Forecasting Ascospore Dose of *Venturia inaequalis* in Commercial Apple Orchards

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ABSTRACT

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Factors affecting potential ascospore dose (*PAD*) of *Venturia inaequalis* were studied in commercial apple orchards from 1981 to 1984. *PAD* was the product of the numbers of scab lesions per square meter of leaf tissue on terminal shoots at leaf fall, pseudothecia per lesion, asci per pseudothecium, ascospores per ascus, and the proportion of the orchard floor covered by leaf litter at bud break. The number of lesions per square meter of leaf tissue was estimated from the numbers of lesions counted and terminal shoots examined, and the estimated leaf area per shoot. Most lesions on overwintered leaves bore aborted (rather than mature) pseudothecia; however, even when the incidence of infected leaves approached 0%, approximately 3% of the lesions produced mature pseudothecia. Neither the numbers of mature pseudothecia per fertile lesion nor asci per pseudothecium differed significantly ($P = 0.05$) on McIntosh, Cortland, or Delicious leaves, hence they were set at 21.6 and 122, respectively, in calculations of *PAD*. Most leaf decay occurred during winter, and leaf litter density decreased by only 16% from bud break to petal fall. The number of lesions per square meter of leaf tissue at leaf fall was the major determinant of the variance of *PAD* in the predictive model. *PAD* ranged from 13 to 44,544 ascospores/m^2/yr when terminal leaf infection was 0.04 and 9.32%, respectively, in autumn of the previous year. Time shifts in disease progress curves were computed based on infection rates and differences in *PAD*. Delays of 2–22 days suggested that spray programs for apple scab could be delayed in orchards with low amounts of overwintering inoculum. The significance of *PAD* to predictions of ascospore maturity, spore trapping, and the use of postharvest eradicant treatments for management of apple scab were also discussed.

Additional key words: disease management, epidemiology, inoculum density.

In 1980, F. H. Lewis (29) chronicled the evolution of the chemical control program for apple scab. Although application schedules, fungicides themselves, and equipment for applying fungicides had changed through the years, the strategy of chemical control remained essentially unchanged from that recommended by Keitt and Jones in 1926 (26). Lewis recognized the inherent inflexibility of some chemical control programs and proposed a multifactored system to adjust the rate and timing of fungicide applications. MacHardy and Jeger (31) came to a similar conclusion, and described an analysis that related mathematically the components contributing to disease occurrence. One part of the analysis dealt with density of overwintering populations of *Venturia inaequalis* (Cke.) Wint., or potential ascospore dose (*PAD*) expressed as the total seasonal production of ascospores per square meter of orchard floor.

The effects of *PAD* on disease development are poorly understood (18,31), are not considered in most disease management programs, and are likely to remain so without further investigation. Two fundamental assumptions implicit in many apple scab management programs are that inoculum is sufficiently abundant at bud break to require fungicidal protection (18), and that even orchards with low amounts of inoculum are subjected to influxes of wind-dispersed ascospores from abandoned orchards. These assumptions were undoubtably valid in the 1940's, when 10% foliar infection was a characteristic of a successful control program. However, modern fungicides and spray equipment have greatly reduced the incidence of apple scab in commercial orchards (29). Several researchers have shown that reducing the amount of overwintering inoculum does affect disease incidence and severity (1,3,5,7,14,16,21,22,27,34,35). Furthermore, ascospores of *V. inaequalis* are discharged and dispersed during rain; a time when mass flux is strongly downward (19). Many studies indicate that the incidence of apple scab is a function of the amount of inoculum within an orchard, not that from outside an orchard.

PAD must be measured at the levels of infection common in commercial orchards, and ideally should be forecasted to allow time for the information to be used in decisions to either manipulate *PAD* or alter other management practices to reduce the cost of controlling apple scab without jeopardizing efficacy of control. The model proposed by MacHardy and Jeger (31), although theoretical, established the framework for an investigation to develop a working model to forecast *PAD*. Our objective was to work within this framework to produce a functional model to forecast *PAD* in commercial orchards.

MATERIALS AND METHODS

Orchard sites. Studies conducted in nine commercial orchards in New Hampshire will hereafter be identified by the following codes: I, Apple Acres, Windham; II, Applecrest Orchards, Hampton; III-A and III-B, Avaloch Farm, Loudon, eastern and western plantings, respectively; IV-A and IV-B, Gould Hill Orchards, Contoocook, semidwarf and standard plantings, respectively; V, Moose Hill Orchards, Londonderry; VI, Poverty Lane Orchard, West Lebanon; VII, Sunnycrest Orchards, Londonderry; VIII, Wildwood Orchard, Northwood; and IX, Woodmont Orchards, Winn Mountain. Studies were also conducted at three research orchards at the University of New Hampshire: X, Kingman Farm Orchard, Madbury; XI, Mast Road Orchard, Durham, where trees were sprayed at 7- to 14-day intervals with the fungicides captan (XI-A), Dikar (XI-B), or thiophanate-methyl (XI-C); and XII, Woodman Horticultural Farm, Durham.

Disease incidence and severity. We conducted our studies in plantings of cultivars McIntosh, Cortland, and Delicious. Over 90% of New Hampshire's apple acreage is comprised of these cultivars and they were present at each commercial orchard site. Assessment of disease incidence and severity was restricted to leaves of terminal shoots for simplicity, because lesions are most frequently found on later-formed vegetative shoots that continue growth after cessation of the spray program (21), and because preliminary observations indicated that approximately 75% of the

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foliage of McIntosh, Cortland, and Delicious trees was borne on vegetative shoots.

Disease incidence and severity were recorded just before leaf fall in 1981, 1982, and 1983 at locations in Table 1. The numbers of infected leaves and lesions per scabbed leaf were recorded on 20 terminal shoots of 10 McIntosh, Cortland, and Delicious trees at each commercial orchard and at site XII. Disease incidence and severity were also assessed by examining 20 terminal shoots on each of three McIntosh trees used for the previously described fungicide trials at site XI. Records of the fungicide spray programs were obtained for each site.

In September of 1981, 1982, and 1983, the leaves of 30 terminal shoots selected at random from McIntosh, Cortland, and Delicious trees at sites III-A, IV-A, V, and VII were counted and the total leaf area of each shoot was measured with a leaf area meter (LI-COR model LI-3000; Lambda Instruments Corp., Lincoln, NE). Comparisons of mean leaf area per terminal shoot and mean number of leaves per shoot were made based on year of collection, site, and cultivar to determine if significant differences ($P = 0.05$) in area or leaves per shoot were caused by these factors.

Pseudothecia per lesion. Between 100 and 300 scabbed leaves collected from McIntosh trees at each site listed in Table 1 were overwintered in wire mesh trays at site XI. Once asci had begun to form in the spring, the leaves were incubated at 10 C, 90% RH for 7–14 days. The leaves were then examined using a transmitted-light dissecting microscope (×25) and the number of ascocarps of *V. inaequalis* associated with each lesion was recorded. Fruiting bodies not identified at ×25 were removed and examined at × 100–675 as described by Gadoury and MacHardy (10).

In October of 1983, scabbed leaves collected from McIntosh, Cortland, and Delicious trees at site V were overwintered in wire mesh trays at site XI until 10 February 1984. Twenty leaves of each cultivar were then incubated for 30 days at 10 C, 90% RH, and the number of pseudothecia that formed per lesion was determined as above.

Asci per pseudothecium. The number of asci that formed in pseudothecia of *V. inaequalis* was assessed as previously described (10) at weekly intervals during 1981–1983 at site XI and during 1982 at sites IV-A and V.

Scabbed leaves collected in October of 1983 from McIntosh, Cortland, and Delicious trees at site V were overwintered in wire mesh trays at site XI until 10 February 1984. Twenty leaves of each cultivar were then incubated as above, and the number of asci that formed in ascocarps from leaves of each cultivar was assessed (10).

Leaf litter density. Four orchards were selected for variability with respect to age, topography, cultivars, and planting density. Site X, established in 1965, covered 0.6 hectares. The trees were semidwarf McIntosh and Cortland on MM-106 rootstock planted at 222 trees per hectare. Site III-A covered 12 hectares of rolling hills and was established in 1975. The trees were semidwarf McIntosh, Cortland, Delicious, and Empire on M-7 rootstock planted at 282 trees per hectare. Site IV-B was established in 1913 in the foothills of the White Mountain range, contained numerous cultivars on seedling rootstock, and was planted at 62 trees per hectare. Site V was established in 1960 on 12 hectares of flatland in the Merrimack River Valley, contained semidwarf McIntosh, Cortland, and Delicious trees on M-7 rootstock, and was planted at 353 trees per hectare.

A point-intercept method (32) was used to assess leaf litter density (*LLD*). At four trees randomly selected from each orchard, four transects were run on diagonals across the adjacent rows. A measuring tape was stretched along each transect, and beginning 0–30 cm from the end of the tape, and at 30 cm intervals thereafter, the presence of leaves under the tape was noted. *LLD* was computed as the proportion of the points under which leaves were found. *LLD* was assessed at leaf fall, and at the silver tip, bloom, and petal fall growth stages of McIntosh fruit buds the following spring.

Leaf decay during spring was monitored at site XI in 1981 and 1982. Three 50-leaf samples collected just prior to bud break were placed in wire mesh trays, and at 2-wk-intervals the area of each sample was measured, the leaves were air-dried for 24 hr, weighed, and then returned to the orchard.

RESULTS

Lesion density. Year of collection and site had no significant effect on either total leaf area of shoots or mean number of leaves per shoot. McIntosh, Cortland, and Delicious trees produced a mean of 15.6, 15.1, and 18.8 leaves per shoot with total leaf areas of 424, 468, and 396 cm^2, respectively. McIntosh and Cortland trees did not differ significantly in number of leaves per shoot or total leaf area per shoot. Delicious trees produced more leaves per shoot than did McIntosh or Cortland, and the total leaf area of Delicious shoots was significantly less that that of Cortland, but not of McIntosh. Combining data from all three cultivars resulted in a mean of 16.5 leaves per shoot with a total leaf area of 430 cm^2.

Disease incidence at leaf fall was low in commercial orchards. In 15 of 19 cases, less than 3% of the leaves were infected, and in 10 cases less than 1% were infected (Table 1). McIntosh, Cortland, and Delicious trees did not differ consistently in percentage of leaves infected or number of lesions per infected leaf. The mode of the number of lesions per infected leaf was 1. Lesions were generally on the adaxial leaf surface, discrete and definitely margined, and less than 1 cm in diameter. Yearly differences in disease incidence were not pronounced except in 1982, when higher incidences of scab existed at sites IV, VI, and IX (Table 1).

Lesion density was computed by dividing the number of lesions counted on leaves of 200 shoots of each cultivar by a mean total leaf area, assuming a mean leaf area per terminal shoot of 430 cm^2. Thus:

$$LD = \Sigma l / \Sigma a$$

in which LD = lesion density (lesions per square meter of leaf tissue at leaf fall), l = lesions counted during assessment, and a = mean leaf area per shoot. The standard error of LD was computed as described by Freese (9).

Pseudothecia per lesion. No consistent relationship was found between the number of mature ascocarps per lesion and fungicide use in commercial orchards, except that the use of fungicides appeared to restrict growth of the subcuticular stromata to the immediate vicinity of the visible lesion. Diffuse stromata as observed by Wilson (38) were found only on leaves from site IX in 1982, where the incidence of disease was unusually high (Table 1).

No significant differences in numbers of mature ascocarps per lesion occurred on McIntosh, Cortland, or Delicious leaves incubated at 10 C; they formed 16, 21, and 13 mature ascocarps per lesion, respectively. Most lesions on McIntosh leaves collected in commercial orchards failed to form mature ascocarps (Table 2). When infertile lesions were examined microscopically, numerous aborted ascocarps of *V. inaequalis* were found in the leaf tissue surrounding the stromata (Fig. 1). The percentage of leaves infected at leaf fall was proportional to the percentage of lesions that produced mature pseudothecia. However, even when the incidence of leaf infection approached 0%, approximately 3% of the lesions still formed mature ascocarps. Regression of the percentage of lesions that produced mature pseudothecia against the percentage of terminal leaves infected at leaf fall yielded a quadratic equation ($R = 0.90$) that allowed fertility to be estimated from assessments of disease incidence (Fig. 2).

Combining data from all sites yielded a mean of 21.6 mature ascocarps per lesion with a standard error of 2.61. Pseudothecial density (PD), the number of mature ascocarps per visible lesion, was computed as the product of lesion fertility and the number of mature pseudothecia per fertile lesion:

$$PD = f \cdot k$$

in which f = the estimated proportion of the lesions that are fertile (Fig. 2), and k = the mean number of mature ascocarps formed per fertile lesion. The standard error of PD was calculated by using an algebraic method (33).

Asci per pseudothecium. Cultivar had no significant effect on the number of asci in pseudothecia. Ascocarps from McIntosh, Cortland, and Delicious leaves produced 101, 103, and 111 asci per

TABLE 1. Incidence and severity of apple scab on shoots in commercial and research orchards in New Hampshire during September of 1981–1983

Year	Orchard	Leaves infected (%)[x]				Lesions per infected leaf				Lesions per 200 shoots			Lesion density (no./m²)[y]
		M	C	D	Mean	M	C	D	Mean	M	C	D	
1981–1982	I	1.13	1.21	1.21	1.18	1.0	1.5	1.2	1.2	37	60	47	5.58
	III-A	3.51	2.90	2.56	2.99	1.3	1.3	1.0	1.2	146	125	85	13.80
	V	0.29	0.20	0.36	0.28	1.1	1.3	2.0	1.5	11	8	24	1.67
	XI-A	0.20	nd[z]	nd	nd	1.0	nd	nd	nd	6	nd	nd	0.70
	XI-B	0.40	nd	nd	nd	1.1	nd	nd	nd	14	nd	nd	1.63
	XI-C	0.46	nd	nd	nd	1.0	nd	nd	nd	15	nd	nd	1.74
1982–1983	III-A	0.22	0.18	0.24	0.21	3.1	1.0	4.8	3.0	23	6	38	2.60
	III-B	0.03	0.06	0.03	0.04	1.0	1.0	1.0	1.0	1	2	1	0.16
	IV-A	9.32	5.45	4.54	6.44	2.2	1.8	2.5	2.2	667	329	368	52.87
	IV-B	4.75	6.06	7.27	6.03	1.6	2.5	1.4	1.8	257	500	331	42.17
	V	0.23	0.30	0.12	0.22	1.1	1.0	1.0	1.1	8	10	4	0.85
	VI	20.16	18.48	21.81	20.15	2.9	2.6	2.4	2.7	1,949	1,603	1,756	205.74
	VII	2.54	2.02	3.13	2.56	1.4	1.3	1.5	1.4	120	87	150	13.84
	VIII	0.52	0.80	0.00	0.44	1.6	1.8	nd	1.7	28	47	0	2.91
	IX	47.82	48.58	58.18	51.49	nd	nd	nd	nd	nd	nd	nd	nd
	XII	0.34	0.00	0.18	0.17	1.0	nd	1.1	1.1	12	0	6	0.70
1983–1984	II	1.81	1.29	2.04	1.71	1.9	1.2	1.8	1.6	114	53	120	11.12
	III-A	0.06	0.00	0.03	0.03	2.0	nd	1.0	1.5	4	0	1	0.19
	IV-A	1.27	1.31	1.71	1.43	1.4	1.2	1.5	1.4	57	53	87	7.64
	V	0.15	0.30	0.00	0.15	1.8	2.3	nd	3.0	8	23	0	1.20
	VII	0.03	0.03	0.00	0.02	1.0	1.0	nd	1.0	1	1	0	0.08
	XII	0.12	0.10	0.03	0.08	2.3	1.0	1.0	1.1	8	3	1	0.47

[x]Estimated percentage of leaves infected based on 16.5 leaves per shoot. M = McIntosh, C = Cortland, and D = Delicious.
[y]Lesion density, expressed in lesions per square meter of leaf tissue, was based on the total leaf area of shoots examined using an average leaf area per shoot of 430 cm².
[z]No data.

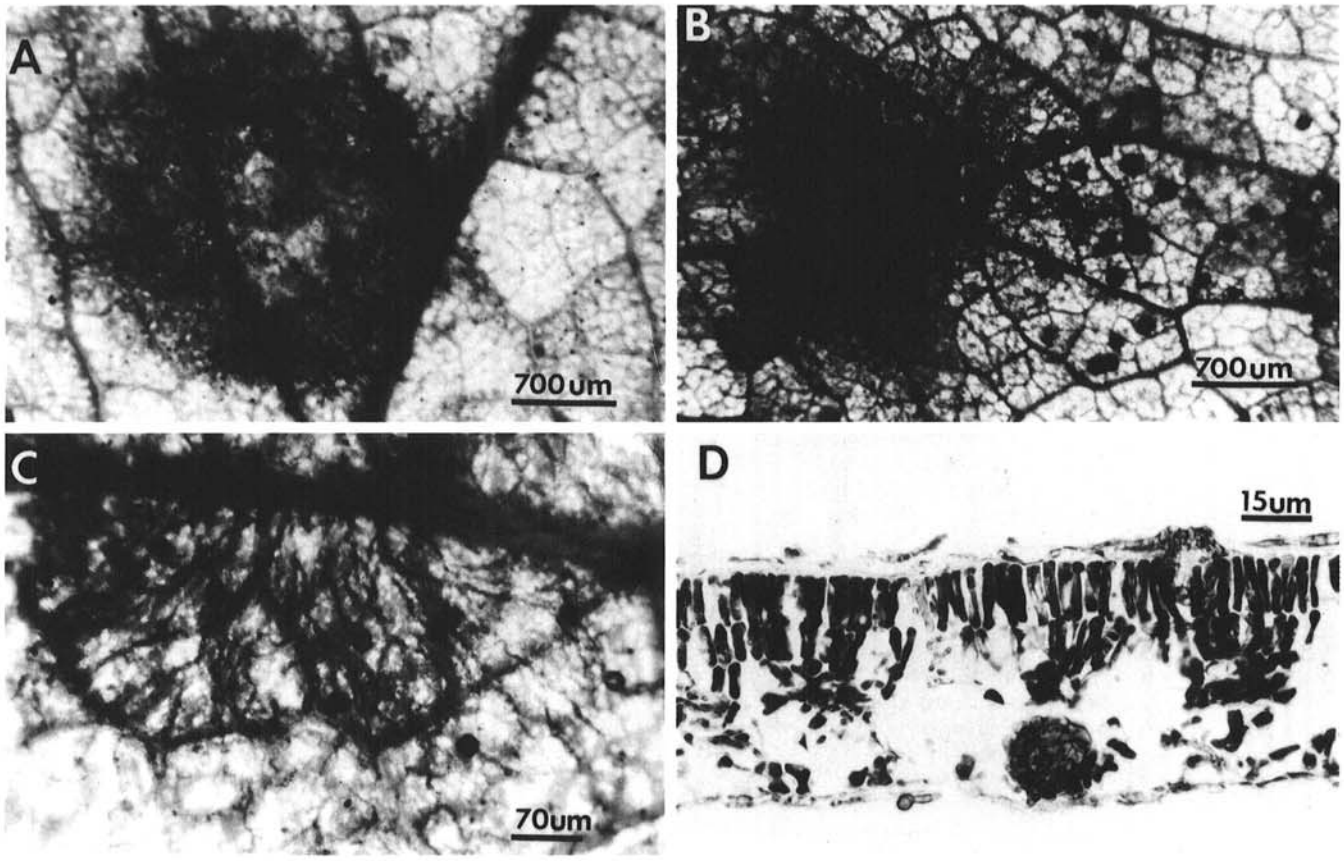

Fig 1. Sterile and fertile stromata, and aborted ascocarps of *Venturia inaequalis*. **A,** Sterile stroma from a fungicide-sprayed leaf 5 mo after leaf fall. **B,** Fertile stroma with mature pseudothecia. **C,** Aborted ascocarps from the periphery of a sterile stroma. **D,** Cross section of aborted ascocarp from the periphery of a sterile stroma.

ascocarp when incubated at 10 C. Pseudothecia from McIntosh leaves overwintered at site XI produced 115, 107, and 139 asci per ascocarp in 1981, 1982, and 1983, respectively, while those overwintered at sites IV-B and V in 1982 formed 109 and 125 asci per ascocarp, respectively. When combined with data reported earlier by Gadoury and MacHardy (10), a mean ascal density (AD) of 122 asci per ascocarp and a standard error of 7.9 was calculated.

Leaf litter density. LLD decreased continuously from leaf fall in late autumn to petal fall the following spring (Table 3). Reductions in LLD averaged 33% from leaf fall to bud break, but only 16% from bud break to petal fall. No consistent relationships were found between LLD, site, year, and planting density. Assessment of LLD at bud break provided an estimate of LLD that did not decrease greatly during the primary infection season. The area and dry weight of the caged leaves at site XI did not decrease significantly ($P = 0.05$) during 1981 or 1982.

Summary of components to forecast *PAD*. An equation for forecasting PAD was constructed by multiplying the above described density functions. The equation was: $PAD = LD \cdot PD \cdot AD \cdot LLD \cdot n$, in which LD was lesion density (lesions per square meter of leaf tissue at leaf fall), PD was pseudothecial density (mature ascocarps per visible lesion), AD was ascal density (asci per ascocarp), LLD was leaf litter density (proportion of the orchard floor covered by leaf litter), and n was the number of ascospores per ascus. For example, at site III-B in 1982–1983, a total of four lesions were counted on 600 terminal shoots (200 shoots from each of three cultivars). The mean leaf area per terminal shoot was 430 cm^2. Therefore, LD = four lesions/25.8 m^2, or 0.155 lesions per square meter. Only 0.04% of the leaves were infected at site III-B in 1982–1983; thus by the equation shown in Fig. 2, it was estimated that 2.67% of the lesions would produce mature pseudothecia. It was estimated that each fertile lesion would produce 21.6 ascocarps, hence $PD = 0.0267 \cdot 21.6$, or 0.577 mature pseudothecia per visible lesion. With AD set at 122 asci per acocarp, there remained only the assessment of LLD. At site III-B in 1982–83, LLD at bud break was 0.292. Therefore, PAD at the site was $0.155 \cdot 0.0267 \cdot 21.6 \cdot 122 \cdot 0.292 \cdot 8$, or 25.48 ascospores per square meter per year. The standard error of the product PAD, computed as described by Freese (9), was 13.

An interactive FORTRAN program was written to forecast PAD and the standard error of PAD. At a low level of infection, such as that at site VII in the fall of 1983 (Table 1), the standard error of PAD was 71% of the forecasted value of PAD, primarily due to the error inherent in assessing LD at low levels of infection (Table 4). The precision of the forecast of PAD increased as leaf infection increased up to approximately 10% infection, again due to a decrease in the error associated with assessment of LD (Table 4). As leaf infection increased above 10%, precision in forecasts of PAD again declined, in this case due to increased error in predicting lesion fertility as the range of data used to develop the equation shown in Fig. 2 was exceeded.

TABLE 2. Incidence of apple scab, lesion fertility, and number of pseudothecia formed per lesion on McIntosh leaves collected in commercial and research orchards during September of 1981–1983

Year	Orchard	Leaves infected (%)	Lesions fertile (%)[z]	Pseudothecia per fertile lesion
1981–1982	I	1.13	3.0	31.0
	III-A	3.51	6.0	20.0
	V	0.29	3.0	13.0
	XI-A	0.20	3.4	42.7
	XI-B	0.40	3.0	11.3
	XI-C	0.46	3.0	8.0
1982–1983	III-A	0.22	3.0	24.7
	III-B	0.03	3.0	39.0
	IV-A	9.32	18.0	10.0
	IV-B	4.75	9.0	22.1
	V	0.23	3.0	16.3
	VI	20.16	28.0	9.8
	VII	2.54	5.0	19.8
	VIII	0.52	3.3	57.0
	IX	47.82	30.0	17.3
	XII	0.34	2.8	21.3
1983–1984	II	1.81	2.6	27.3
	III-A	0.06	2.1	19.7
	IV-A	1.27	2.9	11.3
	V	0.15	2.0	18.0
	VII	0.03	2.5	20.7
	XII	0.12	1.3	14.0

[z]Lesion fertility was expresed as the percentage of scab lesions that produced mature pseudothecia during spring of the year following collection of the infected leaves.

DISCUSSION

Lesion density. The method used to estimate LD required approximately 90 min per orchard and provided a precise estimate of leaf area, but an imprecise estimate of low incidences of disease. Examination of 600 terminal shoots with a mean of 16.5 leaves per shoot yielded a sample size of 9,900 leaves with a combined area of 25.8 m^2 and a standard error of 0.38 m^2, or approximately 1% of the estimated value. However, a sample size of 9,900 was too small to

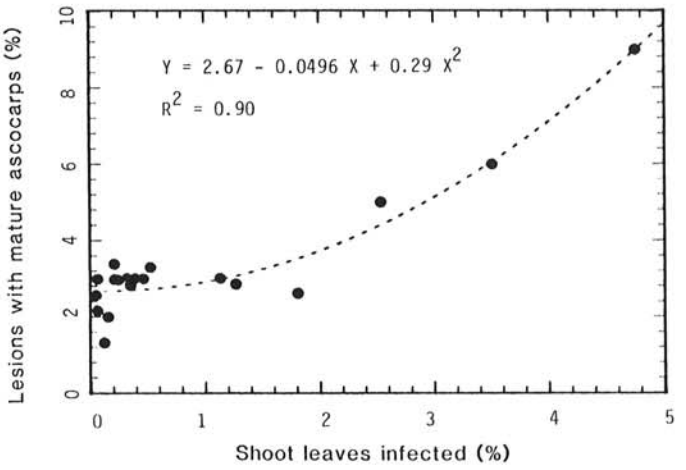

Fig. 2. Relationship between disease incidence at leaf fall and the percentage of lesions that produced mature pseudothecia of *Venturia inaequalis* on leaves collected from McIntosh trees at eleven New Hampshire orchards during September of 1981–1983.

TABLE 3. Proportion of the orchard floor covered by leaf litter in four orchards from leaf fall to petal fall during 1981–1983, and decay of leaf litter between phenological stages of the cultivar McIntosh

Orchard	Year	Leaf litter density[x,y] LF	BB	B	PF	Loss of leaf litter between events (%)[z] LF and BB	BB and PF
III-A	1981–1982	0.44	0.29	0.24	0.23	36	19
	1982–1983	0.38	0.29	0.27	0.24	24	17
IV-B	1981–1982	0.55	0.41	0.37	0.38	25	9
	1982–1983	0.53	0.28	0.26	0.23	48	16
V	1981–1982	0.71	0.57	0.51	0.49	20	14
	1982–1983	0.61	0.46	0.40	0.39	25	15
X	1981–1982	0.56	0.35	0.31	0.30	37	15
	1982–1983	0.67	0.36	0.33	0.28	46	24

[x]Leaf litter density was the proportion of the orchard floor covered by leaves.

[y]Phenological events in the development of the cultivar McIntosh. LF = leaf fall, BB = bud break, B = bloom, and PF = petal fall.

[z]Loss of leaf litter between FL and BB was computed as 100 − [(leaf litter density at BB)/(leaf litter density at LF)] × 100. Loss of leaf litter between BB and PF was computed as 100 − [(leaf litter density at PF)/(leaf litter density at BB)] × 100.

precisely estimate disease incidence in most commercial orchards. Doubling or tripling the sample size would have little effect on the precision of estimates of *LD* at low levels of disease because the error associated with measuring disease incidence increases exponentially as disease incidence falls below 1% (9). More than any other factor, the error associated with *LD* determined the precision of forecasts of *PAD* when the incidence of infection was below 1%.

Pseudothecia per lesion. Although McIntosh, Cortland, and Delicious trees differ in susceptibility to infection, this was not reflected in the suitability of dead leaves as a substrate for saprophytic growth. The number of ascocarps formed per lesion on the three cultivars did not differ significantly. Jeger et al (25) found that lesions on McIntosh leaves produced a mean of 32 and 20 ascocarps in 1979 and 1980, respectively, and that lesions on Delicious leaves produced a mean of 27 and 23 ascocarps during the same period. Our use of 21.6 as an estimate of the number of mature pseudothecia formed per fertile lesion approximated values reported by other researchers (25) for McIntosh and Delicious leaves, and values for McIntosh, Cortland, and Delicious leaves in the present study. Many lesions on leaves collected in commercial orchards produced only aborted ascocarps of *V. inaequalis*, similar in morphology to those described by Keitt and Palmiter (28) in pairings of incompatible mating types. This similarity and the correlation of lesion fertility with disease incidence (Fig. 2) suggest that the abortion of ascocarps may have been due to the heterothallic nature of the fungus, i.e., as the frequency of infection increases, so does the probability of pairing of compatible mating types. However, even as the incidence of infection approached 0%, approximately 3% of the lesions still formed mature ascocarps (Fig. 2). By an unknown mechanism, *V. inaequalis* reproduced sexually when the probability of pairing of compatible mating types was remote. One possible explanation is that ascospores may occasionally be discharged and dispersed as diads, triads, etc., resulting in a single lesion that is self-fertile.

Jeger (24) reported that disease severity, measured as the proportion of a leaf surface covered by scab lesions, had little effect on the number of ascocarps formed per unit of leaf area. However, Jeger (24) used leaves from an unsprayed orchard where there was a high incidence of disease. The least severely infected leaves used by Jeger (24) bore "few, discrete lesions," while the more heavily infected leaves had 10–50% of the leaf surface infected. Disease incidence and severity were far lower in the commercial orchards in which our research was conducted. Thus, it appears that disease incidence and severity affect *PD* when both incidence and severity are low, i.e., when less than 5% of the leaves are infected and there are one to two lesions per infected leaf (Table 1), but that disease incidence and severity have little effect on *PD* when both incidence and severity are high.

Asci per pseudothecium. During the period of ascus formation, orchard temperatures in Durham, NH, averaged 4 C for the years 1959–1981, with a standard error of 0.3 C (17). Gadoury and MacHardy (11) reported a change of approximately six asci per ascocarp per Celsius degree of incubation temperature during the period of ascus formation. We used a constant value with a known standard error for *AD* in calculations of *PAD*. However, it could be necessary to use a different value for *AD* in other locations due to the effects of spring temperatures on *AD*.

Leaf litter density. *LLD* was precisely measured in less than 20 min per orchard. Because of the ease in measurement of *LLD*, and because *LLD* decreased by an average of only 16% during the primary infection season (Table 3), *LLD* was not estimated from orchard characteristics or environmental factors. *LLD* was measured only once: shortly before bud break in the spring.

The distribution of inoculum in commercial orchards. *PAD* is expressed as ascospores per square meter per year. However, ascospores will be concentrated in foci at the locations of fertile scab lesions. The small number of foci per hectare at low levels of disease (Table 4) has important implications in spore discharge and dispersal studies conducted in commercial orchards, for not only must spore traps be extremely efficient to detect ascospores at low doses, but the number of traps must be sufficient to insure adequate sampling in a focal distribution. Most currently available spore traps (8,13,19,36) are unlikely to provide an accurate measurement of airborne ascospore dose when *PAD* is low. If a *PAD* of 500 ascospores per square meter per year, 10% of which was mature, was instantaneously discharged and uniformly dispersed in the air 1 m above the orchard floor for 10 min, the airborne ascospore dose would still be at or below the detection threshold of most spore traps. In reality, detection of the airborne spores would be even more unlikely than in the above example, due to concentration of the inoculum in foci.

TABLE 4. Comparison of values, standard errors (SE), and coefficients of variability (CV) of potential ascospore dose and some component variables at commercial and research orchards in New Hampshire during 1981–1984

Year	Orchard	Lesion density (m^2)			Leaf litter density at bud break			Potential ascospore dose (m^2)			Fertile lesions per hectare[w]	Δt (days)[x]
		Value	SE	CV	Value	SE	CV	Value	SE	CV		
1981–1982	I	5.58	0.95	17	0.40[y]	0.07	18	1,185	306	26	564	11
	III-A	13.80	2.17	16	0.29	0.04	3	3,142	681	22	1,495	9
	V	1.67	0.38	23	0.57	0.06	11	510	136	26	243	13
1982–1983	III-A	2.60	0.45	17	0.29	0.05	17	412	105	25	196	14
	III-B	0.16	0.07	47	0.29	0.05	17	25	13	52	12	21
	IV-A	52.87	7.14	14	0.35[z]	0.05	15	44,544	9,506	21	21,193	2
	IV-B	42.17	5.01	12	0.41	0.02	6	37,269	5,632	15	17,731	2
	V	0.85	0.22	25	0.46	0.02	5	212	56	27	101	15
	VI	205.74	17.53	9	0.35[z]	0.05	15	1,505,027	650,453	43	716,045	0
	VII	13.84	1.66	12	0.36	0.02	6	3,442	514	15	1,638	8
	VIII	2.91	0.84	29	0.35[z]	0.05	15	533	176	33	254	13
	XII	0.70	0.21	30	0.35[z]	0.05	15	132	44	34	63	17
1983–1984	II	11.12	1.65	14	0.35[z]	0.05	15	2,247	484	22	1,069	9
	III-A	0.19	0.11	58	0.35[z]	0.05	15	38	23	60	18	20
	IV-A	7.64	1.11	15	0.35[z]	0.05	15	1,427	309	22	679	11
	V	1.20	0.39	32	0.35[z]	0.05	15	229	83	36	109	15
	VII	0.08	0.05	69	0.35[z]	0.05	15	15	11	71	7	22
	XII	0.47	0.16	35	0.35[z]	0.05	15	89	35	39	43	18

[w] Fertile lesions per hectare based on PAD·10,000/asci per ascus/asci per pseudothecium/pseudothecia per fertile lesion.

[x] Values of Δt were calculated from the formula: $\Delta t = 1/r \ln X_o/X_{os}$. The initial inoculum ($X_o$) was a potential ascospore dose of 98,388 ascospores per square meter per year (equivalent to approximately 10% leaf scab). X_{os} was the forecasted PAD of the sample orchard. Infection rate (r) was 0.40/day.

[y] Leaf litter density estimated from mean values for New Hampshire for 1982–1983 (Table 3).

[z] Leaf litter density estimated from mean values for New Hampshire for 1983–1984 (Table 3).

In commercial orchards, the focal distribution of inoculum and the low incidence of apple scab are obstacles to any validation of our model by direct measurement of *PAD* or measurement of airborne ascospore dose (21). We have included what we believe to be the most significant determinants of *PAD*, and have computed the precision of the estimates of each component variable of the model. The best approach to validation of the model may be to forecast *PAD* in commercial orchards and then observe the seasonal development of apple scab on sprayed and unsprayed trees in the orchards (16).

***PAD* and ascospore maturity.** Forecasts of *PAD* can be further refined when information on ascospore maturity and discharge is available. Squash mount asessments (10) or models of ascospore maturity could be used to estimate (12,23) or forecast (30) ascospore maturity. *PAD* could then be adjusted for the proportion of inoculum available for discharge.

***PAD* and the epidemiology of apple scab.** *PAD* could be used to forecast the onset of apple scab epidemics in commercial orchards. Van der Plank (37) first described the general mathematical relationship between inoculum and development of compound interest diseases:

$$\Delta t = 1/r \ln X_o/X_{os}$$

in which Δt = the delay of an epidemic or the shift in time of a disease progress curve due to the eradication of a portion of the initial inoculum, r = the rate of disease increase ($X = X_o e^{rt}$), and X_o/X_{os} = the ratio of the amount of inoculum before eradication (X_o) to the amount of inoculum surviving eradication (X_{os}). To demonstrate the use of the above analysis, we assumed that a traditional spray schedule (2) beginning at bud break would control apple scab in an orchard with 10% leaf infection at leaf fall, that infected leaves bore 1.3 lesions each, and that *LLD* was 0.35 at bud break. *PAD* in such an orchard would be 98,388 ascospores per square meter per year. This value was used as X_o in Vanderplank's (37) equation to estimate Δt in orchards with less than 10% leaf infection. If r was 0.4/day, a high value for apple scab development on a susceptible cultivar under conditions favorable for apple scab, Δt for site V in 1981–1982, when *PAD* equalled 510 ascospores per square meter per year, could be calculated as: $\Delta t = 1/0.4 \ln 98{,}388/510$, or 13 days. Thus, spraying might have been delayed by 13 days, resulting in a savings of one to two fungicide applications. Values of Δt for other commercial orchards are presented in Table 4. Although extensive testing of this strategy is needed before it can be recommended to commercial growers, preliminary studies conducted at site XII have been successful (14,16).

The logarithmic relationship between *PAD* and Δt indicates that our relatively imprecise forecasts of *PAD* at low levels of disease may not be serious problems in using the model to estimate Δt. Using the example of site V in 1981–1982:

PAD = 510 ascospores per square meter per year, SE = 136 (Table 4);

therefore, *PAD* = 510 ± 231 ascospores per square meter per year ($P = 0.10$); and Δt = 12–15 days ($r = 0.4$/day).

Reducing *PAD* to control apple scab. Reducing *PAD* will delay an epidemic, but not necessarily prevent it or reduce the final amount of disease in the absence of other control measures (37). This principle has not been considered in dealing with the effects of initial inoculum on development of apple scab. Some researchers have used postharvest eradication as a replacement for the regular spray program (3,4,5,21,27,34) while others have either decreased the number of applications, decreased the rate of application, or increased the interval between applications (6,35). Neither has the severity of disease in orchards prior to application of postharvest eradicants been considered in most evaluations of such treatments. Consequently, the effect of postharvest eradication has been unpredictable; even though often beneficial, postharvest eradicant treatments have never been widely applied in commercial orchards. The coupling of forecasts of *PAD* before eradication, estimates of the degree of eradication, and Vanderplank's (37) analysis of the effects of initial inoculum on Δt will allow the costs and benefits of postharvest eradication to be fairly evaluated.

Tactics that greatly reduce *PAD* may be valuable when *PAD* is already at the low levels common in commercial orchards. For example, application of certian fungicides (15,35), or a spore suspension of an antagonistic fungus (20), just before leaf fall could reduce *PAD* by 99% and increase Δt by 12 days. In five commercial orchards that we studied, this might have eliminated the need for the first four fungicide applications. Delaying the onset of a spray program for apple scab beyond the bloom stage would be of little value in New England, because fungicides are applied in late spring to control fruit rots and rust (2). However, elimination of earlier sprays would be desirable because these sprays are applied only to control apple scab. Manipulation of *PAD* might also allow the integration of fungicide and insecticide schedules (16) by delaying the need for fungicidal sprays to coincide with later applications directed against certain insect pests.

Our objective was to produce a practical, functional model to forecast *PAD* in commercial orchards. When we learned that precise prediction of certain component variables of *PAD* did not result in a commensurately precise forecast of *PAD*, simplicity and utility were emphasized over precision. The model we developed is simple to use. Only two measurements, requiring a total of approximately 2 hr per orchard, are needed: disease incidence and severity must be assessed just before leaf fall, and leaf litter density must be assessed at bud break. The model to forecast *PAD* was encoded in a FORTRAN program for use in research, but it could be reduced to a series of graphs or tables for other applications. We are currently investigating the potential value of forecasts of *PAD* as a basis for altering the rate and timing of fungicide applications in commercial orchards (14,16).

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