correlations between coffee rust incidence and environmental variables

	Incidence	Mean Temp	Max Temp	Min Temp	RH	Mean Wind Vel	Max Wind Vel	Accum Precipitation	Leaf Moisture
Incidence	Spearman correlation	−.511*	−.623**	−.097	.556*	−.484*	−.323	.221	.505*
	p	.026	.004	.694	.013	.036	.177	.363	.027

*$p < 0.05$

**$p < 0.01$

threshold for the germination and development of this fungus (Nutman et al., 1963). However, low temperatures, followed by favorable humidity and temperature, have also been reported to increase the germination capacity of *H. vastatrix* urediniospores (Nutman et al., 1963). For this reason, it is interesting to note that the cold winter of the first months of 2015 played a fundamental role in favoring the infection process and the spectacular increase in spores as that which occurred in Teocelo in 2015 and is observed in Principal Component Analysis where the minimum temperature is closely linked to the number of urediniospores collected and the strong negative correlations between temperature and coffee rust incidence. During March and April 2014, the number of collected urediniospores gradually increased, which was associated with an increase in temperature above the minimum development threshold (19 °C), coupled with

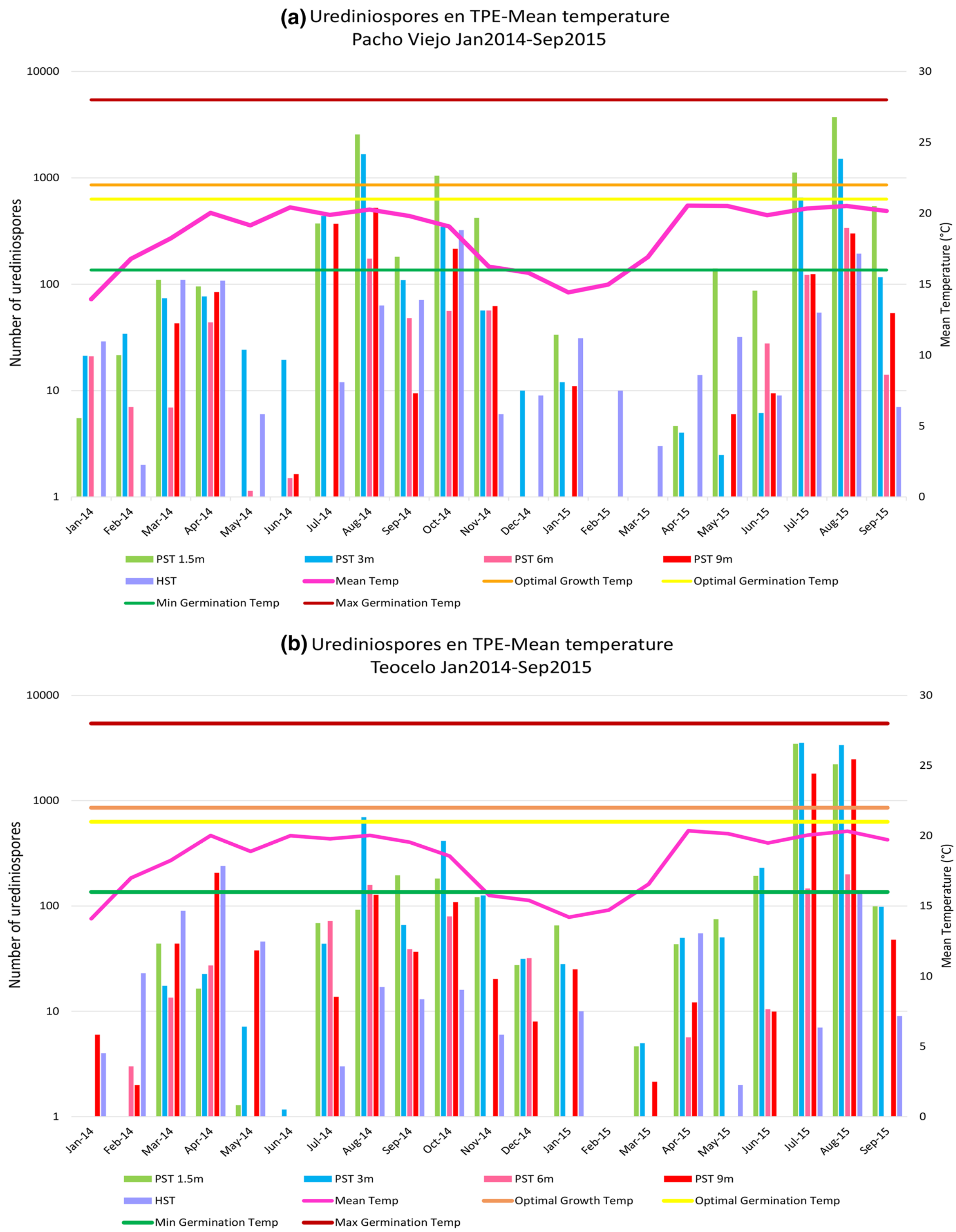


Fig. 5 Mean temperature and collected urediniospores with PST and HST samplers from January 2014 to September 2015 in Pacho Viejo (**a**) and Teocelo (**b**)

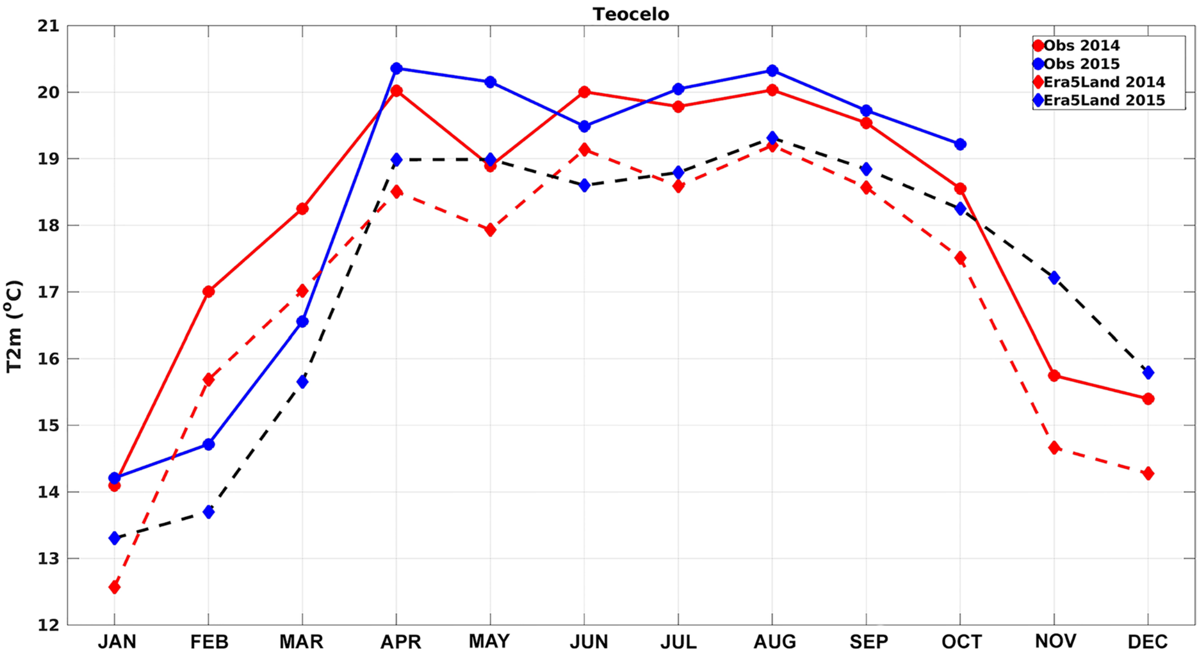


Fig. 6 The mean temperature recorded in Teocelo during 2014 and 2015 and Era5 reanalysis for the same years

light rains in late February and during March (accumulated precipitation for the period of 25–60 mm), which allowed the germination and release of urediniospores during April. This was because *H. vastatrix* requires a month after germinating to form new pustules and release the urediniospores (latency period), as reported by Rivillas et al. (2011). However, in March 2015, urediniospore records were null; this was due to an extraordinary increase in precipitation in the region, which reached values of up to 197 mm above the monthly typical (58 mm) for this region (CONAGUA-SMN, 2015), causing the wet deposition of urediniospores. In this way, the negative effect that abundant rainfall can have on the dispersal of urediniospores in the air was demonstrated. In mid-May and June of both years, the average temperature rose to between 20 and 21 °C, which, together with the beginning of the rainy season (rainfall above 300 mm per period), provided the temperature conditions and adequate water for the germination and development of the fungus. Although the collection of urediniospores decreased during this period due to wet deposition, the incidence of rust on coffee trees began to increase from these months in Pacho Viejo. A month later, in late July and August, the mid-summer drought (MSD) phenomenon occurred. This condition, present only in Mexico and some Central American countries, consists of an increase in temperature and a decrease in rainfall, which causes a bimodal distribution in annual precipitation, with maximums in June and September–October (Magaña et al., 1999). Thus, the increase in temperature close to the optimum for development (21–22 °C) and the decrease in precipitation (30–100 mm per period) resulted in the highest record of urediniospores collected with the PST and SSS in both years, reaching average values during August 2015 of up to 29,823 urediniospores in SSS at 1 m in Pacho Viejo as well as the maximum count found in 9 m PST, by 2469 urediniospores in Teocelo, Therefore, this period was crucial for the release, transport, and spread of the disease in this region of Veracruz. During September, October, and November 2014, and September 2015, high amounts of urediniospores were recorded, despite the rain increasing again, which indicated that this period was essential for development after the maximum dispersal period of *H. vastatrix*. This was reflected in a rapid increase in the incidence of disease from September, one month after the highest peaks of airborne urediniospores were collected, which coincides with the latency period of *H. vastatrix*. The development of this disease in the crop

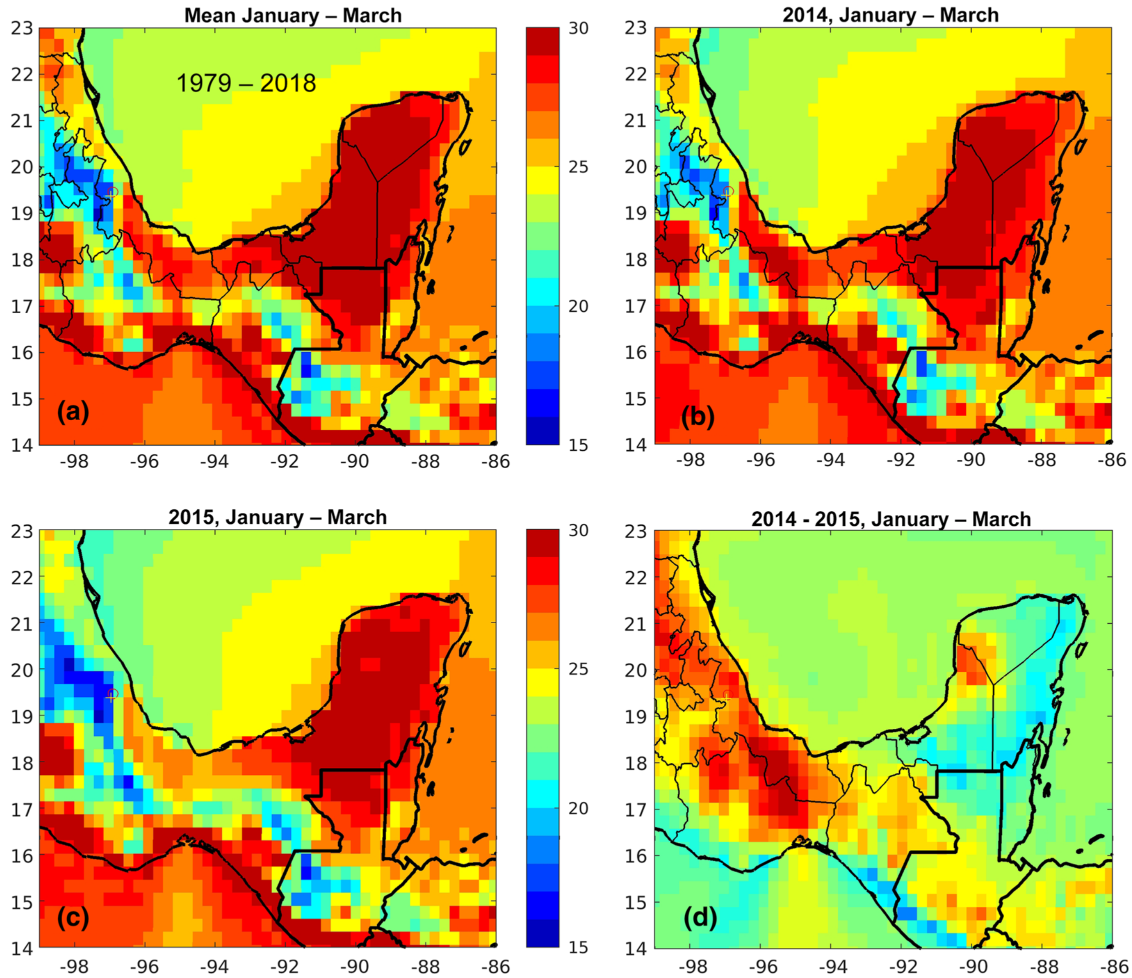


Fig. 7 Mean temperature values from January to March. Average temperature values for the period 1979–2018 (**a**). Mean temperature values for the years 2014 and 2015: (**b**), and (**c**). We estimated temperature anomalies for 2015 concerning 2014 by subtracting the mean temperature values from 2015 from 2014 (**d**)

lasted until November when the temperature again fell below the minimum for germination and development. Principal component analyses and some correlations (Pearson $p < 0.05$) showed that temperature is the determining factor for the development and transport of the fungus since the presence of urediniospores is almost nil when it has values close to or below 16 °C. Conversely, when the optimum germination temperature is approached, it increases significantly. The daily relative humidity was greater than 60% throughout the year, which is always favourable for the development and germination of the fungus. However, when it is greater than 90%, the release and dispersal of urediniospores by the wind decreases significantly as it results in negative correlations between RH and urediniospores counts. Likewise, leaf moisture with values close to 15 (presence of liquid water) is favorable for the start of urediniospore germination, as reported by Nutman et al. (1963), but not for its release and dispersal by the wind, since, for this, conditions with lower leaf humidity are required (< 10). However, it was observed that both conditions could occur on the same day due to dew formation, as reported by López-Bravo et al. (2012) and Avelino et al. (2015). Moderate precipitation (30–100 mm per period) plays a fundamental role in the germination and development of the fungus. However, high precipitation values before the period of greatest

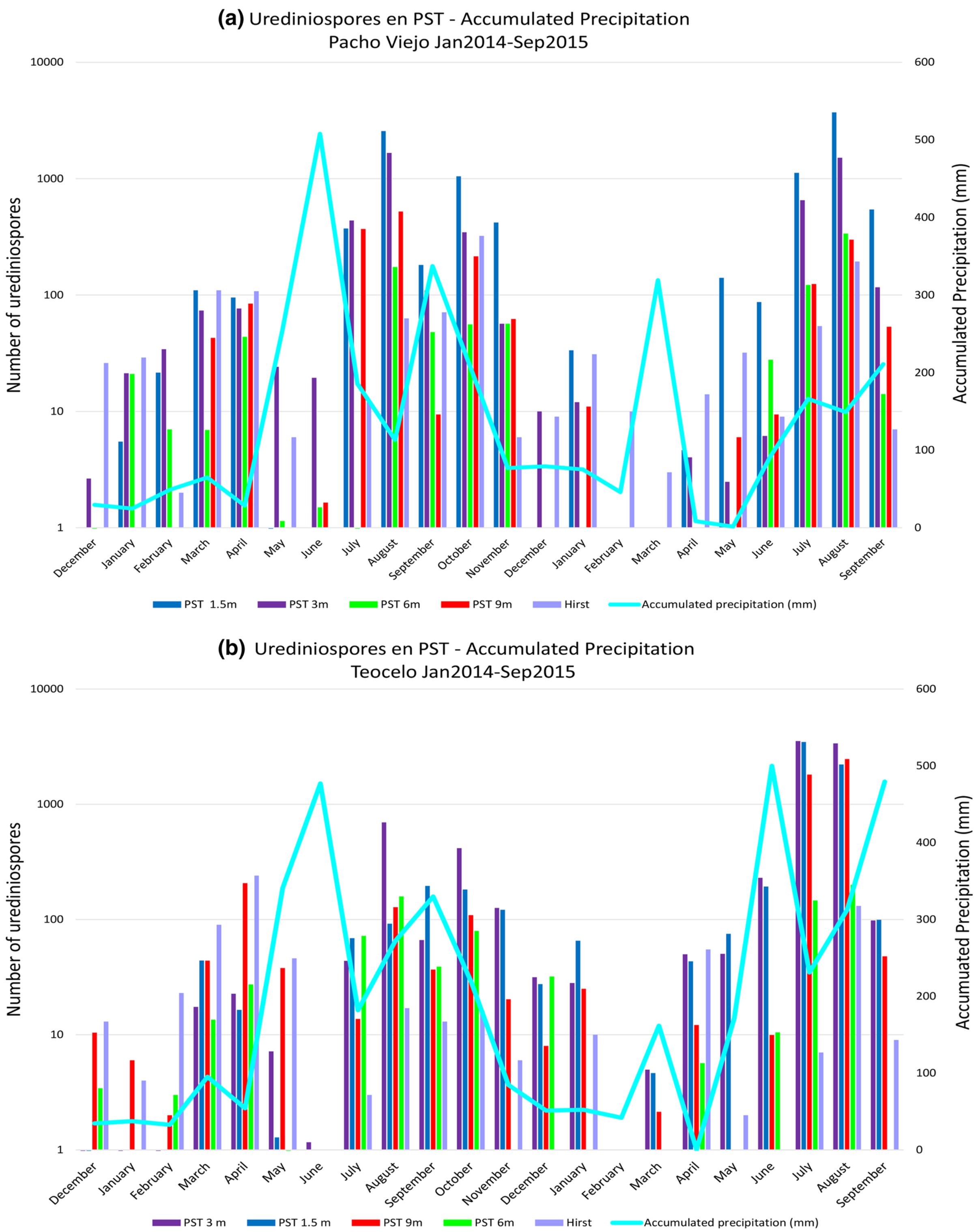


Fig. 8 Accumulated precipitation and counts of urediniospores collected with PST and HST from Pacho Viejo (**a**) and Teocelo (**b**) from January 2014 to September 2015

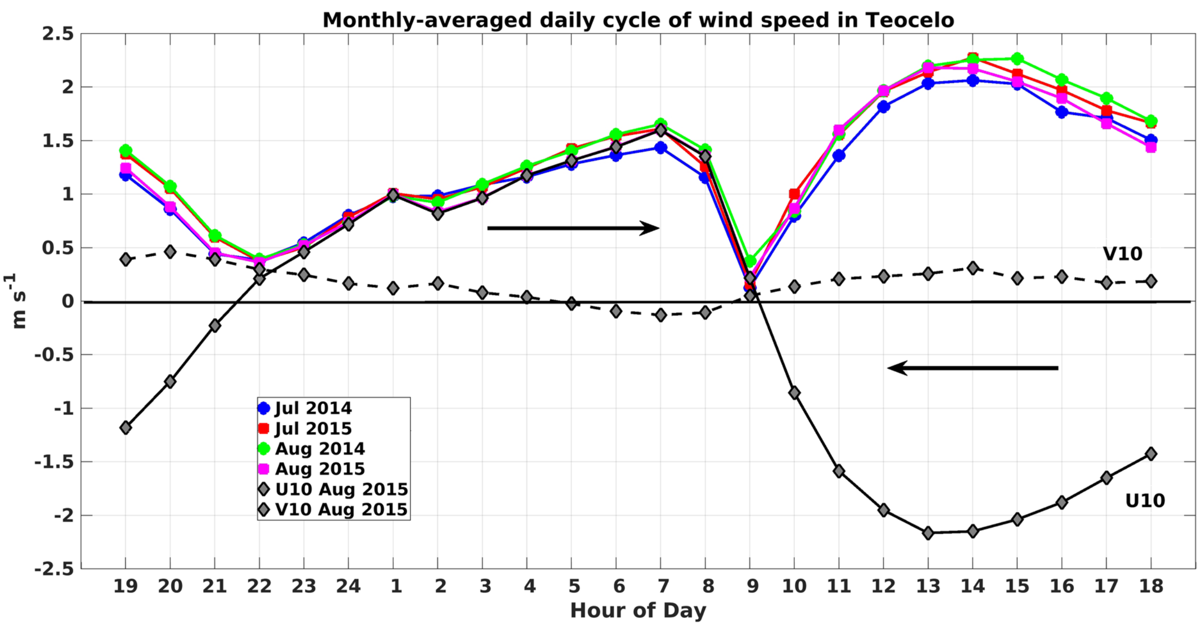


Fig. 9 Wind regime during Teocelo July and August from 2014 and 2015

Table 5 Pearson correlations ($p<0.05$) between number of collected urediniospores and environmental conditions in Pacho Viejo

	Mean temp	Max temp	Min temp	HR	Mean wind Vel	Max wind Vel	Accum precipitation	Leaf moisture
PST 1.5 m	0.367	−0.259	0.437	−0.059	0.132	−0.525*	0.069	0.230
PST 3 m	0.342	−0.309	0.276	−0.304	0.557*	−0.013	0.186	0.174
PST 6 m	0.187	−0.274	0.104	−0.275	0.074	−0.400	−0.276	0.088
PST 9 m	0.107	−0.056	0.009	−0.484	0.389	−0.153	−0.396	−0.057
SSS_1m	0.292	−0.431	0.229	−0.695*	0.242	−0.477	−0.559	0.020
HST	0.314	−0.009	0.292	−0.391	0.198	−0.103	−0.136	0.113

*$p<0.05$

**$p<0.01$

Table 6 Pearson correlations between number of collected urediniospores and environmental conditions in Teocelo

	Mean temp	Max temp	Min temp	HR	Mean WINDVEL	Max wind Vel	Accum precipitation	Leaf moisture
PST 1.5 m	0.393	−0.210	0.435	−0.021	0.174	−0.079	0.330	−0.279
PST 3 m	0.375	−0.203	0.319	−0.124	0.214	−0.135	0.211	−0.245
PST 6 m	0.451	−0.141	0.514	−0.108	0.279	−0.090	0.187	−0.292
PST 9 m	0.578**	0.105	0.405	−0.187	0.347	0.023	0.352	−0.224
HST 1.5 m	0.346	0.506*	0.031	−0.481*	0.390	0.074	−0.037	−0.365

*$p<0.05$

**$p<0.01$

incidence (> 300 mm) cause the washing of urediniospores into the soil, which prevents its dispersal through the wind and its fixation on the leaves. The analysis of the magnitude and direction of the wind is not associated with the increase and occurrence of peaks in the amounts of urediniospores collected during July and August since there are no significant differences concerning convergence-divergence phenomena that could influence it. In previous work, we reported that the convergence of the winds was an essential factor for the temporary increase in pollen concentrations in Mexico City (Calderon et al. 2018). However, this process seems to be marginal in Teocelo, since it only registered an important period of convergence at the end of August 2015. However, some correlations (Pearson < 0.05) between counts of the 1.5 m and 3 m PST and wind velocity can be related to turbulences into the crop.

A significantly greater number of urediniospores was collected in the SSS placed at 1 m (ANOVA $P < 0.05$), indicating the importance of local transport by wet and dry deposition, as well as the splashing of water droplets in rainy seasons, as reported Nutman et al. (1960) and Boudrot et al. (2016). However, there were not found significative differences between PST at different heights, which means that urediniospores spatial distribution at these stages are homogeneous. Urediniospores were collected in PST 1.5 m and PST 3 m, despite registering wind speeds of less than 1 m/s; this was due to intermittent turbulence movements inside the crop, since the canopy surface is irregular, generating thermal differences that can remove and re-suspend the urediniospores, favoring turbulences. This was reported with the urediniospores of *Puccinia graminis* (Sache, 2000), as well as by the action of rain splashing, reported Boudrot et al. (2016), for the collection of *H. vastatrix* urediniospores; however, the records obtained from PST urediniospores, both at 6 and 9 m, suggest that urediniospores can be released and transported at high altitudes, even above the canopy of a culture of traditional polyculture, therefore enabling them to be transported over long distances, even in shady conditions. This was also observed in periods where the PST at 9 m showed counts greater than PST 6 m and even than PST 3 m and the punctual counts of urediniospores in periods where wind gusts were greater than 5 m/s. This fact could indicate that urediniospores collected above the canopy could come from another source and even have the potential to travel long distances, as reported by Bowden et al. (1970) in a study that showed the transatlantic air transport of *H. vastatrix* urediniospores from Angola to Bahia, Brazil in 1970 (Brown & Hovmøller, 2002). This was in contrast to that which was recently reported by Boudrot et al. (2016), who suggest that wind gusts did not affect shaded conditions because the canopy blocked the wind. Likewise, it has already been demonstrated that the morphological and structural characteristics, such as proteins in the wall of the urediniospores of *H. vastatrix* (β-glucomannans of hydrophobic nature), are quite similar to those of *Puccinia graminis* f. sp tritici and *Uromyces phaseoli,* which are widely recognized for their ability to transport distances (Leal et al., 1983).

No significant differences were found between HST and PST urediniospores counts, so a cheaper and more extensive PST monitoring in crops can be done, collecting periods could be adjusted to the crop needs and the availability of the staff. A more significant number of urediniospores were collected with the SSS concerning the 3 m, 6 m, and 9 m PST, but no in the case of the 1.5 m PST (ANOVA $p < 0.05$), therefore it is needed additional studies at different heights to determine if SSS has a significant capacity of collection.

The monitoring of these pathogens in the atmosphere, as well as the generation of knowledge of how biological and meteorological factors and events can modulate their transport on a small and large scale, could be an excellent tool for making future forecasts of the dispersal of plant pathogens that will allow effective quarantine measures to be established (Schmale & Ross, 2015), as well as in the climatic change context, where the temperature increase could favor the pathogen dispersal and boost the incidence of this disease in México as suggested by Castillo et al. (2020). The dispersal pathogens in the atmosphere comprise complex processes that are interconnected, and only their knowledge will allow the comprehensive management of them.

5 Conclusions

Punctual observations of the daily monitoring of urediniospores with the TEH showed that the environmental variables that influence liberation and transport of urediniospores in the air are: (1) average temperatures between 19 and 23 °C; (2) relative humidity less than 85%; (3) mean wind velocity of 1 m/s with wind gusts greater than 5 m/s; c) a high degree of humidity on leaves.

The mid-summer drought (MSD) causes an increase in temperature and a decrease in rainfall, which provides more favorable environmental conditions for the release, transport, and spread of the disease in this region of Veracruz.

Low temperatures, followed by favorable humidity and temperature, increase *H. vastatrix* urediniospores capacity since the winter's cold winter of the first months of 2015 played a fundamental role in favoring the infection process and the spectacular increase in spores that occurred in Teocelo in 2015.

The wind magnitude and direction analysis are not associated with the increase and occurrence of peaks in the amounts of urediniospores collected during July and August.

Higher urediniospores counts that were observed in punctual observations with wind gusts greater than 5 m/s, and the fact that urediniospores reached heights in the air of up to 9 m (above the canopy) in coffee crops suggest that wind can carry them long distances.

The monitoring of these pathogens in the atmosphere, as well as the generation of knowledge of how biological and meteorological factors and events can modulate their transport on a small and large scale, could be an excellent tool for making future forecasts of the dispersal of plant pathogens that will allow effective quarantine measures to be established.

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