CLIMATE, POWDERY MILDEW, SAINFOIN RESISTANCE AND YIELD

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SUMMARY

Associations between dry matter yield (DM), 120 powdery mildew epidemics, six climatic variables, and resistance index were assessed during three growing seasons in 40 sainfoin accessions. In contrast to a two-year greenhouse study, powdery mildew developed on all sainfoin accessions in field experiments. During three growing seasons, plant reactions to powdery mildew varied by accession and study year. Only one accession, Oshnavieh, was rated tolerant to powdery mildew. According to contingency and correspondence analyses, high DM yield in sainfoin crops corresponded to 17-23 days with average relative humidity (RH) below 50%, 13 days with maximum temperatures above 25°C, 4-7 days with average temperatures within 15-20°C and RH above 50%, powdery mildew severity lower than 40%, and 0-3 mm rainfalls during four weeks before disease assessments. Greater disease severity (>40%) was associated with lower DM yield levels (≤0.150 t/ha), fewer (12) days with average RH below 50%, 23-28 days with maximum temperatures above 25°C, no exposure to daily maximum temperatures above 35°C, 14 days with average temperatures within 15-20°C and RH above 50%, fewer (2-4) days with average temperatures within 20-25°C and RH below 50%, and total rainfall as high as 13 mm. Such field-scale epidemiological findings provide useful information to develop accurate predicting models for sainfoin powdery mildew.

Keywords: *Leveillula taurica*, *Onobrychis sativa*, weather.

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INTRODUCTION

Sainfoin (*Onobrychis* spp.) is a leguminous perennial herb grown in Asia, Europe and western North America (Frame, 2005). This forage crop is cultivated on irrigated and rainfed lands in Iran for animal consumption. Sixty out of the 100 worldwide known species of this forage crop have been found in Iran (Mozafarian, 2007). Sainfoin is an important crop in the light of a good adaptation to alkaline soils and semi-arid regions, improvement of protein digestion by reducing animal bloat, ability to fix nitrogen, tolerance to low phosphorus content of soil, and usefulness in honey production (Maurice *et al.*, 1985). Iranian farmers commonly grow sainfoin mixed with alfalfa to benefit from the above-mentioned advantages. However, productivity in the main sainfoin growing regions is threatened by *Leveillula taurica* (namorph *Oidiopsis taurica*) which causes powdery mildew disease (Majidi, 2010). The reduction of forage yield at the second and third harvests during the growing season has restricted the cultivation of sainfoin in Iran and in Zanjan province. Although environmental conditions, air temperature and relative humidity (RH) in particular have been reported as the most commonly influential factors on the development of mildews by *L. taurica* (Guzman-Plazola *et al.*, 2003; Elad *et al.*, 2007; Jacob *et al.*, 2008; Brand *et al.*, 2009), the disease-environment-sainfoin interplay at field scale is little understood.

In Israel, Elad *et al.* (2007) found that severe infections by *L. taurica* on sweet pepper leaves occurred at 15 to 20°C in commercial greenhouses. They also determined a negative correlation of disease severity with lengthy periods of temperatures >25°C (Elad *et al.*, 2007). In California, temperatures of ≥30°C and RH levels as low as 20-40% inhibited tomato mildew development and the rate of disease progress was higher at 20°C than at 25°C, and at RHs within 50-70% (Guzman-Plazola *et al.*, 2003). In controlled environments, tomato powdery mildew did not develop at 28°C (Jacob *et al.*, 2008) and was more severe when the daily temperature varied within 15-25°C in comparison with the 10-20°C range, and when the minimum RH was 50% compared to 85% (Reuveni and Rotem, 1973). Severity of tomato powdery mildew was correlated negatively with temperatures within 5-15°C during four weeks before disease evaluation (Jacob *et al.*, 2008). Although a predictive model was developed based on microclimate data collected in 1993 and 1994 from a total of five tomato greenhouses in California (Guzman-Plazola *et al.*, 2011), further validation of its discriminant function to concisely rank climatic events favorable to powdery mildew epidemics in a larger number of cultivars and under diverse environmental conditions is still required. Because previous studies relied on greenhouse assessments of *L. taurica* epidemics, the field-scale epidemiological basis of the disease in interaction with weather patterns remains unknown.

Moreover, environmental conditions could also affect the morphological and agronomical properties, in particular dry matter yield in Spanish sainfoin crops (Delgado *et al.*, 2008). However, the interaction among environment, powdery mildew, and sainfoin yield is little investigated. In addition to fewer flowers and lower yields in powdery mildew-affected peppers, leaf shedding was considered as a damage indicator and increased following long periods of temperatures > 20°C and < 13°C, and RHs < 75% (Elad *et al.*, 2007). Therefore, the interaction of productivity with environmental conditions in a mildew-sainfoin pathosystem deserves consideration.

The development of a plant disease epidemic depends on the presence of an aggressive pathogen, a susceptible host plant, and favorable environmental conditions. All these three aspects of the mildew-sainfoin-climate interaction have been summarized into a number of descriptors in the present work.

MATERIALS AND METHODS

The purpose of this study was to identify climatic and plant factors conducive to the development of powdery mildew epidemics and subsequent reductions in sainfoin yield. To achieve these goals, two closely related experiments, consisting of a greenhouse study (2008-2009) and a separate field study (2009-2011) were performed on 40 sainfoin accessions in the Zanjan province of Iran. This region has a cold semi-arid climate, with a hot and dry season from June to September. The normal growth season of sainfoin, which is commonly cultivated as an alfalfa-sainfoin mixture in Zanjan, involves seeding in autumn (October) or early spring (April) and harvesting at three times in late spring (June), mid-summer (August) and early autumn (September).

To conduct the greenhouse study, four pots including three replicate treatment pots and one control pot were planted for each sainfoin accession. Seed of 40 accessions of *Onobrychis sativa* was obtained from the Research Institute of Forests and Rangelands, Tehran, Iran. Thus, 160 pots (4 × 3 × 4 cm), each containing three sainfoin plants, were prepared and watered as required. To prevent soil-borne pathogens, the pot soil as a mixture of field soil and compost (1:1) was autoclaved at 121°C for 20 min. Naturally infected plants covered with powdery mildew were collected from sainfoin producers' farms to be used as inoculum sources. The causal agent was identified as *O. taurica* in the laboratory (Mukerji, 1968). Morphological characteristics of the asexual form of fungus, which was isolated from symptomatic leaves collected from sainfoin commercial fields, were in accordance with the descriptions provided by Mukerji (1968). Large conidia were produced on short hyphal branches in two different forms, cylindrical and navicular. Because this is an obligate biotrophic pathogen, the inoculation of sainfoin seedlings was conducted immediately after the inocula collection. The complete details concerning pot preparation, inocula collection, fungal identification, and inoculation are provided by Naseri and Alizadeh (2011). When seedlings had 8-10 fully opened leaves, the entire treatment plants were sprayed with a conidial suspension of *O. taurica* containing 0.05% Tween 80 as a surfactant. Conidial suspensions were prepared by gently brushing conidia from sporulating leaves into sterile distilled water. Concentration was adjusted to 10^6 conidia/ml using a hematocytometer. Control seedlings were sprayed with sterile water. During the day, the greenhouse temperature varied from 16 to 24°C, with night temperatures ranging from 5 to 15°C over the study period. The average daily RH was ≤ 50% during the greenhouse study.

Three field experiments were conducted from 2009 to 2011 to examine the climate-sainfoin-powdery-mildew interaction. The field trial was conducted during the three growing seasons at Zanjan Agricultural and Natural Resource Research Station (*ca*. 27 km west of Zanjan). All trials were infected by windspread, natural epidemics of powdery mildew. On May 5, 2009, 40 sainfoin accessions were sown in the experimental field. Each accession was sown into 2 × 4 m row plots at 20 g seed/plot in a randomized block design with three replicates. The distance between seed rows was 0.6 m and drip irrigation was applied at a weekly interval. The crops were subjected to fertilization, weed and insect controls according to standard commercial practices. However, no fungicide for powdery mildew management was applied to the trials. Crops were harvested one time in 2009, three times in 2010, and four times in 2011.

Assessment of disease and productivity. Each year, powdery mildew was assessed late in the season, just before the last cutting, when approximately 10% of the plants per plot had flowered as follows: on 18 September in 2009, on 30 August in 2010, and on 9 October in 2011. The disease severity was determined on three randomly selected plants per experimental plot. Then three compound leaves per plant and three leaflets per leaf were examined and the disease severity was expressed as percentage of leaf area infected by the pathogen according to the following scale: 1 = no detectable mildew on leaf, resistant; 2 = 0-25% leaf area covered with mildew, tolerant; 3 = 25-50% mildewed, moderately susceptible; and 4 = 50-100% mildewed, susceptible. The resistance index was calculated as the difference between 100 and the highest disease severity recorded for each sainfoin accession over the study. To measure dry matter (DM) yield, sainfoin foliage per plot was harvested, air-dried, and then placed in an oven at 100°C for 48h. The DM yield was detected at the last cutting every year. Due to a slow and weak growth of all the accessions in the first year of cultivation, only one harvest was performed at the end of growing season in 2009. Since powdery mildew covered leaf area in most accessions tested, no measurement of DM yield was made in the first year of field trial.

Assessment of weather data. Weather data were obtained from a standard weather station located at the experimental site. The following climatic variables were determined for statistical analysis during four weeks before disease evaluation: the number of days (ND) with average relative humidity (RH) below 50%, ND with maximum temperature above 25°C, ND with maximum temperature above 35°C, ND with average temperature within 15-20°C and RH above 50%, ND with average temperature within 20-25°C and RH below 50%, and total rainfall. These climatic factors were selected from a larger number of variables based on a preliminary analysis of their significant associations with powdery mildew or yield descriptors. Furthermore, certain temperatures and RH levels were considered according to previous documents on similar pathosystems (Guzman-Plazola *et al.*, 2003; Elad *et al.*, 2007; Jacob *et al.*, 2008; Brand *et al.*, 2009). All weather data were recorded hourly and then daily data were determined accordingly.

Analytical methods. Disease severity data for powdery mildew-infected crops were arcsine square root transformed to create a normal distribution. Then, the disease and DM yield data were analyzed by two-way factorial analyses of variance in randomized complete block designs using GenStat 6.1 (Rothamsted Experimental Station, Harpenden, UK). Factors were sainfoin accession and study year. The least significant difference (LSD) at 0.05 probability level was used to compare mean values for the disease severity and DM yield. This allowed us to test differences between sainfoin accessions under natural infection conditions.

During the present study from 2009 to 2011, the singular and combined associations of 120 (40 epidemic levels per study year) powdery mildew epidemics and DM yield of 40 sainfoin accessions with the six climatic variables and accession resistance index were evaluated using contingency tables (CT) and correspondence analyses (CA), respectively. In the classification of variables, attempts were made to respect the condition of χ^2 test validity which demonstrates that up to 20% of the classes could involve less than five members (Gibbons, 1976). In CT analysis, the variables with high χ^2 value ($P \leq 0.05$) were considered important due to linkage with powdery mildew or yield. In the next step, the climatic, disease, resistance and yield variables were subjected to a CA. Interpretations of CA results were made using the percentage of total inertia explained by principal axes and the coordinates of variable classes. The CA recognized the most relevant indicators of sainfoin production in the form of a matrix with the categories of climatic, disease and resistance variables in columns and the classes of DM yield in rows. The coordinate above 0.30 was used to identify a significantly correlated descriptor to the crop yield.

RESULTS

In the present research, no disease symptom appeared on the inoculated seedlings over the two-year greenhouse study. Artificially inoculated sainfoin seedlings were examined on a weekly basis; however, no detectable mildew developed on the leaf of any sainfoin accession. The tests were terminated at 6 and 10 weeks after inoculation in 2008 and 2009, respectively.

Powdery mildew developed on all 40 sainfoin accessions in the two field trials, in 2009 and 2011 (Table 1). A wide range of plant reactions to powdery mildew was observed among the accessions tested. During the field study, the lowest disease incidence (59%) was determined in Oshnavieh in 2009. Mean disease incidence of 36 accessions ranged from 80 to 90% in 2009. The lowest mean value for disease severity was also detected in Oshnavieh, 19.1% in 2009 and 18.6% in 2011. Thus, Oshnavieh was rated as the only powdery mildew-tolerant accession among the sainfoin accessions studied. In 2009, six accessions were moderately susceptible, with the remaining 33 accessions being highly susceptible to powdery mildew. In 2010, no powdery mildew was detected on any of the three cuttings of the 40 sainfoin accessions examined. In 2011, mean values for the disease incidence in seven accessions were greater than those recorded in 2009. In contrast, mean incidence on cvs Asad abad, Poly-cross, and Kordestan was lower in 2011 compared to 2009. Lower mean severity values were obtained for 37 accessions in 2011 compared to 2009. Due to more severe mildews developed on the accessions in 2009, the powdery-mildew-resistance was rated according to field examinations in the first year of this research. There were higher mean DM yield for 12 sainfoin accessions examined in 2011 compared to 2010 (Table 1).

Based on CT results, the categories of six and four climatic characteristics were associated ($P \leq 0.05$) with powdery mildew and sainfoin-yield classes, respectively (Table 2). The classes of sainfoin yield were linked to the categories of powdery-mildew-severity. According to CA results, the first principal axis explained 100% of the variance in the data that demonstrated a perfect fit of the ordination to the data set. The principal axis best represented the classes of the disease severity, ND with average RH below 50%, ND with maximum temperatures above

Table 1. Incidence and severity of powdery mildew, and dry matter yield examined in 40 sainfoin accessions.

Cultivars	Disease incidence		Disease severity		Dry matter yield (t/ha)	
	2009	2011	2009	2011	2010	2011
Khalkhal	85.7	90.0	64.3	42.0	.137	.183
Gorjan	90.0	90.0	67.9	13.9	.101	.180
Sarab	85.7	90.0	56.6	13.9	.183	.207
Ahar	72.8	90.0	50.5	14.1	.137	.250
Haris	83.7	90.0	56.7	13.3	.150	.257
Asad abad	90.0	77.9	63.4	8.3	.137	.263
Arak	78.1	90.0	36.6	20.6	.147	.127
Khomein 1	85.7	85.7	37.3	13.3	.100	.210
Bonab	75.0	90.0	57.4	14.0	.133	.240
Marand	90.0	90.0	76.1	14.0	.155	.173
Khounsar 1	78.1	85.7	48.7	22.9	.163	.147
Damavand	90.0	80.0	58.3	10.5	.133	.240
Varzaghan	90.0	83.9	64.1	19.3	.150	.260
Songhor	90.0	90.0	74.1	30.1	.130	.180
Khoram abad	69.2	90.0	36.8	15.7	.107	.207
Feridan 1	83.9	90.0	65.7	19.2	.101	.227
Aligoudarz 1	90.0	90.0	69.0	30.7	.200	.217
Azna	82.4	80.0	46.8	13.5	.093	.220
Meshkin	78.1	90.0	43.5	37.1	.091	.170
Zanjan	85.7	83.9	39.9	40.7	.127	.237
Kaboutar abad 1	76.3	90.0	32.4	15.8	.117	.190
Kahloran	90.0	82.4	53.4	17.7	.130	.210
Khoram abad	90.0	90.0	76.2	15.4	.143	.207
Aligoudarz 2	90.0	90.0	77.0	27.1	.177	.233
Feridoun shahr	90.0	90.0	65.4	31.0	.217	.160
Feridan 2	85.7	90.0	51.8	19.1	.135	.130
Khonsar	90.0	90.0	62.0	19.8	.157	.237
Khomein 2	90.0	83.9	71.2	15.4	.100	.230
Oroumieh	90.0	79.6	74.9	15.2	.173	.193
Miandoab	90.0	85.7	80.4	14.6	.170	.267
Silvelna	90.0	90.0	83.2	29.8	.140	.135
Sanadaj	90.0	90.0	72.0	20.0	.130	.063
Poly-cross	90.0	76.3	68.5	11.6	.157	.067
Aligoudarz 3	90.0	90.0	62.5	17.5	.130	.283
Azna 2	90.0	90.0	67.2	45.1	.150	.207
Kermanshah	82.4	90.0	59.0	30.1	.197	.223
Oshnavieh	59.0	83.9	19.1	18.6	.143	.173
Kaboutar abad 2	90.0	90.0	74.9	21.0	.187	.253
Azar shahr	89.7	90.0	59.4	23.5	.121	.287
Kordestan	90.0	55.9	69.7	9.9	.183	.203
	LSD = 11.5		LSD = 14.2		LSD = .101	

25°C, ND with average temperatures within 15-20°C and RH > 50%, and total rainfall variables (Table 3). The principal axis was an axis of decreasing sainfoin production from high (> 0.150 t/ha) to low levels (≤ 0.150 t/ha) of DM yield. The contributions of low and high sainfoin yield to the principal axis were 0.38 and –0.53, respectively. Based on coordinates, 13 days with maximum temperatures above 25°C was strongly linked (coordinate = –0.88) to high sainfoin yield. There were also moderate associations of high production with 17-23 days with average RH below 50%, 4-7 days with average temperatures within 15-20°C and RH above 50%, powdery mildew severity lower than 40%, and 0-3 mm rainfalls. Low production corresponded to 12 days with average RH < 50%, 23-28 days with maximum temperatures above 25°C, 14 days with average temperatures within 15-20°C and average RH > 50%, the severity of powdery mildew greater than 40%, and 13 mm total rainfall.

According to both CT and CA results, the disease severity ≤ 40% was associated with DM yield higher than 0.150 t/ha, 17-23 days with average RH below 50%, fewer days with maximum temperatures above 25°C, two days with maximum temperatures above 35°C, fewer days with average temperatures within 15-20°C and RH above 50%, 16 days with average temperatures within 20-25°C and RH below 50%, and total rainfall as low as 0-3 mm. Greater disease severity (> 40%) corresponded to lower DM yield levels (≤ 0.150 t/ha), 12 days with average RH below 50%, 23-28 days with maximum temperatures above 25°C, the absence of daily maximum temperatures above 35°C, 14 days with average temperatures within 15-20°C and RH above 50%, 2-4 days with average temperatures within 20-25°C and RH below 50%, and total rainfall as high as 13 mm.

DISCUSSION

The present research is an attempt to contribute to the growing body of knowledge about powdery mildew epidemics occurring in sainfoin crops. Although the inoculation method used in the present study followed standard methods, the two-year attempted efforts to incite powdery mildew on sainfoin seedlings failed. One explanation for this failure may be due the lack of proper RH or temperature for the development of powdery mildew in the greenhouse. Although the average daily temperature ranging from 16 to 24°C in the greenhouse might have favored the disease establishment according to the present findings and earlier reports (Guzman-Plazola *et al*., 2003; Elad *et al*., 2007; Jacob *et al*., 2008), the average daily RH ≤ 50% may have suppressed infections following artificial inoculations. In fact, low RH levels of ≤ 50% in this study and ≤ 40% in the studies conducted by Guzman-Plazola *et al.* (2003), Elad *et al.* (2007), and Jacob *et al.* (2008) reduced powdery mildews in various crops. Thus, the present plot-scale findings could be useful in organizing future controlled-environment experiments on sainfoin powdery mildew.

The diverse reactions to powdery mildew evaluated among the accessions tested in this study suggested that the sainfoins contain different sources of resistance to the pathogen. Alizadeh and Jafari (2013) also reported various reactions of sainfoin crops to the disease epidemics occurred in different parts of Iran in which 2 out of 40 accessions were rated tolerant, Oshnavieh and Poly-cross. However, the reaction of Poly-cross accession to the disease was rated susceptible in Zanjan. This discrepancy might be partially attributed to environmental differences between the study areas which have been briefly represented by Alizadeh and Jafari (2013). There are a number of documents on temperature and relative humidity influencing the development of powdery mildew epidemics in various crops (Guzman-Plazola *et al.*, 2003; Elad *et al.*, 2007; Jacob *et al.*, 2008; Brand *et al.*, 2009). To the best of our knowledge, the present study is the first attempt to unravel interactions of sainfoin powdery mildew with air temperature and RH at field scale. Forty sainfoin accessions with a wide range of reactions to the disease were included to allow a systematic understanding of the climate-mildew-sainfoin-yield interaction. Based on the magnitude of CA coordinates, the six climatic descriptors tested in our study were more influential on powdery mildew and DM yield than the resistance index. Definitely, these preliminary associations encourage further characterization of climatic and resistance variables for this pathosystem.

According to the findings of this plot-scale study, 17-23 days with average RH<50%, 13 days with maximum temperatures >25°C, and two days with maximum temperatures >35°C corresponded to low levels of sainfoin powdery mildew. Reverse relationships of powdery mildew with lengthy periods of temperatures >25°C, with temperatures ≥30°C and within 35-40°C, and with low RH levels ≤40% (Guzman-Plazola *et al.*, 2003; Elad *et al.*, 2007; Jacob *et al.*, 2008) have been reported earlier. Furthermore, short daily periods (2-3 daily exposures of at least 2 h) at 35°C reduced mildew development in tomatoes by 70-92% (Guzman-Plazola *et al.*, 2003). However, all the above-mentioned studies were performed in controlled environments and on crops other than sainfoin, or there was no evaluation of climatic conditions influencing powdery mildew epidemics occurred across a wide range of host plant genotypes. In the present field study, even two days with maximum temperatures exceeding 35°C and more frequent exposures to daily average RHs<50% appeared inhibitory to sainfoin powdery mildew. Furthermore, daily maximum temperatures >25°C were required as frequently as 23-28 days to intensify the disease in sainfoins.

The present research also revealed the association of a more severe sainfoin-mildew with the presence of 14 daily average temperatures within 15-20°C and RHs>50% during four weeks before disease evaluation at field scale. Likewise, severe infections by *L. taurica* on pepper or tomato leaves occurred at 15 to 20°C and RH levels ≥50% in commercial greenhouses (Guzman-Plazola *et al.*, 2003; Elad *et al.*, 2007; Reuveni and Rotem, 1973). Elsewhere, severity of tomato powdery mildew was positively linked to the duration of exposure to either temperatures ranging from 15 to 25°C or RH levels of 60 to 90% during four weeks before disease assessment (Jacob *et al.*, 2008). In attempting to predict tomato powdery mildew based on greenhouse findings, the number of hours with temperatures between 17.5 and 22.5°C and RH≥40% was positively linked to the development of powdery mildew (Guzman-Plazola, 1997). In addition to supporting previous documents, our field-scale findings provide useful information to develop predicting models for *L. taurica* epidemics.

According to CT analyses in the present field experiments, 16 days with average temperatures varying within 20-25°C and RH below 50% appeared suppressive to sainfoin mildew in comparison with 2-4 days exposures to

Table 2. Contingency tables analysis of associations between climatic, powdery mildew, resistance and productivity variables in sainfoin field.

Variables[a]	Variable classes	Powdery mildew severity		χ^2 Prob.	Dry matter yield t/ha		χ^2 Prob.
		≤40	>40		≤.150	>.150	
AvgRH<50%[b]	12 days	1	39	.001	40	0	.001
	17-23 days	70	10		30	50	
MaxT>25°C	23-28 days	41	39	.013	64	16	.001
	13 days	30	10		6	34	
MaxT>35°C	2 days	40	0	.001	24	16	.793
	0 day	31	49		46	34	
AvgT15-20°C	4-7 days	70	10	.001	30	50	.001
AvgRH>50	14 days	1	39		40	0	
AvgT20-25°C	2-4 days	31	49	.001	46	34	.793
AvgRH<50	16 days	40	0		24	16	
Powdery mildew severity	≤40%	–	–	–	30	41	.001
	>40%	–	–		40	9	
Rain	0-3 mm	70	10	.001	30	50	.001
	13 mm	1	39		40	0	
Resistance index	<10	52	38	.592	49	41	.134
	≥10	19	11		21	9	

[a] Avg = average; Max = maximum; RH = relative humidity; T = temperature.

[b] Climatic data were recorded during four weeks before disease assessments.

Table 3. The contribution of climatic conditions, disease severity, and resistance index to the inertia explained by the first axis of correspondence analysis.

Variables[a]	Coordinates	
Dry matter yield	≤.150 (0.38)	>.150 (–0.53)
AvgRH<50%	12 days (0.85)	17-23 days (–0.42)
MaxT>25°C	23-28 days (0.44)	13 days (–0.88)
MaxT>35°C	2 days (0.03)	0 day (–0.02)
AvgT15-20°C AvgRH>50	4-7 days (–0.42)	14 days (0.85)
AvgT20-25°C AvgRH<50	2-4 days (–0.02)	16 days (0.03)
PM severity	≤40% (–0.33)	>40% (0.47)
Rain	0-3 mm (–0.42)	13 mm (0.85)
Resistance index	<10 (–0.08)	≥10 (0.24)

[a] Avg = average; Max = maximum; RH = relative humidity; T = temperature.

these conditions. Although temperatures at 25°C and RH levels ≤ 40% also suppressed tomato powdery mildew in controlled environments (Guzman-Plazola *et al.*, 2003; Jacob *et al.*, 2008), an additional finding was that exposures to average daily RHs < 50% for up to 15 days favored sainfoin mildew as discussed earlier. Whereas only 2-4 days with average RHs < 50% appeared conducive to sainfoin powdery mildew in our study when daily average temperatures ranged from 20 to 25°C. Such field-scale information suggests the dependence of RH impact on temperature in this pathosystem. Definitely, this observation needs further investigation in future. It is also believed that the reaction to RH may change with the host plant. For instance, continued exposure to RH levels of 80-95% reduced tomato mildew progress, but intensified the disease on pepper (Reuveni and Rotem, 1973). Furthermore, Diop-Bruckler (1989) added that such effects of RH may be changed by plant cultivars. Moreover, the optimal temperature for infection by powdery mildews is commonly close to the optimal temperatures for their hosts. For instance, powdery mildews with relatively low optimal temperatures attack the cool-weather plants such as cereals (Schnathorst, 1965). Therefore, it seems necessary to characterize the interactions of environmental conditions, in particular air RH and temperature, with a specific pathogen-plant combination. From this viewpoint, the present work addressed a number of climatic-mildew-sainfoin associations.

Although Willocquet *et al.* (1998) concluded that continuous rainfall is unfavourable to grape powdery mildew due to disrupting hyphal webs, weakening conidiophores, enhancing leaf wetness (detrimental to spore germination), and washing off of *Uncinula necator* conidia, light rainfall allowed proper conidia dispersal. However, the interaction of rainfall with powdery mildews caused by *L. taurica* is little understood. Our field-scale finding is the first reported evidence of the linkage between high total rainfall and severe powdery mildew epidemics in sainfoin crops. It should be noted that daily rainfalls ranged from 0.1 to 8 mm in this study, with four (2009), one (2010) and three (2011) rainy days being recorded during four weeks before the disease assessments.

In field trials, regrowth yields of sainfoin decreased with air temperatures above 30°C (Mowrey and Matches, 1991) and severe defoliation occurred at 35°C (Kallenbach *et al.*, 1996). However, the climate-mildew-yield interaction in sainfoin crops is little understood. Powdery mildew reduced pepper yield by shedding leaves which increased following long periods of temperatures > 20°C and RHs < 75% (Elad *et al.*, 2007). Elsewhere, defoliation of infected peppers was lower at 25°C than at 30°C and at 10-20°C (Reuveni *et al.*, 1974). In this field-scale research, less frequent exposures to either daily maximum temperatures > 25°C or daily average temperatures within 15-20°C and RHs > 50% corresponded with greater DM yield levels, presumably by reducing sainfoin mildew. The associations of higher DM yield levels with more frequent exposures to daily average RHs < 50% and with lower total rainfall also appeared to highlight the reverse linkage of DM yield with mildew. In other words, sainfoin yield increased with decreasing powdery mildew under the climatic conditions encountered in this study. Furthermore, future research could include additional eco-physiological parameters to examine the negative impacts of powdery mildew on sainfoin yield.

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REFERENCES

Alizadeh M.A., Jafari A.A., 2013. Evaluation of sainfoin populations in reaction to powdery mildew disease in different climatic conditions of Iran. *Forage Research* **39**: 10-15.

Brand M., Messika Y., Elad Y., Rav David D., Sztejnberg A., 2009. Spray treatments combined with climate modification for the management of *Leveillula taurica* in sweet pepper. *European Journal of Plant Pathology* **124**: 309-329.

Delgado I., Andrés C., Muñoz F., 2008. Effect of the environmental conditions on different morphological and agronomical characteristics of sainfoin. *Options Méditerranéennes* **79**: 199-202.

Diop-Bruckler M., 1989. Dévelopement de *Leveillula taurica* en function des facteurs climatiques et sensibilité de *Capsicum annuum* a different stades végétatifs. *Journal of Phytopathology* **126**: 104-114.

Elad Y., Messika Y., Brand M., Rav David D., Sztejnberg A., 2007. Effect of microclimate on *Leveillula taurica* powdery mildew of sweet pepper. *Phytopathology* **97**: 813-824.

Frame J., 2005. Forage Legumes for Temperate Grasslands. Science Publishers Inc., Enfield, NH, USA.

Gibbons J.D., 1976. Non-Parametric Methods for Quantitative Analysis. Holt, Rinehart and Winston, New York, USA.

Guzman-Plazola R.A., 1997. Development of a spray forecast model for tomato powdery mildew (*Leveillula taurica* (Lev) Arn.). Ph.D. Thesis. University of California, Davis, USA.

Guzman-Plazola R.A., Davis R.M., Marois J.J., 2003. Effects of relative humidity and high temperature on spore germination and development of tomato powdery mildew (*Leveillula taurica*). *Crop Protection* **22**: 1157-1168.

Guzman-Plazola R.A., Fajardo-Franco M.L., Coffey M.D., 2011. Control of tomato powdery mildew (*Leveillula taurica*) in the Comarca Lagunera, Coahuila State, Mexico, supported by the spray forecast model Tomato PM. *Crop Protection* **30**: 1006-1014.

Jacob D., Rav David D., Sztjenberg A., Elad Y., 2008. Conditions for development of powdery mildew of tomato caused by *Oidium neolycopersici*. *Phytopathology* **98**: 270-281.

Kallenbach R.L., Matches A.G., Mah J.R., 1996. Sainfoin regrowth declines as metabolic rate increases with temperature. *Crop Science* **36**: 91-97.

Majidi M.M., 2010. Study of genetic variation of sainfoin genotypes under salt tolerance. *Iranian Journal of Field Crop Science* **41**: 645-653.

Maurice E., Robert H., Darral S.M., 1985. Forages. The Science of Grass Land Agriculture. 4th Ed. Iowa State University Press, Ames, IA, USA.

Mowrey D.P., Matches A.G., 1991. Persistence of sainfoin under different grazing regimes. *Agronomy Journal* **83**: 714-716.

Mozafarian V., 2007. A Dictionary of Iranian Plant Names. Farhang Moasser Publication, Tehran, Iran.

Mukerji K.G., 1968. *Leveillula taurica*, Descriptions of pathogenic fungi and bacteria. No. 182. Commonwealth Mycological Institute, Kew, Surrey, UK.

Naseri B., Alizadeh M.A., 2011. Evaluation of resistance to powdery mildew disease in sainfoin accessions (*Onobrychis sativa*). Technical report 91/5508-20. AREEO, Tehran, Iran.

Reuveni R., Perl M., Rotem J., 1974. The effect of *Leveillula taurica* on leaf abscissions in peppers. *Journal of Phytopathology* **80**: 79-84.

Reuveni R., Rotem J., 1973. Epidemics of *Leveillula taurica* on tomatoes and peppers as affected by the conditions of humidity. *Journal of Phytopathology* **76**: 153-157.

Schnathorst W.C., 1965. Environmental relationships in the powdery mildews. *Annual Review of Phytopathology* **3**: 343-366.

Willocquet L., Berud F., Raoux L., Clerjeau M., 1998. Effects of wind, relative humidity, leaf movement and colony age on dispersal of conidia of *Uncinula necator*, causal agent of grape powdery mildew. *Plant Pathology* **47**: 234-242.

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