Predicting apple leaf emergence from degree-day accumulation during the primary scab period

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Carisse, O., Jobin, T. and Bourgeois, G. 2008. Predicting apple leaf emergence from degree-day accumulation during the primary scab period. Can. J. Plant Sci. 88: 229–238. The severity of primary infections of apple scab (Venturia inaequalis) is mainly determined by three components: the amount of primary inoculum, climatic conditions, and the amount of unprotected susceptible leaves. Prediction tools are available for the first two components but there are no tools to predict the emergence of apple leaves. The objective of this study was to develop degree-day models to predict emergence of both cluster and terminal shoot leaves during the primary scab period. The number of leaves per shoot was monitored during the primary infection period from 2003 to 2005 on three replicate apple trees of the cultivar Summerland McIntosh grafted on different rootstocks (M.9, MM.111, M.26) at one site and on trees of the cultivars Cortland, Empire, Lobo, McIntosh, Paulared and Spartan at two sites. There were no significant differences in the area under the leaf emergence curve (AULEC) for the different rootstocks and cultivars. The models were thus developed on data pooled over years, sites and cultivars. The rate of change in apple leaf emergence in response to degree-days (base temperature 5°C) accumulated from Apr. 01 was nonlinear with an initial lag phase followed by a linear response reaching a maximum after which the rate remained low or reached zero (no more new leaves). This response was well described by the Richards ($R^2 = 0.91$) and the Weibull ($R^2 = 0.96$) functions for the emergence of cluster and terminal shoot leaves, respectively. The models were tested against data not used for model development and provided an adequate prediction of the number of leaves per shoot $(R^2 = 0.92 \text{ and } 0.97)$. This new tool can be used to improve timing of fungicide applications against primary apple scab infections.

Key words: Leaf development, phenology model, Malus domestica Borkh., Venturia inaequalis (Cke.) Wint

Carisse, O., Jobin, T. et Bourgeois, G. 2008. Prévision de l'émergence des feuilles de pommier à partir de l'accumulation des degrés-jours durant la période de tavelure primaire. Can. J. Plant Sci. 88: 229–238. La sévérité des infections primaires de la tavelure (Venturia inaequalis) est déterminée par trois facteurs: la quantité d'inoculum primaire, les conditions climatiques, et la quantité de feuilles sensibles non-protégées. Des outils prévisionnels sont disponibles pour les deux premiers facteurs mais pas pour la prévision de l'émergence des feuilles. L'objectif de cette étude était de développer des modèles de prévision de l'émergence des feuilles de pousses de bouquet floral et de pousses végétatives durant la période des infections primaires à partir des degrés-jours. Le nombre de feuilles par pousse a été noté durant la période des infections primaire de 2003 à 2005 sur trois pommiers de la variété Summerland McIntosh greffés sur différents porte-greffes (M.9, MM.111, M.26) sur un site et des variétés Cortland, Empire, Lobo, McIntosh, Paulared et Spartan sur deux sites. Aucune différence significative entre l'aire sous la courbe d'émergence foliaire obtenue pour les différents porte-greffes et variétés n'a été observée. Le modèle a donc été développé à partir des données combinées. Le taux d'émergence en fonction de l'accumulation des degrés-jours (température de base 5°C) depuis le 1^{er} avril était non-linéaire avec une phase de latence initiale suivie par une phase d'augmentation linéaire du taux jusqu'à l'atteinte d'un plateau. Le patron d'émergence foliaire a été bien décrit par les modèles de Richards ($R^2 = 0.91$) et de Weibull ($R^2 = 0.95$) pour les feuilles de pousses de bouquet floral et de pousses végétatives. Ces modèles, testés avec des données indépendantes ont permis une bonne prévision du nombre de feuilles par pousse ($R^2 = 0.92$ et 0.97). Ce nouvel outil pourra être utilisé pour améliorer le positionnement des applications de fongicides durant les infections primaires de tavelure.

Mots clefs: Développement foliaire, Malus domestica Borkh., modèle phénologique, Venturia inaequalis (Cke.) Wint

In most non-arid growing areas, the primary disease affecting apple is apple scab [Venturia inaequalis (Cke.) Wint.] and most fungicide treatments are directed at its management (MacHardy 1996). Epidemics of apple scab are initiated by ascospores produced on infected leaves that have overwintered from the previous

season. These ascospores are released over a period of 5 to 10 wk, with a period of high ascospore ejection during the pink to petal fall apple phenological stages and infect the newly emerged leaves (Szkolnik 1974). Each primary apple scab lesion will produce large amounts of conidia that are responsible for summer epidemics. Most management strategies aim at controlling ascospore infections in order to avoid summer epidemics. In the spring, growers time their fungicide sprays based on a calendar program or based on risk

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of scab development (MacHardy 1996). In the latter case, the risk is estimated mainly from the stage of ascospore maturation and the severity of the infection period (Gadoury and MacHardy 1982; MacHardy and Gadoury 1989; Mills 1944; Schwabe et al. 1989). However, the risk of infection is also influenced by apple leaf development since apple leaves are susceptible to infection by *V. inaequalis* only when they are expanding and become resistant once fully expanded (Schwabe 1980; MacHardy 1996; MacHardy et al. 2001). As a consequence, the risk of apple scab infection varies during the spring according to apple leaf emergence.

Apple (Malus domestica Borkh.) physiology has been extensively studied (Corelli-Grappadelli and Lakso 2004; Johnson and Lakso 1985; Wünsche and Lakso 2000a,b). Vegetative apple development includes extension of shoots, leaves, thickening of stems and expansion of the rooting system. Early-season growth relies on stored carbohydrate and nitrogenous reserves produced from photosynthetic activity of the previous season (Lakso et al. 1999). The rate of development of apple trees is dependent on several environmental factors including temperature, light and humidity. The effect of temperature on growth and fruit production is complex affecting all physiological processes. However, each stage of tree development requires a certain amount of thermal units to reach the following stage (Seem and Szkolnik 1978; Corelli-Grappadelli et al. 1994).

In theory, the number of thermal units required to complete an organism's development does not vary and the combination of temperature, between the minimum and maximum thresholds, and time will always be the same (Bonhomme 2000). This combination of temperature and time is often expressed in degree-days, growing degree-days or degree-hours (Bonhomme 2000). To our knowledge, there is no information available on apple leaf emergence in relation to climatic conditions with the exception of Johnson and Lasko (1985) who reported that vegetative shoot extension was linearly related to degree-days.

The foliage of apple can be classified as terminal (or vegetative) or cluster (or spur). The proportion of each leaf group depends on tree age and vigor, crop load, training system and pruning practices. Generally, young trees will have a high proportion of terminal leaves and this trend reverses as the tree ages and begins to bear fruits. The goal of this research was to examine the pattern of apple leaf emergence during the primary scab period for Summerland McIntosh on three rootstocks and for six other apple cultivars, and to predict leaf emergence on cluster and terminal shoots as a function of degree-day accumulation.

MATERIALS AND METHODS

Influence of Rootstocks and Cultivars on Leaf Emergence

To evaluate the influence of rootstock on apple leaf emergence, a first set of experiments was conducted during the springs of 2003 and 2004 at a commercial orchard located in Saint-Grégoire, Quebec, Canada (lat. 45°36′00″N; long. 73°15′00″W). Apple leaf emergence was monitored on mature trees of the cultivar Summerland McIntosh grafted on rootstocks M.9, M.26, and MM.111 planted at a distance of about 4.5 m between rows and 2.5 m within rows. Early in the season, before bud break, three trees per rootstock were selected at random and 10 to 15 terminal shoots per tree were tagged. The number of unfolded leaves per shoot was counted every 2 to 3 d from Apr. 30 to Jun. 10 and from Apr. 22 to Jun. 17 in 2003 and 2004, respectively. An unfolded leaf was defined as a leaf showing a "U" shape with an angle of at least 45° between upper surface edges.

To evaluate the influence of cultivar on leaf emergence, a second set of experiments was conducted during the springs of 2003, 2004, 2005 at the Agriculture and Agri-Food Canada experimental farm located in Frelighsburg (lat. 45°4′00″N; long. 73°15′00″W) and at a commercial orchard located in Saint-Paul d'Abbotsford (lat. 45°44′00″N; long. 72°87′00″W), Québec, Canada. At each site, leaf emergence was monitored on six apple cultivars: Cortland, Empire, Lobo, McIntosh, Paulared and Spartan grafted on various rootstocks planted at a distance of about 4.5 m between rows and 2.5 m within rows. These cultivars were selected because they represent up to 85% of the cultivars grown in Quebec, Canada. At the beginning of the spring before bud break, three trees per cultivar were selected at random within the orchard blocks. For each tree, 10 shoots were selected at random for both the cluster and terminal shoot leaves. On each tree, care was taken for selecting 50% of the shoots as terminals and 50% as clusters even though this proportion changed slightly later in the season because of the difficulty of determining terminal and cluster shoots before bud break. The number of unfolded leaves per shoot was counted every 2 to 3 d from Apr. 30 to Jun. 19, from Apr. 21 to Jul. 01, and from Apr. 18 to Jul. 06, in 2003, 2004, and 2005, respectively.

Data on the effect of rootstock and cultivar on leaf emergence were analyzed with the analysis of variance of area under the leaf emergence curve (AULEC). The AULEC was calculated using Eq. 1:

$$AULEC = \sum_{i=1}^{n} ((y_i + y_{i-1})/2)^* (t_i - t_{i-1})$$
 (1)

in which n is the number of assessment times, y is the mean number of leaves per shoot and t is time in days. Analysis of variance (ANOVA) was used to test the

effects of rootstock and cultivar on AULEC. Fisher's LSD was used to detect significant differences among means (AULEC) at P = 0.05. Statistical analyses were conducted using the SAS software program (SAS Institute, Inc. version 9.1, Cary, NC.).

Model Development

Data collected from the experiments on the effects of cultivar on leaf emergence conducted from 2003 through 2005 were used for the model parameterization. Each year, 20 shoots out of a total of 30 shoots (3 trees \times 10 shoots per tree) were selected at random and used for model development for a total of 720 data sets (3 years $\times 2$ sites $\times 6$ cultivars $\times 20$ shoots). Each year, 10 shoots per set of three trees were selected at random and not used for model development for a total of 360 data sets (3 years \times 2 sites \times 6 cultivars \times 10 shoots). An additional year of data was collected in 2006 at the Agriculture and Agri-Food Canada experimental farm, in Frelighsburg from Apr. 18 to Jun. 25 following the methodology described above for a total of 60 data sets (6 cultivars \times 10 shoots).

Daily maximum (T_{max}) and minimum (T_{min}) temperatures were obtained from weather stations located at the experimental farm and at less than 5 km from the commercial orchards. Degree-days (DD) were calculated using the minimum-maximum method with a base temperature (T_{base}) of 5°C (Johnson and Lakso 1985) and accumulated from 01 April. Daily degree-days were calculated as:

$$DD = [(T_{max} + T_{min})/2] - 5$$
 (2)

To describe the pattern of cluster and terminal shoot leaf emergence as a function of degree-days, selected response models were fitted to the data. Based on the observed pattern of leaf emergence, three non-linear sigmoid models; Richards (3), Weibull (4), and logistic (5) (Campbell and Madden 1990) were tested for their reliability in predicting the number of leaves per shoot.

LE = B{1 - [1 - D^(1-E)]
×exp(-Cx)}^[1/(1-E)] where E
$$\Leftrightarrow$$
 1 (3)

$$LE = B\{1 - \exp[-(Cx)^{D}]\}$$
 (4)

$$LE = B/[1 + (1/D - 1) \exp(-Cx)]$$
 (5)

where LE is the leaf emergence expressed as the number of leaves per shoot, DD is degree-days in Base 5°C accumulated from Apr. 01, and B, C, D and E are regression parameters. In these equations, A is the intercept and x = 0 when DD <A, and to x = DD-Awhen DD \geq A. DD is the number of cumulative degreedays (Tbase = 5° C, from 1 April). For the purpose of measuring the accuracy of the model fittings, error sum squares (SSE), root mean squares error (RMSE),

and coefficient of determination R^2 were considered. Analysis of residual was also used as a model selection criterion, which included randomness, normality and distribution of residuals. All models were also evaluated by performing a simple regression analysis between the predicted values and the corresponding observations as paired data (goodness of fit between predicted and observed values). Analyses of these regressions were done by testing whether the intercept was significantly different from zero, the slope from one and if the appropriate F value was significant (Dent and Blackie 1979).

RESULTS

For both cluster and terminal shoot leaves, the patterns of leaf emergence over time on trees grafted on different rootstocks were similar (Fig. 1). For the cluster leaves, leaf emergence was delayed on the rootstocks MM.111 and M.26 rootstock in 2003 when compared with the other rootstocks (Fig. 1A). However, the area under the leaf emergence curve for rootstocks MM.111 (AULEC = 9.87), M.9 (AULEC = 9.45), and M.26(AULEC = 9.46) was not significantly different at the 0.05 level of confidence (LSD value = 1.22). For the terminal shoot leaves, the pattern of leaf emergence over time was similar for all rootstocks (Fig. 1B). Similarly, the area under the leaf emergence curve for rootstocks MM.111 (AULEC = 21.68), M.9 (AULEC = 30.87), and M.26 (AULEC = 29.68) was not significantly different at the 0.05 level of confidence (LSD value = 3.41).

Over the 3 yr of the experiment and for both sites the pattern of leaf emergence within the same year and the same site was similar among the six cultivars (Figs. 2 and 3). The first cluster leaf emerged on Apr. 30 (day 120) to May 10 (day 130) depending on year and site. The subsequent leaves emerged rapidly until about May 10 (day 130) to May 20 (day 140) to reach a maximum of six to eight leaves. From that point on, almost no new leaves emerged on cluster shoots (Fig. 2). When the AULEC for the cluster leaves were analyzed, there was a significant effect of year and site (P = 0.0023, 0.0082,respectively) but not of cultivar (P = 0.1421).

The pattern of leaf emergence was different for the terminal leaves when compared with the cluster leaves. On terminal shoots, the first leaf emerged from May 01 (day 121) to May 10 (day 130) depending on year and site. Emergence of subsequent leaves was gradual until the end of the sampling period, which was fixed at the end of the primary scab period. When the AULEC for the terminal leaves were compared, there was a significant effect of years and sites (P = 0.0009, 0.0006,respectively) but no significant effect of cultivars (P =0.2690).

When all observations were pooled, the number of leaves per cluster shoot was low until approximately 25 degree-days were accumulated from Apr. 01, then the number of leaves per shoot increased rapidly to reach a maximum of six to eight leaves per shoot when 180 to 200 degree-days were accumulated. All models provided

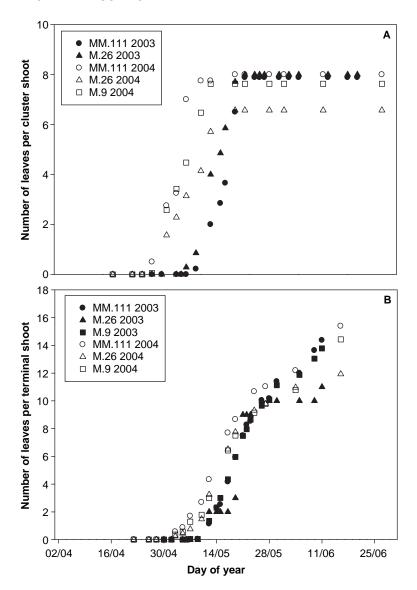


Fig. 1. Number of leaves per cluster (top) and terminal (bottom) shoot in 2003 and 2004 on apple trees grafted on different rootstocks (M.9, MM.111, M.26).

adequate fit to the observed data (Table 1). Selection of the best model was thus made based on smallest SSE and on distribution of residuals. Based on these criteria, the Richards model was selected because of random distribution of residuals and proportionally small residuals from 25 to 200 cumulative degree-days, the period during which most cluster leaves emerged (Fig. 4). The model that fit best the data was of the form:

LE = 7.4284
$$\{1-[1-0.0008^{(1-1.6516)}]$$

 $\times \exp(-0.0507x)\}^{[1/(1-1.6516)]}$ (6)

where x = 0 when DD < 24.2193 x = DD - 24.2193 when DD ≥ 24.2193 where LE is the number of leaves per cluster shoot and DD is cumulative degree-days. The regression of the predicted values against the observed values was significant (P < 0.0001, $R^2 = 0.91$). The intercept was 0.0286, which was not significantly different from zero (P = 0.6697) and the slope was 0.9959, which was not significantly different from 1 (P = 0.7002).

When all observations were pooled, the number of leaves per terminal shoot was small until approximately 110 degree-days, and then the number of leaves per shoot increased gradually to reach 14 to 20 leaves per shoot when about 700 degree-days were accumulated. All models provided adequate fit to the observed data (Table 2). Selection of the best model was thus made based on the smallest error sun of squares (SSE) and on

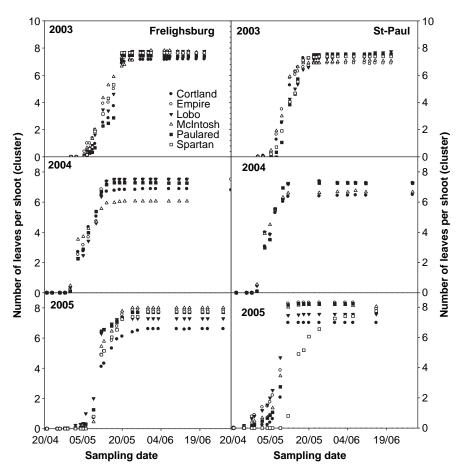


Fig. 2. Number of leaves per cluster shoot in 2003, 2004 and 2005 on apple trees of the cultivars Cortland, Empire, Lobo, McIntosh, Paulared and Spartan at the Frelighsburg (Quebec) and St-Paul (Quebec) sites.

distribution of residuals. Based on these criteria, the Weibull model was selected because of random distribution of residuals and proportionally small residuals from 100 to 600 degree-days, the period during which most terminal leaves emerged (Fig. 5). The model that fit best the observation was of the form:

LE = 23.0231
$$\{1 - \exp[-(0.0025x)^{0.8380}]\}$$
 (7)

where x = 0 when DD < 110.3238 x = DD-110.3238 when $DD \ge 110.3238$

where LE is the number of leaves per terminal shoot and DD is cumulative degree-days. The regression of the predicted values against the observed values was significant (P < 0.0001, $R^2 = 0.96$). The intercept was 0.0182, which was not significantly different from zero (P = 0.7444) and the slope was 1.0019 which was not significantly different from 1 (P = 0.7797).

Both models were validated against data not used for model development. A total of 480 data sets were used to compare predicted and observed number of leaves per cluster or terminal shoot (Figs. 6 and 7). With the

exception of a few cluster leaves that emerged before the predicted time, the model adequately predicted cluster leaf emergence from cumulative degree-days. The regression of the predicted values against the observed values was significant (P < 0.0001, $R^2 = 0.92$). The intercept was 0.0370, which was not significantly different from zero (P = 0.6829) and the slope was 0.9671, which was not significantly different from 1 (P = 0.6345). For the terminal leaves, the model provided a good prediction of leaf emergence at degree-days from 0 to about 600 after which the model tended to underestimate the number of leaves per terminal shoot (Fig. 7). The regression of the predicted values against the observed values was significant (P < 0.0001, $R^2 =$ 0.97). The intercept was -0.0942, which was not significantly different from zero (P = 0.2041) and the slope was 1.0194 which was not significantly different from 1 (P = 0.3697).

DISCUSSION

Emergence of cluster and terminal apple leaves was monitored over several years for different rootstocks, cultivars and sites. The pattern of both cluster and

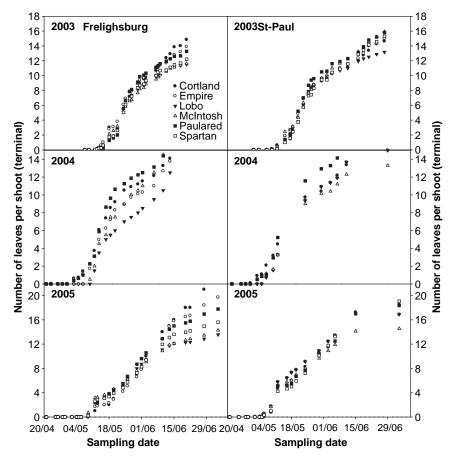


Fig. 3. Number of leaves per terminal shoot in 2003, 2004 and 2005 on apple trees of the cultivars Cortland, Empire, Lobo, McIntosh, Paulared and Spartan at the Frelighsburg (Quebec) and St-Paul (Quebec) sites.

Table 1. Parameter estimates for each model fitted to the observations of the number of leaves per cluster shoots								
Model ^z	Parameter estimated	Asymptotic standard error	R^2	SSE^y	RMSE ^x	F value		
Richards								
A	24.2193	264.2450	0.91	782.8788	0.9597	2168.00		
В	7.4284	0.0487						
Č	0.0507	0.0053						
Ď	0.0008	0.0373						
E	1.6516	0.2446						
Logistic								
A	22.3777	9.36E + 06	0.91	784.7622	0.9603	2886.44		
В	7.4130	0.0474						
Č	0.0575	0.0143						
D	0.0023	1259.74						
Weibull								
A	48.2875	14.0735	0.91	789.67	0.9633	2866.73		
В	7.4144	0.0477						
C	0.0112	0.0018						
D	2.9931	0.5767						

^zThe models used were: Richards $LE = B \{1-[1-D^{(1-E)}] \exp(-Cx)\}^{[1/(1-E)]}$, where E <>1 (Eq. 3), Weibull $LE = B \{1-\exp[-(Cx)^D]\}$ (Eq. 4) and logistic $LE = B/[1+(1/D-1) \exp(-Cx)]$ (Eq. 5).

ySSE is the error sum of squares.

^{*}RMSE is the square root of error mean square.

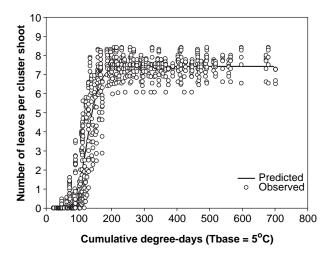


Fig. 4. Number of leaves per cluster shoot in 2003, 2004 and 2005 as a function of degree days (Base 5°C) accumulated from Apr. 01. Each point is an average of 10 observations (10 shoots per tree). The response line was generated from the following equation: LE = $7.4284 \{1-[1-0.0008 (1-1.6516)] \text{ exp}$ (-0.0507x)^[1/(1-1.6516)], x = 0 when DD < 24.2193; x = DD24.2193 when DD ≥ 24.2193 , where LE is the number of leaves per cluster shoot and DD is cumulative degree-days.

terminal leaf emergence was not affected by rootstock or cultivar, although variations were observed among years and sites. Overall, the first cluster leaves emerged from the end of April to early May, and then the number of leaves per cluster shoot increased rapidly to reach a maximum of about eight leaves per shoot in mid-May. The pattern of leaf emergence was different for the terminal leaves; the first leaves emerged during the first week of May and emergence of subsequent leaves was

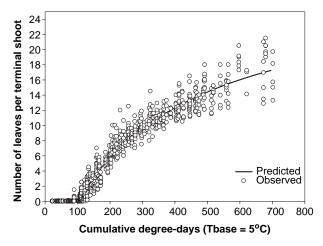


Fig. 5. Number of leaves per terminal shoot in 2003, 2004 and 2005 as a function of degree days (Base 5°C) accumulated from Apr. 01. Each point is an average of 10 observations (10 shoots per tree). The response line was generated from the following equation: LE = $23.0231 \{1-\exp[-(0.0025x)^{0.8380}]\}$, x = 0 when $DD < 110.3238 \text{ x} = DD 110.3238 \text{ when } DD \ge 110.3238, \text{ where}$ LE is the number of leaves per terminal shoot and DD is cumulative degree-days.

gradual and at a lower rate than for the cluster leaves until the end of June, which corresponded to the end of the primary scab infection period. Because temperature has been reported to be the main factor affecting early season leaf emergence (Johnson and Lakso 1985), cumulative degree-days were used as a predictor of leaf emergence. These patterns of leaf emergence on cluster and terminal shoots as a function of cumulative degree-days (Tbase 5°C) were well described with the Richards and the Weibull models, respectively. When

Table 2. Parameter estimates for each model fitted to the observations of the number of leaves per terminal shoots									
Model ^z	Parameter estimated	Asymptotic standard error	R^2	SSE ^y	RMSE ^x	F value			
Weibull A B C	110.3028 23.0231 0.0025	1.4203 1.6880 0.0003	0.96	1069.31	1.2521	6797.13			
D Richards A B	0.8380 105.5689 18.3837	0.0353 1.7401 0.5629	0.95	1095.01	1.1330	4967.36			
C D E	0.0039 0.0012 0.0002	0.0004 0.0042 0.0655							
Logistic A B C D	16.4583 14.2152 0.0219 0.0244	3.68E+07 0.0026 0.0035 14305.20	0.93	1850.71	1.4721	3807.10			

^zThe models used were: Richards $LE = B \{1-[1-D^{(1-E)}] \exp(-Cx)\}^{[1/(1-E)]}$, where E <> 1 (Eq. 3), Weibull $LE = B \{1-\exp[-(Cx)^D]\}$ (Eq. 4) and logistic LE = $B/[1+(1/D-1) \exp(-Cx)]$ (Eq. 5).

ySSE is the error sum of squares.

^xRMSE is the square root of error mean square.

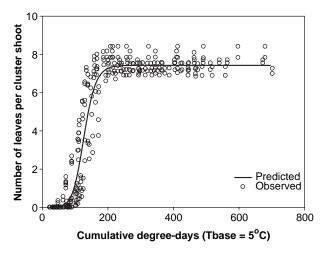


Fig. 6. Number of leaves per cluster shoot in 2003 through 2006 as a function of degree days (Base 5°C) accumulated from Apr. 10. Each point is an average of 10 observations (10 shoots per tree) that were not used to develop the model. The response line was generated from the following equation: LE = 7.4284 {1–[1–0.0008 $^{(1-1.6516)}$] exp(-0.0507x)} $^{[1/(1-1.6516)]}$, x=0 when DD <24.2193; x=DD -24.2193 when DD \geq 24.2193, where LE is the number of leaves per cluster shoot and DD is cumulative degree-days.

adjusted to the observed number of leaves per shoot the models explained 92 and 96% of the variation in number of cluster and terminal leaves per shoot, respectively. The models were validated against independent data and predicted 91 and 97% of the variation

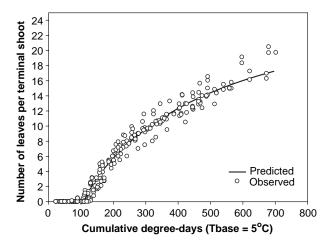


Fig. 7. Number of leaves per terminal shoot in 2003 through 2006 as a function of degree days (Base 5°C) accumulated from Apr. 10. Each point is an average of 10 observations (10 shoots per tree) that were not used to develop the model. The response line was generated from the following equation: LE = 23.0231 {1-exp[$-(0.0025x)^{0.8380}$]}, x = 0 when DD < 110.3238, x = DD-110.3238 when $DD \ge 110.3238$, where LE is the number of leaves per terminal shoot and DD is cumulative degree-days.

in number of cluster and terminal leaves per shoot, respectively.

Apple scab progress is intimately related to apple phenological development. Most years, the first mature ascospores are ready to be discharged at the apple bud break stage and the peak in ascospore release typically occurs from the tight cluster to the petal fall stage, which is also the peak developmental time for apple leaves (Szkolnik 1974). Towards the end of the primary infection period, the rate of leaf emergence is lower than early in the season and most leaves are resistant to V. inaequalis, reducing the risk of scab infection (Schwabe 1980). The critical time for spraying fungicide against apple scab is during the peak of ascospore release and the period of rapid leaf emergence. Currently, most apple scab management programs are "pathogen oriented" in other words based on the estimated amount of mature ascospores of V. inaequalis, and on the predicted severity of ascospore infection (MacHardy 1996). However, another strategy more "host oriented" could be to prevent ascospore infections by protecting new leaves (susceptible to V. inaequalis) with appropriate fungicides. In practice, growers use information on ascospore maturation, severity of infection and, intuitively, the amount of susceptible leaves. The leaf emergences models are intended for growers and advisors to facilitate decision-making on fungicide timing.

There have been many observations, but relatively few studies on the effect of temperature on apple tree growth. Most of these studies were aimed at understanding the effect of temperature on shoot or fruit growth to predict yield (Tromp 1977; Lakso 1980; Bergh 1990). Johnson and Lasko (1985) found that extension shoot growth was linearly related to cumulative degreedays. Tromp (1992, 1993) and Grauslund (1978) reported that in the 12–25°C range, higher temperatures generally stimulated shoot growth. Almost all studies reporting the effect of temperature on shoot growth focused on shoot length. In their study, Johnson and Lakso (1985) found a linear relationship between shoot length and cumulative degree-days (Tbase 4°C) from bud break, between leaf area per shoot and cumulative degree-days (Tbase 4°C) from bud break and between shoot length and leaf area per shoot. They suggested that total leaf area could be predicted from cumulative degree-days. Although total leaf area is a critical factor affecting the probability that an ascospore will reach a leaf and cause an infection, it does not account for ontogenic resistance as it includes all leaf tissues (susceptible and not susceptible). Another approach has been to predict phenophases from cumulative degreedays. Seem and Szkolnik (1978) developed a regression equation that relates apple phenophases to cumulative degree-days and cumulative precipitation. In practice, phenophases are relatively easy to obtain from direct observations in the orchard. Growers intuitively use phenological stages to relax or intensify their fungicide

spray program. In our study we found a nonlinear relationship between number of leaves per cluster or terminal shoot and cumulative degree-days. The Richards and Weibull models provided a good description of the response of leaf emergence to degree-days accumulated. The parameters of both models have biological meaning including the asymptote which represents the maximum number of leaves per shoot and the rate of leaf emergence.

This study was initiated, in part, to address apple growers' concerns regarding the need to improve timing of fungicide applications during the primary scab period under increasing pressure to reduce the environmental impact of fungicide. The objective was, thus, to develop a simple model that could be provided to growers in the form of a table using weather data that are easily available. For these reasons, degree-days were calculated with the minimum-maximum method, a simple method using data that could be collected with a standard min-max thermometer or a more sophisticated device. The biofix (starting point) for degree-days accumulation was set on Apr. 01 based on preliminary analysis, and because at earlier dates, the temperature is generally below the base temperature for apple trees (Johnson and Lakso 1985). Calendar date was chosen as biofix because physiological stages of either the host (e.g., 50% silver tip) or the pathogen (ex. first mature ascospore) are often difficult to estimate and subjective (MacHardy 1996). The biofix will probably need to be validated if the models are to be implemented in other geographical areas. In addition, the models predict leaf emergence rather than leaf area (Beresford et al. 2004) because leaf area must be predicted from hourly temperature, which is not available to most growers. From a management standpoint, it is not necessary to know the exact amount of susceptible leaf tissues, knowing the number of new leaves since the last fungicide application is sufficient for decision making.

Using the models developed in this study, it will be possible for growers to know a few days in advance the expected date for the first leaf emergence, information that could be validated with direct orchard observations. This information could be used to time the first fungicide spray. Subsequent fungicide sprays could then be timed based on the accumulation of degree-days since the emergence of the last leaf or time of last fungicide spray, which is an indication of the number of leaves that are unprotected against V. inaequalis infection.

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