

A NEW MODEL ESTIMATING THE SEASONAL PATTERN OF AIR-BORNE ASCOSPORES OF *VENTURIA INAEQUALIS* (COOKE) WINT. IN RELATION TO WEATHER CONDITIONS

V. Rossi¹, I. Ponti², M. Marinelli², S. Giosuè¹ and R. Bugiani²

¹ *Istituto di Entomologia e Patologia Vegetale, Università Cattolica del Sacro Cuore, Via Emilia Parmense 84, I-29100 Piacenza, Italy*

² *Servizio Fitosanitario, Regione Emilia Romagna, Via di Corticella 133, I-40129 Bologna, Italy*

SUMMARY

A simple model estimating the seasonal pattern of air-borne ascospores of *Venturia inaequalis* was elaborated, by using spore trapping records collected during a 6-year period (1991-1996) in the Po Valley (North Italy). The model estimates the proportion of the season's ascospores trapped by using weather factors which occur after the first appearance of mature ascospores inside the pseudothecia. Temperature and leaf wetness are the driving variables included in the model, expressed as degrees (above 0°C) accumulated daily in the hours when leaves are wet. The model is a non-linear regression that describes the relationship between degree-days and the proportion of the season's ascospores, expressed as a mean and its confidence intervals. The model was verified by comparison with its component data sets, and was validated with additional observations of the ascospore trappings made in 1997 and 1998. Validations showed that the model makes accurate estimates, which could be used in the warning systems for apple scab management, instead of records from spore traps.

Key words: apple scab, ascospore trappings, weather, estimating model.

INTRODUCTION

The apple scab pathogen, *Venturia inaequalis* (Cooke) Wint., overwinters primarily as pseudothecia in apple leaf litter. During spring rains, ascospores are released from the pseudothecia and cause infection. Since significant sources of conidial primary inoculum are usually absent (Kennel, 1990; Becker *et al.*, 1992; Stensvand *et al.*, 1996), control of apple scab is achieved by application of fungicides to prevent infection by ascospores (MacHardy, 1996). Optimal timing

of fungicidal sprays coincides with ascospore discharge, when weather conditions favour the infection process; the former being usually monitored in the field using spore traps (Curtis, 1922; Sutton and Jones, 1976; Gadoury and MacHardy, 1983), the latter being defined according to either the original or the revised Mill's table (Mills, 1944; Schwabe, 1980; MacHardy and Gadoury, 1989; Stensvand *et al.*, 1997). The use of spore traps, however, is time-consuming and requires adequate laboratory equipment; in addition the relatively high cost of traps frequently restricts or prohibits their use. An accurate estimate of ascospore trappings during the primary inoculum season is then crucial for an efficient scheduling of fungicide applications in the absence of a network of spore traps.

Several models have been developed to predict the first ascospore discharge (James and Sutton, 1982b; Proctor, 1982) or the dynamic of ascospore maturity during the season (Massie and Szkolnik, 1974; Gadoury and MacHardy, 1982c; St-Arnaud *et al.*, 1985; Lagarde, 1988; Schwabe *et al.*, 1989) as influenced by the weather.

In a previous work (Rossi *et al.*, 1999), we evaluated the accuracy of the model developed by Gadoury and MacHardy (1982c) in New Hampshire (USA) under the conditions of the Po Valley (North Italy). This model estimates the proportion of the season's ascospores that are mature and ready for discharge during each rain event, as a function of the degree-day accumulation, when weather does not limit the wetting of apple leaves on the orchard floor (MacHardy, 1996). The model did not fit spore trappings accurately under our conditions, because of the effect of dryness: when many consecutive rainless days occurred, the proportion of ascospores trapped was constantly lower than the model estimates, due to a slowed spore maturation. When we modified the New Hampshire model to account for the leaf litter wetness caused by rain and deposition of atmospheric humidity, which frequently occurs with the Po Valley weather, there was a significant improvement in model estimates. Notwithstanding this, differences between the pattern of air-borne ascospores and estimated ascospore maturity were wide.

Corresponding author: V. Rossi

Fax: +39.0523.599256

E-mail: PATOLO@PC.UNICATT.IT

In this work, we devoted further efforts to obtaining a mathematical model estimating the seasonal pattern of air-borne ascospores of *V. inaequalis* on the basis of weather conditions, whose outputs could be used in our regional warning system for apple scab management (Bugiani *et al.*, 1996) instead of the records from the spore traps.

MATERIALS AND METHODS

Ascospore trapping. To elaborate the model, air-borne ascospores of *V. inaequalis* were trapped during a 6 year (1991-1996) period at Passo Segni (Ferrara, North Italy), in a commercial orchard of 9 year-old 'Imperatore' trees, spaced 4 x 1.8 m. To validate the model, ascospores were trapped in 1997 and 1998, at Borgo Panigale (Bologna, North Italy), in a commercial planting of 10 years-old trees cultivar 'Imperatore'.

In both data sets, to obtain a representative level of the overwintering pseudothecia, the trees were sprayed with fungicide each year to control scab, following common practice. No eradicating practices were applied to the leaf litter, which was allowed to decompose naturally.

A 7 day recording volumetric spore sampler (Lanzoni VPPS-2000, Bologna, Italy) was installed in the orchard and operated continuously from March to June. It functioned on a 220 V 50 Hz power source, and was adjusted to sample air at 10 l min⁻¹ at 150 cm above the ground. The tape that served as the trapping surface was 28 mm² h⁻¹ wide; it was removed weekly and dissected for microscopic examination. The tape was examined microscopically (675x) by scanning 4 equidistant transects across the long axis of the tape at 2 mm (1 hour) intervals. The number of ascospores of *V. inaequalis* observed in each 1 hour transect was corrected for the proportion of the tape examined and the volume of air sampled: it was then expressed as trapped spores per m³ of air per hour. The spore counts were not adjusted for trap efficiency.

The cumulative number of trapped spores per m³ of air (that is the 'relative ascospore dose', *sensu* Hirst and Stedman, 1961) was then calculated as the yearly total of hourly ascospore densities; afterwards, the cumulative proportion of ascospores trapped at each discharge was calculated on a 0-1 scale (PAT, proportion of ascospores trapped).

Hourly meteorological data (air temperature, relative humidity, leaf wetness, rain) were measured in an automatic weather station placed in the neighbourhood of the experimental site, during the whole season of ascospore trapping.

Model formulation. In each day of the primary inoculum season, we accumulated air temperatures as follows:

$$DDC_i = \sum_{j=1}^i \sum_{h=1}^{24} (T_{hj} / 24) \quad [1]$$

in which: DDC_i is the degree-day cumulation on the i^{th} day; T_{hj} is the air temperature (in °C) in each hour ($h = 1$ to 24) of the j^{th} day ($j = 1$ to i). When $T_{hj} \leq 0$, or when the leaf wetness sensor measured no wetness, T_{hj} was set at zero; therefore, we accumulated degrees only when the temperature was above 0°C and the leaves were wet. The biofix (*i.e.* the starting point) for degree-day accumulation ($j = 1$) was determined using the model of James and Sutton (1982b), modified by Mancini *et al.* (1984), which estimates the mean development stage of pseudothecial population during winter and early spring as a function of air temperature and leaf litter wetness, using a numerical code ranging from 5 (pseudothecia with lumen filled with pseudoparaphyses, *i.e.* undifferentiated pseudothecium) to 12 (pseudothecia with pigmented and mature ascospores, *i.e.* morphologically mature ascospores). The biofix was set to be equal to the day when the mean development stage was 9.5; in fact, at this stage a small part of the overwintering pseudothecia (about 2%) already contains morphologically mature ascospores, due to variability within the population (James and Sutton, 1982a).

DDC was used as the dependent variable in a nonlinear regression analysis, to fit the cumulative proportion of the season's ascospores trapped on each i^{th} day of each year (PAT_i), according to the following logistic model (Rossi *et al.*, 1999):

$$PAT_i = 1/[1 + \exp(a - b \cdot DDC_i)] \quad [2]$$

in which: a and b are the model parameters. Analysis was performed by the nonlinear regression procedure of the SPSS Advanced Statistics package (SPSS Inc., 1995), which obtains least squares estimates of the parameters using the algorithm developed by Marquardt (1963). In the logistic function we used, the parameter a depends on the length of the initial phase of the seasonal ascospore pattern, when a small part of the spores mature, whereas the parameter b is influenced by the rate of ascospore discharged during the central phase of the primary inoculum season, when most of the ascospores mature.

Like Gadoury and MacHardy (1982c), we calculated a model fitting the average pattern of ascospore discharge over the years, and its confidence intervals. Since in the non-linear regression the residual mean square is not an unbiased estimate of error variance

(Draper and Smith, 1968), we could not calculate the confidence region for the model using tests for the linear models. Therefore, we worked as follows. We calculated the values of $\hat{P}AT$ in each year, by running the equation [2] using the parameters previously estimated, in the interval $DDC = 0^{\circ}C$ to $500^{\circ}C$, step $25^{\circ}C$. Afterwards, we calculated the mean and the standard deviation of $\hat{P}AT$ on each value of DDC , and we used them to calculate the 95% and 99% confidence intervals for the means. We then fitted these data using the equation [2]. Therefore we obtained estimates of the parameters \underline{a} and \underline{b} for the 6-year average of $\hat{P}AT$, and for its confidence intervals ($\hat{P}AT'$ and $\hat{P}AT''$) at the 95% and 99% probability levels.

Model verification and validation. To validate model performances, we plotted actual data collected in 1997 and 1998 (which were not used in model elaboration) against the range of model estimates. Then we counted the number of points which fell inside and outside this range, over the whole season of ascospore trapping, and separately for the lag phase (that is when 20% of the season's ascospores are discharged, $PAT \leq 0.2$), the accelerated phase (when 70% of the season's ascospores are discharged, $0.2 < PAT \leq 0.9$), and the final phase (when the final 10% of the season's ascospores are discharged, $PAT > 0.9$) (MacHardy, 1996); afterwards, we expressed them as relative frequencies. In addition, we counted the number of cases in which the model overestimated and underestimated actual values, and expressed them as relative frequencies. Furthermore, we analysed errors made by the model in estimating PAT , by calculating the differences 'observed minus estimated'.

Ascospore trappings (dependent variable) were regressed against model estimates (independent variable) and the properties of the linear model were examined: the null hypothesis that \underline{a} (intercept of regression line) is equal to zero, and \underline{b} (slope of regression line) is equal to one were tested using the Student t-test: $t_a = (a-0)/SE_a$; $t_b = (b-1)/SE_b$. If the t-test for \underline{a} and \underline{b} was not significant, then both null hypotheses were accepted and the model was considered a statistically accurate estimator of the observed data (Teng, 1981).

RESULTS

Model formulation. The yearly ascospore trappings we observed changed markedly, regarding both the seasonal pattern and the relative ascospore dose. In 1991, the period of ascospore trapping was 42 days long, with two peaks of trapping: the period 23 to 26 March and

April 5, when 76% and 15% of the relative ascospore dose (equal to 6746 spores per m^3 of air) were trapped, respectively. In 1992, the trapping period was shorter (34 days) and the peaks were delayed: on March 30 (1st trapping day) only 11% of total spores (2836 per m^3 of air) were trapped, whereas 35% and 51% of spores were trapped on April 17 and 30, respectively. In 1993, only 360 spores per m^3 of air were trapped during a 28-day period, with a peak on April 15. In 1994, the trapping season was very short because all the spores (10,051 spores per m^3 of air) were trapped in 16 days, with three peaks: on April 2 (35% of relative ascospore dose), April 10 (22%), and April 16 (25%). In 1995, the period of spore trapping was 59 days, but in a 5-day period (April 20 to 24) 85% of the relative ascospore dose (15,378 spores per m^3 of air) was trapped. In 1996, few spores were trapped between April 2 and May 2 (555 spores per m^3 of air), mostly on April 29 (37% of total spores) and May 1 (30%).

The goodness of the fitting of PAT data obtained by the logistic model [2] was evaluated on the basis of the standard error of parameters, the R^2 statistic, and the distribution of residues versus predicted values. The values of R^2 ranged between 0.93 (in 1991) to 0.99 (in 1992 and 1995), but most of them were higher than 0.96, and the fitted curves did not show systematic deviations from actual data (Fig. 1); in addition, the relative deviations were of about the same magnitude over the whole range of actual data (not shown). Standard errors of parameters were constantly low (Fig. 1), and estimates of the model parameters always agreed with their biological means. Based on the previous results, we considered the values of PAT calculated by the model [2] very accurate estimates of the proportion of the season's ascospores ready to be ejected on each discharging occasion.

Equation [2] fitted the average of the $\hat{P}AT$ values over the 6-year period, and its confidence intervals accurately, as the parameter values and the related statistics showed (Table 1).

Model verification. Considering the 99% probability level, the upper and lower limits of the confidence bands were quite wide during the middle of the primary inoculum season (Fig. 2). For example, at the mid-time of ascospore discharge (when $PAT = 0.5$, and $DDC = 197^{\circ}C$), the upper and lower limits for PAT were 0.8 and 0.2, respectively, whereas the limits for DDC were $155^{\circ}C$ and $236^{\circ}C$, respectively. However, the model was more precise at the beginning and at the end of ascospore season. When $PAT = 0.9$ (at $DDC = 260^{\circ}C$), the confidence limits were 0.97 and 0.69 for PAT , $217^{\circ}C$ and $299^{\circ}C$ for DDC .

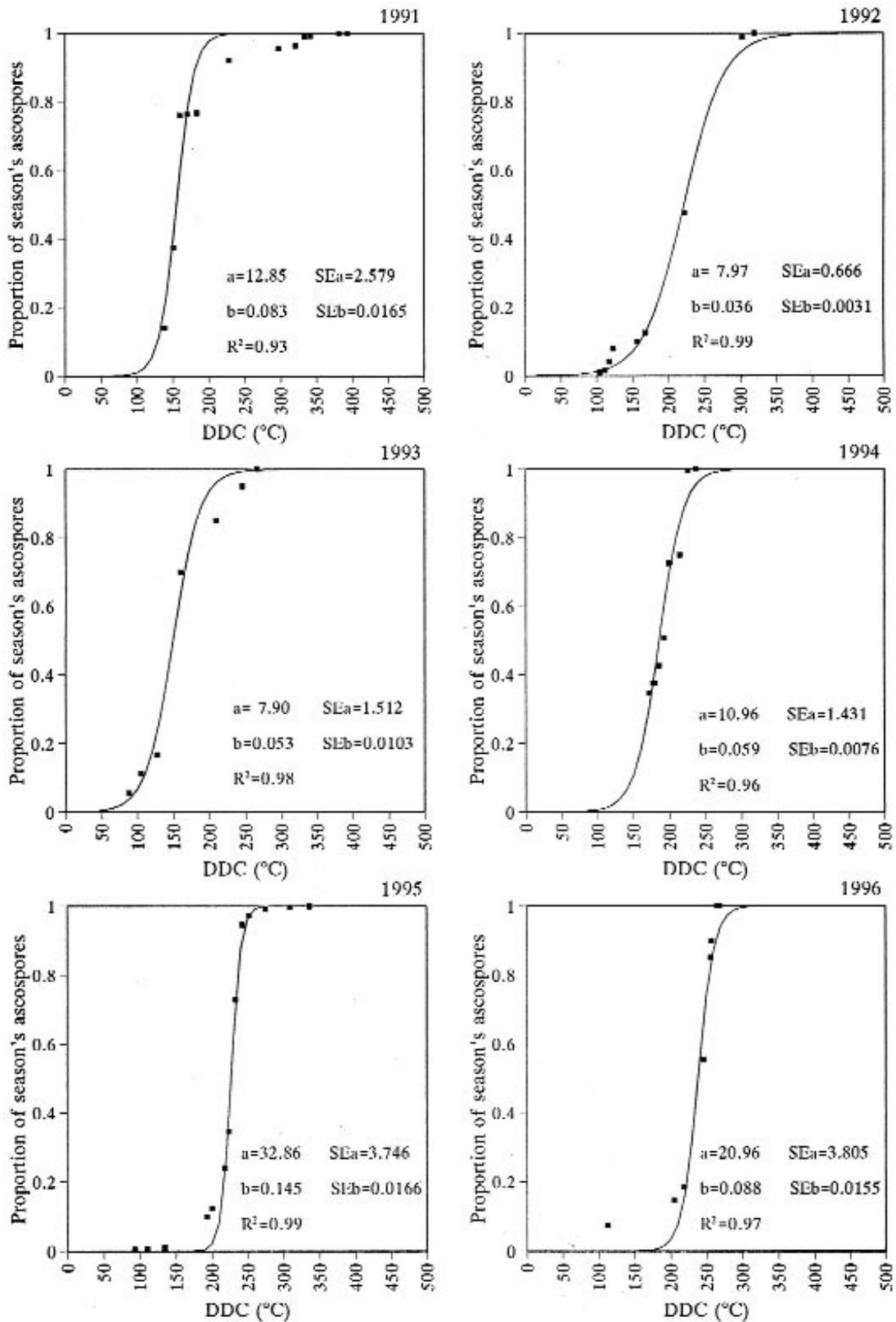


Fig. 1. Dynamic of the proportion of the season's ascospores of *V. inaequalis* trapped during a 6 year period, in relation to the degree-days above 0°C, accumulated when leaves were wet (DDC, °C). Points represent observed values; lines are the values fitted by the logistic model [2]; \underline{a} and \underline{b} are the model parameters, with the respective asymptotic standard errors (SE).

Table 1. Parameters and statistics of the logistic functions [2] used to fit the average cumulative proportion of the season's *V. inaequalis* ascospores trapped (PAT), and its confidence intervals at 95% and 99% probability levels, as a function of the accumulated degree-days (DDC).

	a	SE _a ¹	b	SE _b ¹	R ²⁽²⁾
PAT ³	6.89	0.302	0.035	0015	0.99
PAT' 95% ⁴	5.69	0.082	0.035	0014	0.99
PAT'' 95% ⁵	8.01	0.120	0.035	0014	0.99
PAT' 99%	5.41	0.135	0.035	0016	0.98
PAT'' 99%	8.27	0.176	0.035	0016	0.98

¹ Standard error of model parameters.

² Coefficient of determination.

³ 1991-1996 average.

⁴ Lower limit for the confidence interval.

⁵ Upper limit for the confidence interval.

During the whole period of ascospore trapping, 45 of 60 observed PAT values (75%) fell inside the 99% confidence interval of the values estimated by the model, whereas 15 cases (25%) fell outside, although at a very narrow distance from either the upper or the lower limit (Fig. 2). Six outsiders occurred during the lag phase (30% of total trappings during this phase), 4 occurred during the accelerated phase (20%), and 5 in the final phase (25%). 42% of cases were overestimated, whereas 58% of them were underestimated (Fig. 2).

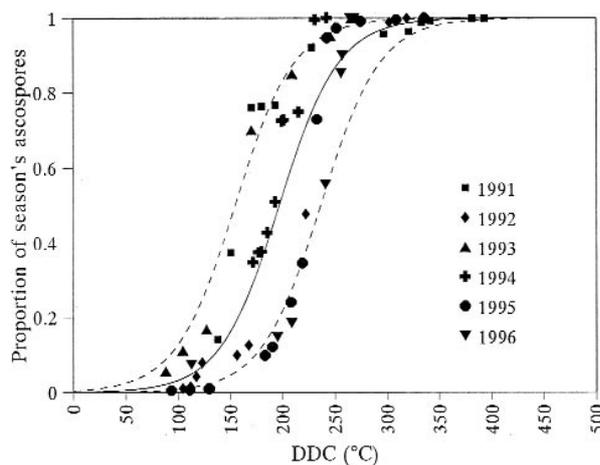


Fig. 2. Comparison between the proportion of the season's ascospores of *V. inaequalis* trapped during a 6 year period (points) and estimated by the logistic model [2] (average and its 99% confidence bands) (lines), over the degree-days above 0°C, accumulated when leaves were wet (DDC, °C) (see Table 1 for model parameters).

Model validation. To validate the model, we compared its estimates to the actual ascospore trappings collected in 1997 and 1998, which were not used in model elaboration. In 1997, the season of primary inoculum discharge was 72 days long, with a peak on May 8, when 62% of total ascospores (274 spores per m³ of air) were trapped. In 1998, a total of 567 spores per m³ of air were collected during a period of 67 days; most of them (74%) were trapped between April 10 and 19. When the actual values of PAT were plotted against the model outputs, 29 of 32 observations (91% of cases) fell inside the 99% confidence bands of the estimates. In 2 outsider cases, observed PATs were very close to the upper limit of the estimates. Compared to the mean value of model outputs, 62% of observed values were underestimated, 19% were overestimated, whereas 19% of them were equal to the estimated values (Fig. 3).

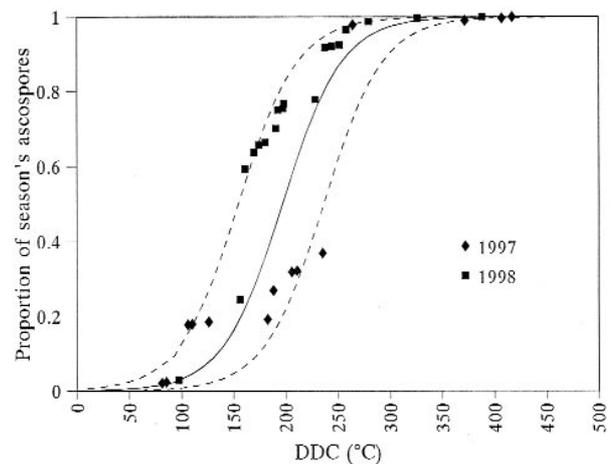


Fig. 3. Comparison between the proportion of the season's ascospores of *V. inaequalis* trapped in 1997 and 1998 (points) and estimated by the logistic model [2] (average and its 99% confidence bands) (lines), over the degree-days above 0°C, accumulated when leaves were wet (DDC, °C) (see Table 1 for model parameters).

The mean error (observed - estimated) in estimating PAT was 0.063 (min -0.423, max 0.373). Error distribution had a mode of about zero, and 50% of data were between 0 and 0.194; the 2 worst estimates may be considered as outliers (Fig. 4).

The linear regression between observed and estimated data showed a significant statistical agreement; in fact, neither \underline{a} (= 0.0242±0.049) nor \underline{b} (= 0.86±0.095) were significantly different from zero and one, respectively. The total variance accounted for by the regression was 73%.

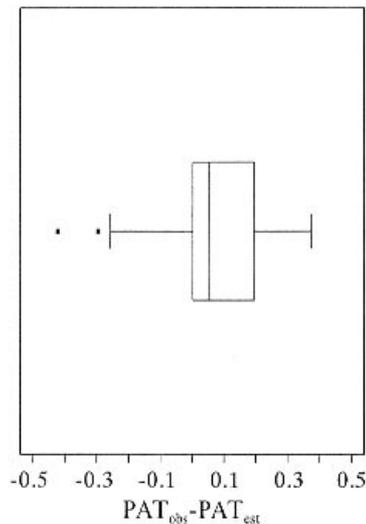


Fig. 4. Box plot representing distribution of the errors in estimating the proportion of the season's ascospores of *V. inaequalis* trapped (PAT) in 1997 and 1998, by means of the logistic model [2]. Errors are expressed as: $PAT_{\text{observed}} - PAT_{\text{estimated}}$; the central box covers the middle 50% of the data, between the lower and upper quartiles, while the whiskers extend out to the min and max values; points are outliers.

DISCUSSION

The model we elaborated estimates the proportion of the season's ascospores which are air-borne on each discharging event (*i.e.*, the response variable), by using weather factors (*i.e.*, the driving variable) which occur after the first appearance of mature ascospores inside pseudothecia (*i.e.*, the biofix).

In our model, we used a response variable different from the one used in some previously elaborated models, especially that elaborated by Gadoury and MacHardy (1982c) in New Hampshire. The previous authors used data from laboratory and field studies to develop a model to estimate the cumulative proportion of mature ascospores, as measured by counting the ascospores discharged in water by pseudothecia (Gadoury and MacHardy, 1982b), or by examining crushed pseudothecia (Gadoury and MacHardy, 1982a). In contrast, we used data on the cumulative proportion of ascospores trapped at each discharge, as recorded by a volumetric spore sampler installed in an apple orchard. We chose this approach because: (i) our aim was to elaborate a model whose outputs could be used in our regional warning system for apple scab management, instead of the records from the spore traps; (ii) estimating spore trapping records could account for all the factors affecting the discrepancies be-

tween ascospore maturation in the leaf litter at the orchard floor and ascospore density in the orchard air, such as, for instance, the dynamic of the discharging events or the rate of leaf litter decomposition (MacHardy, 1996).

The environmental factors involved with our model were air temperature and leaf wetness, expressed as degrees accumulated daily in the hours when leaves were wet. We chose this variable to account for the influence of both temperature and leaf litter wetness on ascospore maturation. Some previously elaborated models showed the great influence of temperature on the seasonal pattern of ascospore maturation (Massie and Szkolnik, 1974; Gadoury and MacHardy, 1982c; St-Arnaud *et al.*, 1985; Lagarde, 1988; Schwabe *et al.*, 1989). On the other hand, MacHardy (1996), by analysing performances of the New Hampshire model (Gadoury and MacHardy, 1982c) at some locations in Norway, showed that the wide discrepancy between the ascospore maturity predicted by the model and the cumulative spore trapped results from the effect of extended dryness on spore maturation. Stensvand *et al.* (1998) obtained a better estimate of spore maturation subtracting the dry days beyond the 4th dry day from the degree-day accumulation than by using the original New Hampshire model. Rossi *et al.* (1999) improved the accuracy of the New Hampshire model outputs in the Po Valley's weather (North Italy) by accumulating degrees only in the days when leaf litter was estimated to be wet.

As Gadoury and MacHardy (1982c) did in their model, we used the first appearance of mature ascospores as the biofix for degree-day accumulation. We chose to estimate the date when mature ascospores first appear, by using the model developed by James and Sutton (1982b), modified by Mancini *et al.* (1984), instead of inducing ascospore discharge or examining crushed pseudothecia. We considered this approach suitable for our advisory system for the following reasons: (i) low daily degree-day cumulation in early spring minimizes errors in choosing the date of biofix (MacHardy, 1996); (ii) the model runs using weather factors, which are measured by a widespread network of meteorological stations; (iii) the model gave an accurate simulation of pseudothecial development under the conditions of the Po Valley (Mancini *et al.*, 1984). In our previous experiments, by setting the biofix when the mean of pseudothecial development is 9.5, it was possible to explain 100% of the earliest dates when ascospores were discharged over a 17 year period (unpublished data), because, at this stage, a small part of the overwintering population contains pigmented and mature ascospores (James and Sutton, 1982a).

The model we elaborated is a non-linear regression that describes the relationship between the weather factors and the proportion of season's air-borne ascospores, expressed as a mean and its confidence intervals; the confidence bands are a part of the model, to allow estimation of the deviation from the expected spore density at various times during the primary inoculum season. Air-borne ascospores are then expressed as an estimate with upper and lower confidence limits.

First validations suggest that our approach can be considered successful, because the model makes accurate estimations based on input data not used in model development, and representing different epidemiological conditions. If further validations confirm the accuracy of the model, it will be used in our warning system for apple scab management to estimate the relative inoculum level within apple orchards, *i.e.* the percentage of the season's primary inoculum that is air-borne at each ascospore discharge.

ACKNOWLEDGEMENTS

This work is part of research promoted and supported by the Emilia Romagna Region (Italy), through the co-ordination of the Centro Ricerche Produzioni Vegetali (CRPV).

REFERENCES

- Becker C.M., Burr T.J., Smith C.A., 1992. Overwintering of conidia of *Venturia inaequalis* in apple buds in New York orchards. *Plant Disease* **76**: 121-126.
- Bugiani R., Tiso R., Butturini A., Govoni P., Ponti I., 1996. Forecasting models and warning services in Emilia-Romagna (Italy). *EPPO Bulletin* **26**: 595-603.
- Curtis K.M., 1922. Ascospore ejection of the apple and pear black-spot fungi. *New Zealand Journal of Science and Technology* **5**: 83-90.
- Draper N.R., Smith H., 1968. Applied regression analysis. John Wiley and Sons, New York.
- Gadoury D.M., MacHardy W.E., 1982a. Preparation and interpretation of squash mounts of pseudothecia of *Venturia inaequalis*. *Phytopathology* **72**: 92-95.
- Gadoury D.M., MacHardy W.E., 1982b. Effects of temperature on the development of pseudothecia of *Venturia inaequalis*. *Plant Disease* **66**: 464-468.
- Gadoury D.M., MacHardy W.E., 1982c. A model to estimate the maturity of ascospores of *Venturia inaequalis*. *Phytopathology* **72**: 901-904.
- Gadoury D.M., MacHardy W.E., 1983. A 7 day recording volumetric spore trap. *Phytopathology* **73**: 1526-1531.
- Hirst J.M., Stedman O.J., 1961. The epidemiology of apple scab [*Venturia inaequalis* (Cke.) Wint.]. I. Frequency of airborne spores in orchards. *Annals of Applied Biology* **49**: 290-305.
- James J.R., Sutton T.B., 1982a. Environmental factors influencing pseudothecial development and ascospore maturation of *Venturia inaequalis*. *Phytopathology* **72**: 1073-1080.
- James J.R., Sutton T.B., 1982b. A model for predicting ascospore maturation of *Venturia inaequalis*. *Phytopathology* **72**: 1081-1085.
- Kennel W., 1990. Die Überwinterung des Apfelschorfs. *Ostbau* **8**: 346-347.
- Lagarde M.P., 1988. Une nouvelle approche de la modélisation a partir de l'évolution de la maturation des ascospores. *Adalia* **7-8**: 14-15.
- MacHardy W.E., 1996. Apple scab. APPS Press, St. Paul, Minnesota.
- MacHardy W.E., Gadoury D.M., 1989. A revision of Mill's criteria for predicting apple scab infection periods. *Phytopathology* **79**: 304-310.
- Mancini G., Cotroneo A., Galliano A., 1984. Evaluation of two models for predicting ascospore maturation of *Venturia inaequalis* in Piedmont (NW Italy). *Rivista di Patologia Vegetale* **20**: 25-37.
- Marquardt D.W., 1963. An algorithm for least square estimation of nonlinear parameters. *Journal of the Society of Industrial and Applied Mathematics* **2**: 431-441.
- Massie L.B., Szkolnik M., 1974. Prediction of ascospore maturity of *Venturia inaequalis* utilising cumulative degree-days. *Phytopathology* **64**: 140.
- Mills W.D., 1944. Efficient use of sulfur dusts and sprays during rain to control apple scab. *Cornell Extension Bulletin* **630**: 1-4.
- Proctor J.T.A., 1982. Prediction of apple scab ascospore discharge using degree days. *Hort Science* **17**: 496.
- Rossi V., Ponti I., Marinelli M., Giosuè S., Bugiani R., 1999. Field evaluation of some models estimating the seasonal pattern of air-borne ascospores of *Venturia inaequalis*. *Journal of Phytopathology* **147**: 567-575.
- Schwabe W.F.S., 1980. Wetting and temperature requirements for apple leaf infection by *Venturia inaequalis* in South Africa. *Phytophylactica* **12**: 69-80.
- Schwabe W.F.S., Jones A.L., van Blerk E., 1989. Relation of degree-day accumulations to maturation of ascospores of *Venturia inaequalis* in South Africa. *Phytophylactica* **21**: 13-16.
- SPSS inc., 1995. Statistical package for social science, ver 6.1 for Windows. Chicago, Michigan.

- St-Arnaud M., Coulombe L.J., Neumann P., Jacob A., 1985. La maturation et l'éjection des ascospores du *Venturia inaequalis* à Frelighsburg (Québec) en relation avec la température et la pluie. *Phytoprotection* **66**: 153-161.
- Stensvand A., Amundsen T., Semb L., 1996. Observations on wood scab caused by *Venturia inaequalis* and *V. pirina* in a apple and pear orchards in Norway. *Norwegian Journal of Agricultural Sciences* **10**: 533-540.
- Stensvand A., Gadoury D.M., Amundsen T., Semb L., Seem R.C., 1997. Ascospore release and infection of apple leaves by conidia and ascospores of *Venturia inaequalis* at low temperatures. *Phytopathology* **87**: 1046-1053.
- Stensvand A., Gadoury D.M., Seem R.C., Amundsen T., Falk S.P., 1998. Some recent advances in epidemiology of apple scab. *Proceedings of 7th International Congress of Plant Pathology, Edimburg* 1998, 3: 6.50. (Abstract).
- Sutton T.B., Jones A.L., 1976. Evaluation of four spore traps for monitoring discharge of ascospores of *Venturia inaequalis*. *Phytopathology* **66**: 453-456.
- Teng P.S., 1981. Validation of computer models of plant disease epidemics: a review of philosophy and methodology. *Journal of Plant Disease and Protection* **88**: 49-63.

Received 15 February 1999

Accepted 24 February 2000