DEVELOPMENT OF *XANTHOMONAS ARBORICOLA* PV. *PRUNI* EPIDEMICS ON PEACHES

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SUMMARY

Infections of Xanthomonas arboricola pv. pruni (Xap) on peaches have become more important in northern Italy since the late '80s. Therefore, a three year (1993 to 1995) epidemiological study was conducted in two peach orchards affected by Xap in the district of Verona. Both disease onset and progress over time were considered. The incidence of affected leaves or fruits and disease severity were assessed in relation to meteorological data. Primary infections appeared on leaves between the end of May and the middle of July. The disease progressed with variable incidence and severity, the former ranging from very slight to more than 70% of leaves affected. Fruits were less severely affected. Rainfall played a predominant role in Xap infections. Primary infections were always established following at least 3 successive rainy days, with temperatures between 14 and 19°C. Disease progress was closely correlated with the number of rainy days after disease onset. The use of the latter variable in a logistic regression model accounted for 85% of variability in disease incidence and for 96% of variability in disease severity. A more complex model, also considering the time of disease onset, increased accountable variability to 93% and 97%, respectively.

RIASSUNTO

SVILUPPO DELLE EPIDEMIE DI *XANTHOMONAS ARBORICOLA* PV. *PRUNI* SU PESCO. Xanthomonas arboricola pv. pruni (Xap) ha assunto sviluppo epidemico nel Nord Italia a partire dalla fine degli anni '80, principalmente su pesco. Al fine di studiare alcuni aspetti epidemiologici della malattia, nel triennio 1993-1995, sono stati eseguiti sopralluoghi in due pescheti infetti siti in provincia di Verona, per rilevare la data di comparsa dei primi sintomi di Xap e la successiva evoluzione della malattia. Sono state determinate sia l'incidenza di foglie o frutti infetti che la gravità dei sintomi; inoltre sono state studiate le relazioni intercorrenti fra la malattia e le condizioni meteorologiche. Le prime infezioni sono comparse fra la fine di Maggio e la seconda decade di Luglio, sulle foglie. La malattia si è quindi sviluppata con incidenza e gravità variabili, passando da una presenza in tracce ad incidenze superiori al 70% delle foglie. I frutti hanno viceversa mostrato infezioni sempre contenute. La pioggia ha avuto un ruolo preminente nello sviluppo delle infezioni di Xap. In tutti i casi, le infezioni primarie si sono verificate dopo un periodo di almeno tre giorni consecutivi con pioggie, con temperature comprese fra 14 e 19°C. Il successivo sviluppo delle epidemie è risultato strettamente correlato al numero di giorni piovosi: l'impiego di questa variabile in un modello di regressione logistica ha permesso di spiegare l'85% della variabilità sperimentale nel caso dell'incidenza di malattia, ed il 96% nel caso della gravità. L'uso di un modello più complesso, che tiene conto anche dell'epoca di comparsa delle infezioni primarie, ha aumentato la variabilità spiegata al 93% e 97% rispettivamente.

Key words: bacterial spot, epidemiology, disease progress, weather, mathematical models.

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INTRODUCTION

Bacterial spot on stone fruits, caused by Xanthomonas arboricola pv. pruni (Vauterin et al., 1995; syn. X. campestris pv. pruni (Smith) Dye, hereafter cited as Xap) occurs in most countries where stone fruits are grown. It is more common and most severe in areas where stone fruits are grown on light, sandy soils and the environment is humid and warm during the growing season. The most common hosts include peaches and nectarines, Japanese plums, apricots and almonds (Ritchie, 1995).

Xap has been reported in Italy from time to time (Petri, 1934; Verneau, 1954; Ciccarone, 1958; Ercolani, 1970). Since the late '70s, epidemics of bacterial spot have been noted several times in plum- and peach-growing areas (Bazzi and Mazzucchi, 1980; Stefani et al., 1989; Saccardi and Goio, 1990; Balestra and Varvaro, 1997). In northern Italy Xap is now endemic.

In Italy, bacterial spot symptoms differ somewhat from the traditional description. On peaches and nectarines symptoms occur only on leaves and fruits, while plums also develop cankers on the branches and trunk. Flowers are always symptom free.

According to the traditional disease cycle, sources of primary inoculum on peach are black tips, affected leaf scars, and cankers on branches and trunks. In Italy, affected leaves on the soil surface and secondary hosts, such as plum, probably play as important a role as these primary sources of inoculum (Stefani et al., 1989; Saccardi and Goio, 1990; Zaccardelli et al., 1998). Summer cankers develop only on plum following penetration through leaf scars during the previous autumn (Gasperini et al., 1984).

In several countries Xap is thought to be able to overwinter in terminal and/or axillary buds (Dhanvantari, 1971). In Italy, the pathogen can overwinter in peach buds, but this does not play any role in primary infections, because primary symptoms usually appear in late May-early June, one month after bud break (Mazzucchi, personal communication).

Xap can also be epiphytic on both twigs and buds, on peach or plum, in the absence of symptoms (Shepard and Zehr, 1994), but in Italy Zaccardelli et al. (1998) failed to isolate Xap from symptomless leaves or flowers. Otherwise, Xanthomonads generally can multiply and survive for at least several weeks on the surfaces of hosts without causing disease and can also survive and multiply on nonhost plants under favourable conditions (Timmer et al., 1987).

The occurrence of primary and secondary infections depends entirely on environmental conditions. Frequent periods of moisture from late bloom to a few weeks after petal fall are very conducive to primary infections on fruits and leaves of peaches or nectarines. Wind-driven rain may increase disease severity. Similar environmental conditions during the growing season can favour the development of secondary infections, while few infections occur when it is hot and dry (Ritchie, 1995).

The increasing prevalence of Xap in Italy encouraged a study of its epidemiology at orchard level. We therefore carried out a three-year study in two peach orchards south-east of Lake Garda, in the Veneto region, one of the most important peach-growing areas in the Po valley (North Italy), in order to investigate relationship between disease onset and progress and weather conditions.

MATERIALS AND METHODS

Orchards. Two peach orchards were selected at Valeggio and Sommacampagna (Verona district), each with different amounts of Xap overwintering inoculum. At Valeggio, inoculum was known to be abundant since previous observations indicated high disease incidence; at Sommacampagna the inoculum was presumed to be slight, because little disease had been noted the previous year. In both locations, 'Elegant Lady' peach trees were trained in a vase-shaped system, and standard agricultural practices were followed. Both orchards were flood-irrigated starting from 15 April until 30 September irrespective of rainfall; 100 and 87 mm of water were distributed at Valeggio and Sommacampagna respectively, in each irrigation, which lasted about 1.5 hours. Tipical of the whole peach-growing area, the soil of both orchards was gravelly (about 70% gravel). 'Elegant Lady' leaves have been described as highly susceptible to Xap, whereas the fruits have been considered less susceptible (Werner et al., 1986).

In each orchard, 10 trees were chosen randomly and marked; the trees were checked for 3 years (1993 to 1995), in order to note the appearance of primary Xap symptoms and to follow disease progress during the season. Of each plant, 4 shoots were selected annually in each of the 4 canopy sectors (N-E-S-W), and labelled. All leaves and fruits on each shoot were observed for the presence of Xap spots every 15-30 days, from mid May until late September.

Meteorological data. Air temperature (T), relative humidity (RH), and rainfall (R) were recorded between 1 May and 30 September, using an electronic weather station placed near the experimental sites. Summation of mean daily T (ST), mean daily RH (SRH), and daily R (SR) as well as the number of rainy days (SRD), were calculated starting from the day when disease first appeared. The number of days after disease appearance (SDA) and the number of days after the 1 May (NDM) were also recorded. Daily meteorological data were then plotted in 5-day records (mean of 5 daily values for T and RH; summation of 5 daily values for R) (Fig. 1).

Disease assessment. Leaves and fruits of all marked shoots were noted for presence or absence of Xap symptoms, to calculate disease incidence. Random checks were made on symptoms to identify the presence of Xap. Disease severity of the affected organs was assessed by comparing each leaf or fruit with a standard diagram (Fig. 2), and assigning it to a class. The diagram was previously tested for accuracy, replicability and reproducibility and had 5 classes of disease severity

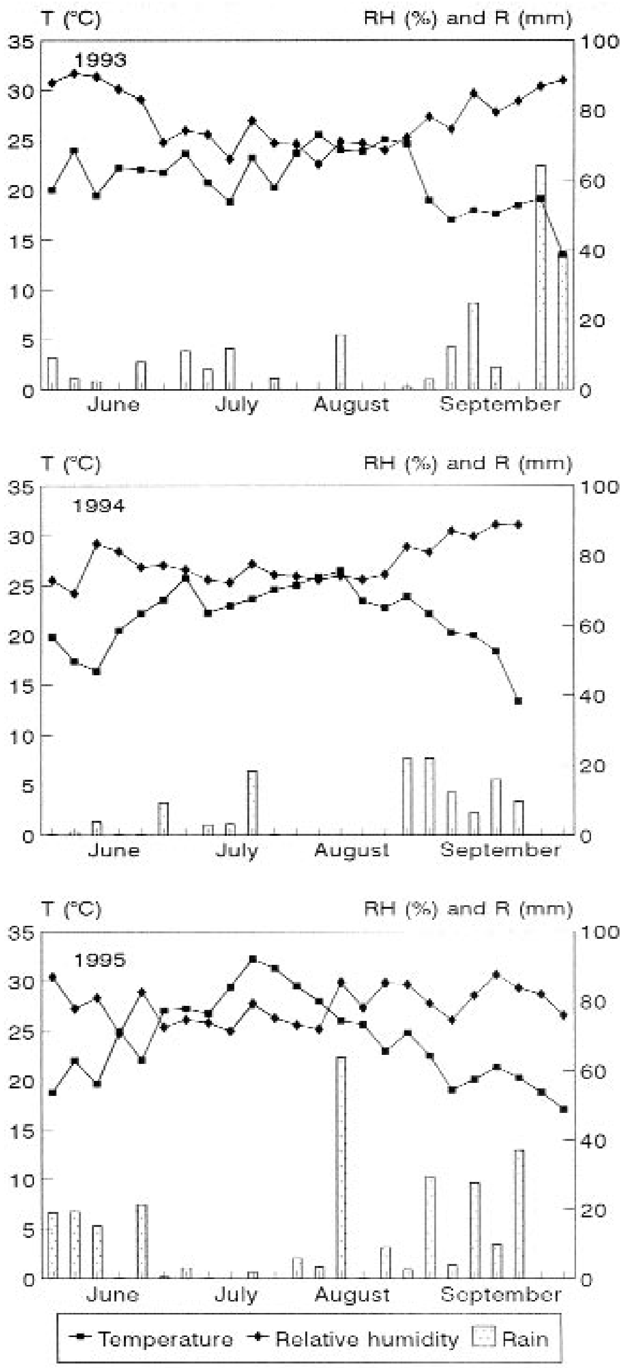

Fig. 1. Five-day records of mean air temperature, mean relative humidity, and total rain registered at Villafranca (Verona, North Italy), in 1993 to 1995.

between 1-24% of affected area. Classes with higher severity were not considered because they do not usually appear under natural conditions in the Po Valley. Early leaf fall is common in severely affected leaves.

Dynamics of disease development. To study the relationship between Xap incidence and severity, the semi-logarithmic regression model previously used by James and Shih (1973) and Seem (1984) for other diseases was employed in the following form:

$$Y = \varphi \cdot \ln(1-X) \qquad [1]$$

where: Y = Xap severity; X = Xap incidence; φ = model parameter. In model [1], omission of the intercept from the model implies that the response variable is zero when the independent variable is zero (Draper and Smith, 1968).

The correlation coefficients between disease incidence and severity and the meteorological variables were calculated to determine their degree of association.

The variables showing highest correlation coefficients with disease incidence or severity were used in a regression analysis, the former being the independent variable, the latter being the dependent one.

Data on both Xap incidence and severity obtained in the different surveys were regressed against each independent variable according to the following regression model:

$$Y = \phi/[1+e^{(\alpha+\beta \cdot X)}] \qquad [2]$$

where: Y = Xap incidence or severity; X = SDA, ST, SRH, SR, or SRD; α, β, ϕ = model parameters. The analysis was performed by the nonlinear regression procedure of SPSS statistical package (SPSS Incorporated, 1994), which obtains least squares estimates of the parameters using the algorithm developed by Marquardt (1963). The goodness of fit was evaluated on the basis of the standard error of parameters, the R^2 statistic (calculated using the corrected sum of squares), and the distribution of residues versus predicted values.

In some analyses, the parameter f, which was an estimate of the upper asymptote of the logistic model, was replaced as follows:

$$\phi = \delta + \lambda \cdot Z \qquad [3]$$

where: Z = the number of days after the 1st of May (NDM); δ and λ = model parameters.

RESULTS

Weather conditions. Weather conditions during the period June to September (when epidemics of Xap develop) varied markedly from one year to another, with regard to both air temperature and rainfall (Fig. 1). The weather in 1993 and 1994 was cooler than in 1995.

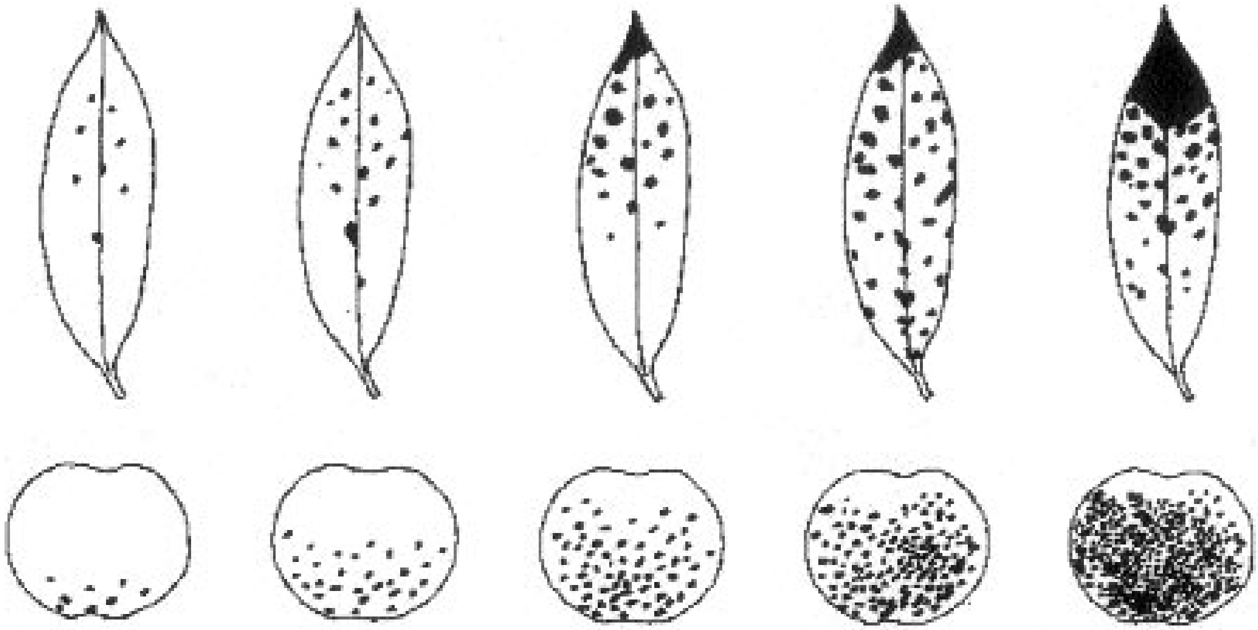

Fig. 2. Standard diagram for assessing the severity of X. arboricola pv. pruni infection on peach leaves and fruits: the 5 classes represent an area affected by 1, 3, 6, 12 and 24%, respectively.

In 1993, the 5 day average of temperature during June, July and August varied between 20 and 26°C, and dropped below 20°C in late August and September. In 1994, temperatures were quite similar to 1993, except in early June, when they were below 20°C. In 1995, temperatures were higher than 25°C from late June to mid August.

Rainfall was more abundant and more regularly distributed in 1993 and 1995 than in 1994. In 1993, the driest period was from mid July to late August, when only two significant rainy periods occurred. In 1994, a prolonged 30 day dry period occurred between late July and 20 August. In 1995, the driest period was in the middle of July, when only 2.2 mm rain fell.

Disease onset and development. In 1993, disease first appeared on leaves on 20 July, at both Valeggio and Sommacampagna. At Valeggio, the number of affected leaves increased until the end of September, when 25% showed Xap symptoms, with a mean disease severity lower than 2% (Table 1). Fruits were not affected. At Sommacampagna, the disease developed very slowly; all trees became affected, but only one month after disease onset (25 August) with one or a few leaf spots on each tree.

In 1994, disease was first observed on leaves on 14 June at both locations. At Valeggio, it developed slowly for about one month, so that incidence in the middle of July was less than 10%; the disease then increased markedly to reach 70% of leaves affected on 20 September, with a mean disease severity of 2.7% (Table 1). Xap spots were not seen on fruits until late July. At harvest, a few fruits showed spots affecting 1-3% of their total surface but most trees bore healthy fruit. At Sommacampagna, there was very little disease on either leaves or fruits during the whole season, and several trees remained symptomless.

In 1995, symptoms first appeared on 26 May at both locations. At Valeggio, 13% of the leaves showed Xap spots on 6 June. Disease incidence increased significantly until 19 July, when the disease affected 65% of the leaves, but it did not increase further until the end of September (73% of affected leaves). Disease severity however increased during the whole period starting from traces to reach 2% of the leaf area on average, 55 days after spot appearance. It then constantly increased to reach a maximum of 5.4% in late September (Table 1). Fruits were infected later; they showed symptoms after only 15 July, with very low incidence and severity. At Sommacampagna, the disease was present in traces only.

Progress of both incidence and severity were different in different years. In 1993, the disease appeared late, developed slowly, and at the end of the season affected about 25% of the leaves; in 1994, it appeared earlier than in 1993, increased slowly over a long period, followed by a period of faster increase, in which the pathogen affected about 75% of the leaves; in 1995, Xap appeared earliest and rapidly increased to affect about 75% of leaves early in the season.

Table 1. Dynamic of the epidemics of X. arboricola pv. pruni (Xap) that occurred at Valeggio (Verona) and releated meteorological variables.

Date	SDA[1]	Xap incidence	Xap severity	ST[2] °C	SRH[3] %	SR[4] mm	SRD[5] no.
1993							
20 July	1	0.03	0.005	0	0	0	0
5 August	17	0.07	0.006	366	1105	3.2	2
25 August	37	0.13	0.007	859	2501	19.6	5
16 September	59	0.14	0.011	1259	4247	79.8	15
29 September	72	0.25	0.016	1489	5368	176.2	21
1994							
14 June	1	0.01	0.001	0	0	0	0
21 June	8	0.02	0.003	143	551	0.6	1
29 June	16	0.04	0.005	324	1177	11.0	5
13 July	31	0.06	0.007	660	2208	30.6	9
28 July	46	0.25	0.011	1024	3342	82.8	14
12 August	61	0.42	0.014	1412	4447	82.8	14
26 August	75	0.54	0.016	1739	5532	135.4	16
20 September	100	0.70	0.027	2221	7676	294.8	28
1995							
26 May	1	0.01	0.0001	0	0	0	0
6 June	12	0.13	0.001	201	905	29.2	7
19 July	55	0.65	0.019	433	1917	64.0	22
28 July	64	0.66	0.024	617	2608	85.4	22
7 August	74	0.62	0.035	828	3282	89.4	25
17 August	84	0.62	0.039	1077	3998	89.4	30
25 August	92	0.65	0.044	1285	4626	91.4	34
7 September	105	0.67	0.046	1611	5579	111.4	41
28 September	126	0.73	0.054	2065	7325	206.0	51

[1] number of days from disease appearance.
[2] summation of mean daily air temperature.
[3] summation of mean daily relative humidity.
[4] summation of daily rain.
[5] number of rainy days.

Disease incidence and severity were significantly correlated ($r = 0.86$, $P \leq 0.01$). The model [1] accounts for 79% of variability in Xap severity in terms of disease incidence, when the rate parameter φ was estimated to be 0.032±0.0023 (Fig. 3).

The progress of both disease incidence and severity was described accurately when the data collected in each year at Valeggio on peach leaves were regressed against the number of days after disease appearance (SDA) using the function [2]. In fact, the standard errors of model parameters were low, the R^2 was constantly higher than 92% (Table 2), and residuals did not show any significant shift from randomness (not shown). The estimated values of model parameters agreed with their biological means, in relation to what occurred in the field: α (which represents the length of the first phase of the S-shaped logistic trend) increased between 1993 and 1995; the absolute value of β (which estimates the rate of increase during the log-phase) increased between 1993 and 1995, whereas ϕ (which was the maximum disease level) was greater in both 1994 and 1995 than in 1993 (Table 2).

The logistic function remained accurate in describing disease progress over time even when data collected during the 3 year period were pooled (Table 2; Fig. 4). In this case, the scatter of data around the fitted curve was greater than observed for the annual data (R^2 dropped to 0.82 and 0.88, for incidence and severity respectively).

Since there was a negative relationship between the day when the disease appeared and the maximum disease level, the use of function [3] in estimating parameter ϕ of the logistic function improved the data fit (Fig. 5). In fact, the model incorporating two independent variables (SDA and NDM) accounted for 95% of variability in both disease incidence and severity, instead of 82% and 88%, respectively, obtained with function [2] (Table 3).

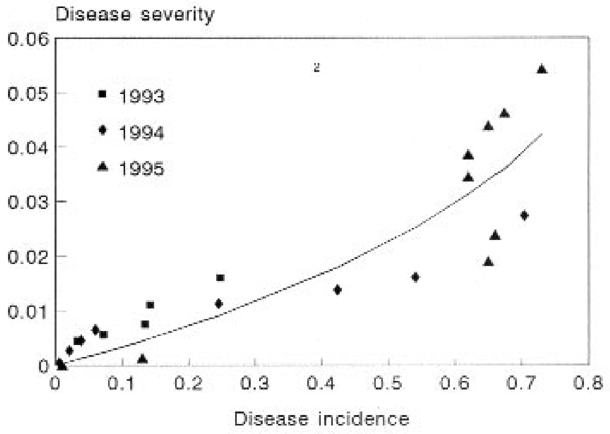

Fig. 3. Relationship between incidence and severity of X. arboricola pv. pruni infections on peach leaves. Points represent actual values, lines fit actual values according to model [1] (see text).

Relationships between disease and weather. In the field, Xap did not cause disease unless at least 3 successive rainy days occurred after the 1st of May. In 1993, the first 3 day rainy period started on 10 July, and leaf spots were observed in the survey of 20 July, 10 days later; mean temperature during the infection period was 18.9°C. In 1994, the first rainy period started on 18 May and lasted 3 days, with a mean temperature of 15.9°C; disease symptoms appeared between 11 and 26 days later. In 1995, rain fell from 10 May to 20 May, with a mean temperature of 13.8°C; Xap symptoms were observed 6 days later.

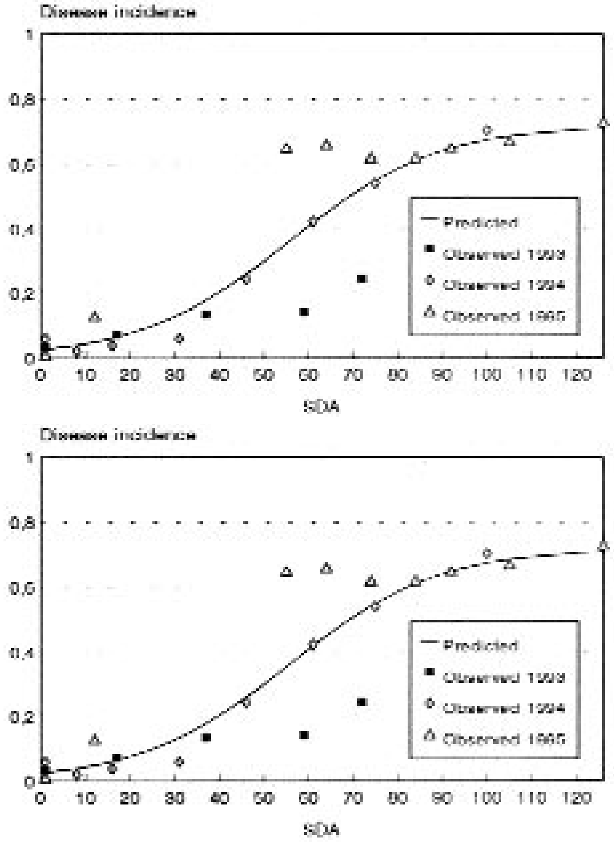

Fig. 4. Progress of the epidemics caused by X. arboricola pv. pruni on peach leaves at Valeggio (Verona, North Italy), in 1993 to 1995, expressed as both disease incidence and severity, as a function of the number of days after disease appearance (SDA). Points represent actual values, lines fit actual values according to model [2] (see Table 2).

Table 2. Parameters and statistics of the 3-parameter equations[1] fitting the progress of X. arboricola pv. pruni (Xap) incidence or severity on peach leaves, as a function of the number of days (SDA) or the number of rainy days (SRD) after disease appearance.

		α	s.e. α	β	s.e. β	ϕ	s.e. ϕ	R^2
Xap incidence								
SDA	1993	2.17	0.501	-0.03	0.011	0.40	0.087	0.92
SDA	1994	4.14	0.362	-0.07	0.007	0.72	0.032	0.99
SDA	1995	4.40	0.465	-0.25	0.034	0.66	0.014	0.98
SDA	pooled	3.33	0.926	-0.06	0.019	0.72	0.092	0.82
SRD	pooled	3.21	0.848	-0.21	0.060	0.70	0.062	0.85
Xap severity								
SDA	1993	2.47	0.405	-0.02	0.012	0.05	0.025	0.94
SDA	1994	2.83	0.309	-0.03	0.008	0.05	0.019	0.98
SDA	1995	3.75	0.380	-0.06	0.006	0.05	0.002	0.99
SDA	pooled	3.42	0.474	-0.04	0.010	0.06	0.014	0.88
SRD	pooled	3.07	0.264	-0.12	0.015	0.06	0.004	0.96

[1] model [2]: $Y = \phi/[1+e^{(\alpha+\beta*X)}]$.

Table 3. Parameters and statistics of the 5-parameter equations[1] fitting the progress of X. arboricola pv. pruni (Xap) incidence or severity on peach leaves, as a function of both the number of days (SDA), or the number of rainy days (SRD) after disease appearance, and the number of days after the 1st of May (NDM).

	δ	s.e. δ	λ	s.e. λ	α	s.e. α	β	s.e. β	R^2
Xap incidence									
SDA - NDM	0.92	0.052	-0.008	0.0011	4.01	0.965	0.093	0.0213	0.95
SRA - NDM	0.87	.054	-0.007	0.0014	4.22	1.218	-0.341	0.0985	0.93
Xap severity									
SDA - NDM	0.07	0.009	-0.0006	0.0001	3.103	0.3959	0.043	0.0078	0.95
SRA - NDM	0.06	0.005	-0.0003	0.0001	2.852	0.2724	-0.118	0.0143	0.97

[1] model [3] : $Y = (\delta+\lambda{*}Z)/[1+e^{(\alpha+\beta{*}X)}]$.

All the meteorological variables were significantly correlated with both Xap incidence and severity, at $P \leq 0.01$ (ST, SRH and SRD) or $P \leq 0.05$ (SR). The highest correlation coefficients were obtained for number of rainy days (0.86 and 0.97 for disease incidence and severity, respectively). Meteorological variables were significantly correlated with each other; the highest correlation was found between summation of mean daily T and summation of mean daily RH (0.99) (Table 4).

Number of rainy days was the most important meteorological variable influencing Xap epidemics, according to Table 4. Regression analysis of the pooled data of both disease incidence and severity at different times against the corresponding values of rainy days, according to model [2], showed a satisfactory fit with the data (Fig. 6). Both the standard error of model parameters and the R^2 showed that number of rainy days was a better indicator of disease than number of days after disease appearance. The accuracy of estimates was not increased significantly by use of the other meteorological variables as regressors in model [2], or by their use in a multiple regression model.

For number of rainy days, the use of model [3], where number of days after the 1st May was used to estimate ϕ in the logistic equation, also allowed better disease estimates, especially for Xap incidence (Fig. 7). In the latter case, model [3] accounted for 93% of total data variability, whereas model [2] accounted for only 85%.

DISCUSSION

During the three years of the study, symptoms of primary infection were observed between late May and middle July, in a 55 day interval. Our data indicate that primary infections developed when at least 3 successive rainy days occurred, with a mean temperature between about 14 and 19°C.

It is known that both leaf wetness and water congestion can markedly influence infection establishment (Zehr and Shepard, 1996). A continuous film of water extending from the leaf surface through stomata into

Table 4. Matrix of correlation between incidence or severity of X. arboricola pv. pruni (Xap) infections on peach leaves and different weather variables.

	ST[1]	SRH[2]	SR[3]	SRD[4]
XAP incidence	0.60**	0.67**	0.57*	0.86**
XAP severity	0.62**	0.69**	0.45*	0.97**
ST	–	0.99**	0.80**	0.70**
SRH		–	0.83**	0.77**
SR			–	0.56*

[1] summation of mean daily air temperature.
[2] summation of mean daily relative humidity.
[3] summation of daily rain.
[4] number of rainy days.
*: significant at $P \leq 0.05$.
**: significant at $P \leq 0.01$.

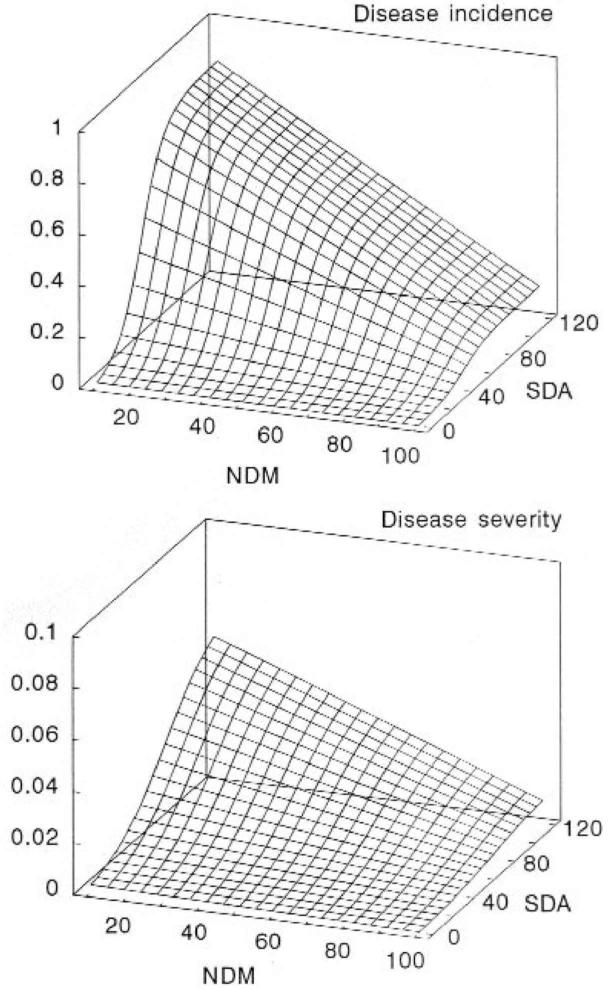

Fig. 5. Progress of the epidemics caused by X. arboricola pv. pruni on peach leaves at Valeggio (Verona, North Italy), in 1993 to 1995, expressed as both disease incidence and severity, as a function of both the number of days after disease appearance (SDA) and the number of days after the 1st of May (NDM), according to model [3] (see Table 3).

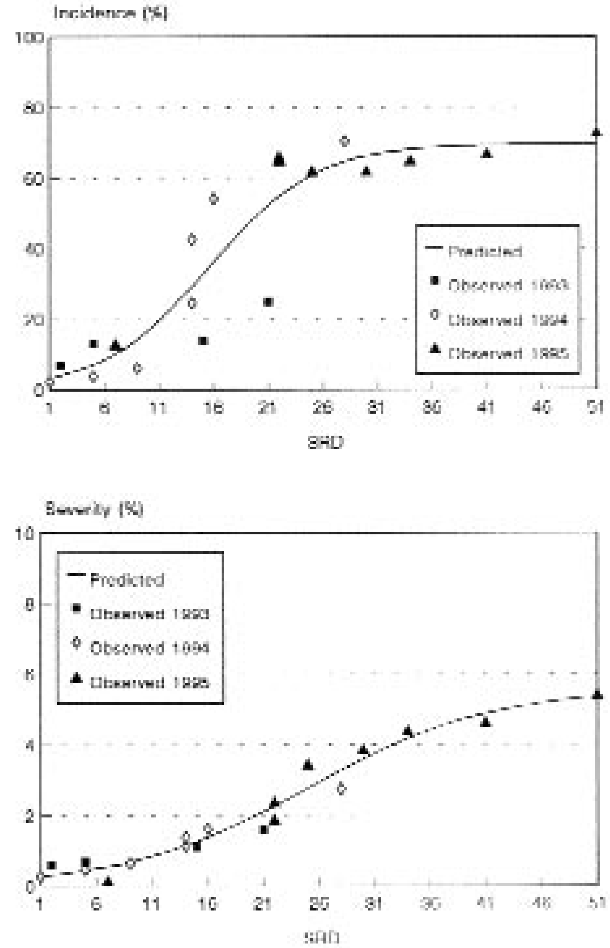

Fig. 6. Progress of the epidemics caused by X. arboricola pv. pruni on peach leaves at Valeggio (Verona, North Italy), in 1993 to 1995, expressed as both disease incidence and severity, as a function of the number of rainy days after disease appearance (SRD). Points represent actual values, lines fit actual values according to model [2] (see Table 2).

the substomatal chamber is necessary for penetration of Xap into peach leaves (Matthee and Daines, 1968; Matthee and Daines, 1969) and development of symptoms (Zehr and Shepard, 1996): in the greenhouse, only slight necrosis developed when water-congested leaves were allowed to dry immediately after inoculation or to remain wet up to 18 hours, whereas necrosis levels increased if leaves remained wet 24 to 48 hours. Our results from the two orchards appear to confirm these findings: probably a 3 day rainy period was necessary to produce, in our conditions, the water congestion and leaf wetness necessary for establishment of infection (Zehr and Shepard, 1996).

In this work irrigation during rainless periods did not favour infection establishment. Because of the soil characteristics, water availability decreases rapidly after irrigation. In fact, after May, plants already become water stressed 2-3 days after irrigation (Xiloyannis et al., 1992). In addition, there is no association between soil moisture and leaf water potential during the day (Xiloyannis et al., 1980).

Leaf spot symptoms were observed 6-26 days after a rainy period favoured establishment of infection. The incubation period of bacterial spot on peaches is very variable, in relation to temperature (Rolfs, 1915; Young et al., 1977; Du Plessis, 1986; Zehr and Shepard, 1996),

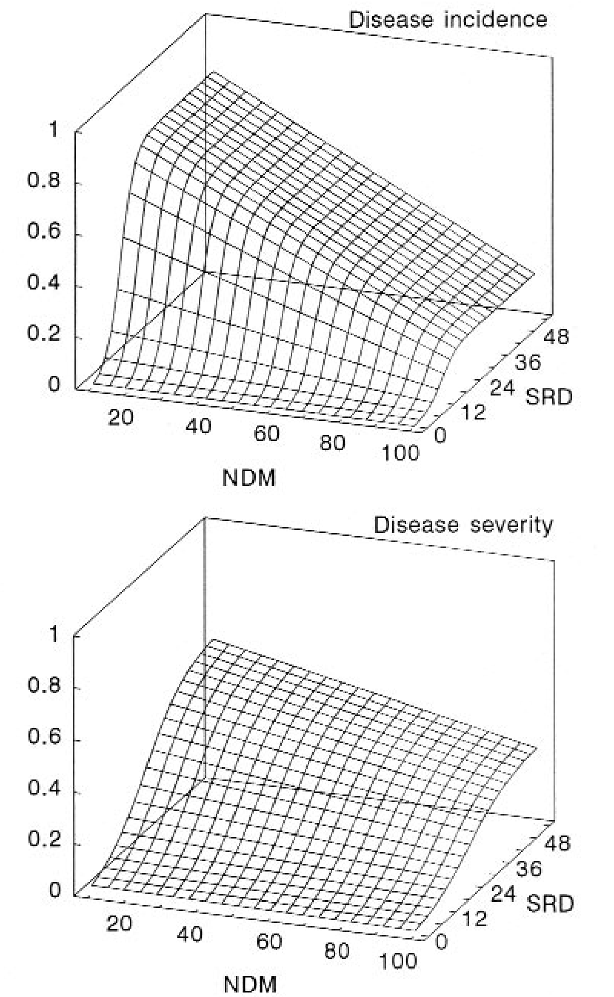

Fig. 7. Progress of the epidemics caused by X. arboricola pv. pruni on peach leaves at Valeggio (Verona, North Italy), in 1993 to 1995, expressed as both disease incidence and severity, as a function of both the number of rainy days after disease appearance (SRD) and the number of days after the 1st of May (NDM), according to model [3] (see Table 3).

leaf wetness duration (Young, 1974; Zehr and Shepard, 1996), and inoculum dose (Randhawa and Civerolo, 1985). The incubation period varies between 7 and 25 days in warm and cold weather, respectively; when the temperature is 24°C, it is 14 days without leaf wetness and 10 days with 48 h of leaf wetness. Incubation period increases from 6 to 14 days when the inoculum concentration decreases from 10^7 to 10^5 cfu ml^{-1}.

Xap developed with variable incidence and severity, the former changing from very light to more than 70% of leaves affected. Both the amount of primary inoculum and rainfall were important in the progress of Xap epiphytotics.

At Sommacampagna, where the initial inoculum level was slight, Xap did not cause severe epidemics, irrespective of weather conditions, while at Valeggio, where the amount of inoculum was high, the disease developed into severe epidemics. Civerolo (1975) found that the number of lesions induced by Xap is directly proportional to inoculum concentration. Evidence of a direct relationship between primary inoculum and disease progress is not yet reported for Xap on peaches, but it is well known for X. campestris pv. citri (Danos et al., 1984).

The progress of both disease incidence and severity on leaves were closely correlated with the number of rainy days after disease onset. The use of the latter variable as regressor in a logistic model accounted for 85% of variability in disease incidence and for 96% of variability in disease severity. Our results were consistent with those of Daines (1961), who found that the number of Xap infections increased with the duration of rain. Similar results were obtained for X. campestris pv. citri (Gottwald et al., 1989) and pv. mangiferaeindicae (Manicom, 1986).

A more complex model which considers time of disease onset in addition to number of rainy days after onset, increased the variability accounted for, especially for Xap incidence. Thus, time of first appearance significantly influenced subsequent disease progress on leaves. Two factors could explain this finding: when disease appears late in the season, (i) the weather is warmer and drier and so less favourable for disease development, and (ii) leaves are more mature and no more leaves grow on shoot. The first explanation is supported by the previously cited knowledge on temperature requirements of Xap; the latter is strengthened by the results of Zehr and Shepard (1996), who found that necrosis after experimental inoculation is most severe on the youngest leaves. In our conditions, the number of leaves per shoot increased progressively until the beginning of August, when shoots ceased growing, without marked differences between years. As a consequence, early Xap infections developed on actively growing shoots bearing many young leaves; on the contrary, late infections affected mature or old leaves only.

In all the cases we observed, fruits were affected later in the season, with lower incidence and severity compared to leaf infection. This could be related to the lower density of stomata on the fruit surface compared to leaves. In addition, fruits are not subject to water congestion because their stomatic chambers are less influenced by the hydrostatic pressure of the xylem (Mazzucchi, personal communication). A delay in disease appearance on fruits has been previously reported (Saccardi and Goio, 1990; Shepard and Zehr, 1994), as well as a lack of correlation between leaf and fruit infection

(Werner et al., 1986). Probably, epiphytic Xap populations produced by pre-symptomatic egress of bacteria (Miles et al., 1977) or by exuding leaf spots, which persist a long time on leaves (Shepard and Zehr, 1994), serve as inoculum for disease development on peach fruits, as is true for plums (Bazzi and Mazzucchi, 1980), for X. campestris pv. juglandis on walnuts (Mulrean and Schroth, 1982), and for X. campestris pv. mangiferaeindicae on mangoes (Manicom, 1986). Because fruit infection was sporadic in our study, we were unable to fully understand disease outbreaks on fruit, and this aspect needs additional research.

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