

C MOIST AIR GERMINATES SOME SPORES ON DRY LEAVES ACCORDI

GERM(1)=CATCH\*GAUSS(RH(I,J),92.,4.,.01)

CATCH=CATCH-GERM(1)

70 IF (DETA

# EPIDEM

**A Simulator of Plant Disease  
Written for a Computer**

**P. E. Waggoner and J. G. Horsfall**

C FECT INCREME

C DRY. INCREASE

C MORE INFECTIO

GERM SPOR. TEMP E

CTIVE WITH JGH AS H

DDAY AND IC IS 2 OF

TEMP=DFEC

IF(W(I,J)) TEMP=1.

IF(TEMP.EQ.0.0) GO TO 79

DO 71 K=2,5

71 NFECT=NFECT+GERM(K)\*2.\*TP(K-1)/(30.+TP(K-1))\*FECT

I \*CL(IC)

IF (DETAIL) CALL CENS

CALCULATE VNV TO MAKE LE.

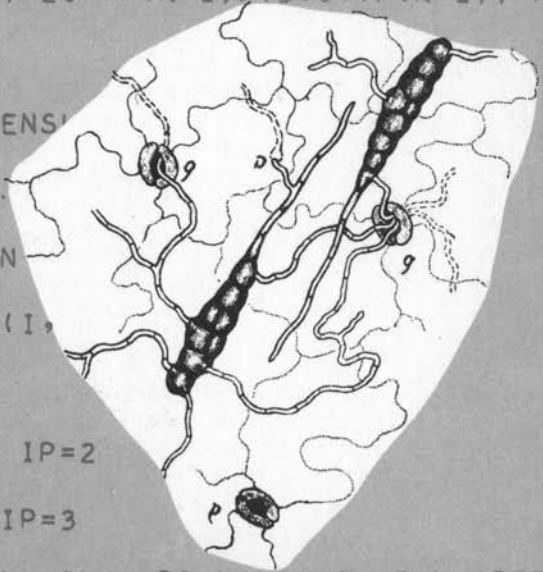
C WET REQUIRED FOR LESION

79 IF(WVNV.AND..NOT.W(I,

IP=1

IF (T(I,J).LT.25.) IP=2

IF(T(I,J).LT.20.) IP=3



C PD IS EFFECT OF TEMP ON VOLV. POUND SAYS COOL SPEEDS.

VNV=VNV+PD(IP) /VDV \*TEMP

C VDV IS PORTION OF FULL EXPANSION POSSIBLE/PERIOD. SUGGE

IF(DETA

**BULLETIN OF THE CONNECTICUT AGRICULTURAL**

**EXPERIMENT STATION, NEW HAVEN • NO. 698 APRIL 1969**

76 FORMAT

T40.E1

## Contents

Summary .....	2
Introduction .....	5
I. Experiments with <i>Alternaria</i> .....	7
A. Materials and Methods .....	8
B. Stalk Formation .....	9
Elongation of stalks .....	10
Effect of light and dark .....	10
Effect of temperature .....	14
Effect of drying .....	16
Effect of nutrients .....	17
Effect of rain .....	18
C. Spore Formation .....	18
Effect of stalk age .....	18
Effect of light and dark .....	19
Effect of temperature .....	19
Effect of drying .....	20
Effect of nutrients .....	21
Succeeding crops of spores .....	22
D. Departure .....	22
E. Survival of germinated spores .....	22
F. Penetration and Enlargement .....	23
II. Integrating the Fungal Cycle and Weather Influences into EPIDEM .....	24
A. Reading the Weather Reports .....	24
B. Fungal Character .....	25
C. The First Day .....	26
D. Stalks Are Formed .....	26
E. Spores Appear .....	29
F. Spores Are Washed Off by Rain and Caught by Leaves .....	31
G. Spores Are Blown by Wind and Caught by Leaves .....	32
H. Spores Germinate .....	34
I. Germinated Spores Invade Leaves .....	34
J. Lesions Enlarge .....	36
K. At Day's End, Lesions and Opportunities for Stalks Appear .....	37
III. What EPIDEM Did When It Saw Actual Weather .....	38
IV. Adequacy of Our Knowledge of Early Blight .....	43
V. Experiments with the Character of Pathogen and Host .....	45
A. How the Pathogen is Blown and Caught .....	45
B. How the Pathogen is Washed and Caught .....	46
C. Susceptibility Changes with Fruit and Sun .....	47
D. Speed of Invasion, The Escape from Weather .....	48
E. Speed of Enlargement and Incubation, Two Long Processes .....	48
VI. Weather Changes that Slow or Speed the Rise of <i>Alternaria</i> .....	52
A. The Wind that Carries Spores .....	52
B. Humidity of the Air that Permits Germination .....	52
C. Dew and Irrigation that Wet the Leaves .....	53
VII. The Summary, EPIDEM, as written in Fortran .....	55
VIII. Symbols .....	77
IX. Literature Cited .....	79

## SUMMARY

An epidemic marching through a population of plants, animals, or men reflects the integration of a very large number of factors in the environment and characteristics in the pathogen and host. These act and interact on each other in a fabulous array that boggles the mind.

Taken in bits and pieces, however, single steps in the life of the pathogen can be re-created in the laboratory of the biologist, and he can measure the effects of the weather, one element at a time, upon a single step. For example, the effects of temperature or light or humidity upon several steps in the life of *Alternaria solani*, the cause of early blight of tomato and potato, have been measured.

With rapid and capacious information machinery at hand, we were encouraged to draw the bits and pieces from the libraries and compose them into the beginnings of a simulator. During the composition, the complete system of weather, pathogen, and host had to be examined, and this led to critical experiments that had been missed. These missing experiments were run, and the simulator was completed.

The simulator, which we call EPIDEM, mimicked several actual epidemics of past years, indicating that the pathology incorporated into EPIDEM was adequate. After the simulator was verified, it provided a guide to the importance or influence of the characteristics of the fungus, the weather, or the host. It also provided a predictor for the outcome of modified weather.

The foregoing overview is now expanded into a fuller summary.

The simulator employs the temperature, relative humidity, wind speed, sunniness, and wetness for each 3 hours of each day. Each 3 hours, it modulates the course of the following fungal stages according to the different, sometimes opposite, effect of the weather factors upon them: formation of conidiophores, formation of spores, departure of spores on wind or rain, finding a host, germination of the spores, penetration of the host, incubation of the infection, and expansion of the lesion.

Information in the literature was adequate to begin composing the simulator. For example, biologists had already carefully measured the different effect of temperature upon sporulation in the light and in the dark. And since the simulator was to be logical and run like the fungus this interaction of temperature and light upon a stage of *Alternaria's* life was incorporated into EPIDEM, exactly as it was observed in the laboratory. All other information available was also employed.

Several phenomena, however, had been overlooked by experimenters, but in attempting to build a logical simulator we found that information about the phenomena was essential. The required experiments were often manageable, they were performed, and are reported here. For example, the speed with which a germinated spore reaches the sanctuary of the leaf interior by penetrating its epidermis, the washing of spores by rain, the fertility of conidiophores that had lost their spores, and the survival after drying of stalks, spores, and germinated spores were all observed.

The simulator is, in fact, a computer program written in Fortran IV. Its composition, fungal stage by fungal stage, is described in detail for it may be a guide to similar analyses of other diseases.

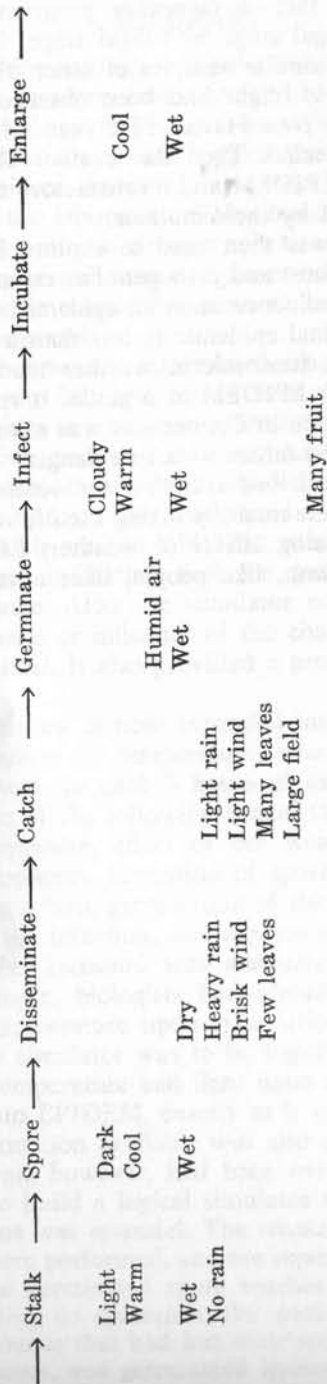
Epidemics of *Alternaria* blight had been observed for many years at the Lockwood Farm near New Haven. Five years of diverse weather and disease severity were selected. Then the weather observations for those years were furnished to EPIDEM and a satisfactory mimicking of the real epidemics was performed by the simulator.

The tested simulator was then used to explore how influential were various characteristics of host and pathogen. For example, slowing sporulation seems to have little influence upon an epidemic, while sterilizing half the stalks decreases the final epidemic to less than a tenth.

Finally, the pathologic feedback in weather modification or climatic variety was explored with EPIDEM as a guide. It revealed, for example, the fear of daytime irrigation in Connecticut was a bugaboo, while dew in Israel was — as claimed by others — a true danger.

Early blight has been described as both a wet weather and a dry weather disease — often by the same man. By taking the life of the fungus step-by-step with the often opposing effects of weather, EPIDEM explains the apparent paradox. *Alternaria*, like people, likes a variety of weather in the right season.

THE MANY DIFFERENT WAYS THAT  
WEATHER AND HOST FAVOR DIFFERENT STAGES IN THE  
LIFE OF *ALTERNARIA*



# E P I D E M

## A Simulator of Plant Disease Written for a Computer

P. E. Waggoner and J. G. Horsfall

The diagram of the life cycle of a pathogenic fungus in the Frontispiece quickly conveys complexity. *Alternaria solani*, the pathogen of the early blight disease of tomato and potato, illustrates the typical complexity through the conflicting effects that wetness, light, or heat have upon different steps in the cycle. We are left wondering whether wet or dry or mixed weather favors early blight. Nevertheless, we must decipher this complexity if we are to design a simulator of epidemics, to test the adequacy of our pathology, to reason which step in the cycle is most strategic for control, and to predict how the disease would fare in a new place or in modified weather.

In this paper, we shall illustrate how building and using an epidemimetic model, a simulator, which we shall call EPIDEM, can accomplish the deciphering, testing, reasoning, and predicting. An abstract of this paper has been published elsewhere (Waggoner and Horsfall, 1968).

EPIDEM is a method for calculation that proceeds through the same steps and considers the same influences as shown in the real cycle of the Frontispiece to predict the course of an epidemic in a certain field and particular weather. EPIDEM, of course, is far from the first integration of epidemiology. The first efforts were those brought forth in an attempt to forecast disease. A classic example is Cook's (1949) effort to employ the correlation between total rainfall plus mean temperature and the outcome of an epidemic.

Perhaps the best known analysis of plant disease is that of van der Plank (1963). He visualized the growth of an epidemic as the growth of money at compound interest. By making the interest rate an explicit, logical function of temperature, Waggoner (1965) brought into consideration at least one factor listed in the Frontispiece. When he synthesized epidemics of *Phytophthora* late blight of potatoes for northern and southern climates, the synthetic epidemics resembled the mean epidemic histories of the two climates. But the success was superficial. We know *Phytophthora* depends more on wetness than on temperature, and we are really more interested in season-to-season than in average predictions.

Thus the two approaches, a rule or an equation, that are so far available to plant pathologists have an ineluctable air of artificiality because common sense tells us that life is not that simple. Common sense tells us that to be realistic, an analysis must deal in season-to-season, even day-to-day and hour-to-hour effects of the fickle weather upon each stage in the fungal cycle rather than in averages. Averages hide too many interactions.

Now, however, speedy and capacious information machines give more latitude to our common sense by letting us include things that formerly had to be discarded in the required simplification. The speedy machine lets EPIDEM take each step in turn and relate it to the weather every 3 hours through the season, while a forecast rule must deal in averages or sums. The capacious machine lets EPIDEM deal with all stages of the fungus and all weather variables, while the simple equation cannot. Thus, a new facility has freed us to produce a simulator that not only can predict but also, step-by-step and interaction-by-interaction, run much like the disease in Nature.

The first simulation that took advantage of these circumstances was of *Phytophthora* late blight of potato (Waggoner, 1968). It incorporated the results of Crosier's (1934) laboratory experiments on the effect of heat and humidity, wet and sun upon each step in the cycle of *Phytophthora*. Three-hourly observations of the weather at Hartford, Connecticut, in 1951, were taken in by the simulator; the progress of the fungus was calculated according to the laboratory information and the 3-hourly weather; and the *Phytophthora* simulator synthesized the famous downy mildew epidemic caused in tobacco in 1951 by a pathogen that has much the same habits as *Phytophthora*.

This was a victory for ordinary common sense. The knowledge gained in the laboratory was fully exploited; the course of the epidemic was modified with every change in the weather; and several weather factors and stages in the fungal cycle — not just a pair — were considered. Finally, history was recreated.

The victory, however, was too easy. The dependence of *Phytophthora* upon water was well known and overwhelming. The information about effects of weather factors on the fungus was easily obtained from a century of investigation of the cause of the Irish Famine. The history of only a single year was available in only anecdotal form, and hence, the match between synthetic and real epidemic needed not be very close to be convincing. *Alternaria* provides a tougher test.

The confusing statements in the literature concerning *Alternaria* and the weather make it a severe and ideal test for a synopsis of pathology and meteorology. If one reads the literature of early blight of tomato and potato he is confused by:

"Following a dry summer, the tubers were heavily infected" (Anon 1954), "Wet weather of June and July favors the disease" (Clinton 1961), and "Early blight is a disease of the drier seasons" (Lutman 1911).

L. R. Jones, who named the disease "early blight," almost states the weather both ways. "The early blight develops and spreads even in cool, dry weather" (1892). "The conditions favoring this disease are . . . hot dry weather followed by a moister period" (1895). Harrison *et al.* (1965) also seems to go both ways. They say, "These results agree closely with those of other workers who have found the disease to be favored by warmer more moist conditions." [but] ". . . Disease severity was as great in [drier] 1964 as in [moister] 1963; apparently sufficient sporulation and infection

occurred even under the cooler, drier season to result in relatively heavy infections" (Harrison *et al.* 1965).

Thus the confusion of *Alternaria* epidemiology offers a challenge to the composer of a simulator. If it can be assembled logically from the bits and pieces of laboratory experiments past and present and of common sense, reproduce actual year-to-year variations of early blight, and rationalize the confusing statements about *Alternaria* and the weather, EPIDEM will have satisfied our hopes.

Our booklet is in four parts. In the first, experiments on sporophore and on spore formation, dissemination, survival, and penetration are presented because we found they were needed before the synopsis could be written. In the second part, the simulator — which we call EPIDEM — is built from the literature, our own experiments, and generous drafts of common sense. In the third part, EPIDEM is tested by offering it our Lockwood Farm weather of 5 years and asking it to duplicate the natural epidemics assessed at that farm in Mt. Carmel, Connecticut, and nearby. Finally, after EPIDEM has passed its test, it is used to experiment with variations in the weather and characteristics of *Alternaria*. Then we shall have learned why *Alternaria* seems a dry weather disease to some, a wet weather disease to others, a mixture to still others.

## I. EXPERIMENTS WITH ALTERNARIA

Composing a simulator is an exercise in feedback from computer program to experiment and back again. Ideally, the composer sits down at his desk and divides the life cycle of the fungus into stages: formulation of conidiphores (here called stalks), formation of spores, departure of spores on wind or rain, finding a host, germination of the spores, penetration of the host, incubation of the infection, and expansion of the lesion. Within each stage, the composer lists the effective host factors: resistance (or susceptibility), plant size, fruit load, and leaf area still uninfected. Next, he adds all the pertinent weather factors: rain and dew, sun and cloud, hot and cold, wind and calm, humid and arid. When the composer tries assembling these parts into a complete and consistent synopsis, however, the feedback begins.

A logical simulator, a synopsis that runs, inevitably requires information that has not yet been gotten. Thus the feedback: try to construct, find parts that are missing; go to the laboratory and get them; modify; try again to build; find more parts that are missing, and around again.

In many cases, the composer simply is incapable of getting the missing piece, and an assumption must be fitted in. But in many cases the laboratory will yield the information, and this section of our booklet presents these experiments we needed and could make. They concern stalk and spore formation, spore departure and survival, and the penetration of a new host. The experiments were called for by the building of EPIDEM, but they are presented first so that the reader will know them when the building is presented.

### A. Materials and Methods

We used laboratory and greenhouse methods for measuring the fungus and host factors. Miss Barbara Wooding performed most of the experiments. When she ran an experiment, she had the opportunity to see things that were not in the plan. She did see new things, and thus we could make the simulator more realistic.

The laboratory method for producing conidiophores (hereinafter called stalks for short) and spores was essentially that of Lukens (1960), who found that *Alternaria solani* produces stalks in the light at room temperature and spores in the dark. The hyphae grown in shake-culture at 23 C in the normal day and night regime were ground in a blender. The resulting fragments of mycelia were washed in deionized water, centrifuged to free them of nutrients, then spread over clean filter paper in petri dishes, and placed in fluorescent light, always at 23 C unless noted otherwise. The fungus, being drastically starved, produced little additional mycelium, but it produced stalks in great abundance within 24 hours. We usually allowed 31 hours or sometimes more.

As long as the stalks were kept in the light, no spores were formed, but as soon as they were put in the dark, conidia were formed overnight. All tests were run in duplicate, repeated at least once unless specified differently. Using a microscope, we counted the number of stalks with and without conidia in ten 0.74 mm<sup>2</sup> fields for each duplicate. Thus, we could study the factors of stalk growth separately from spore formation. They are certainly different.

The effect of light and dark operated precisely the same on lesions on the greenhouse-grown plants as on filter paper in the laboratory.

We obtained greenhouse-inoculated plants through the kind generosity of Dr. B. von Schmeling, our neighbor in the Uniroyal Company, Bethany, Connecticut.

For the purposes of screening new protective fungicides, Dr. von Schmeling inoculates 30-day-old tomato plants (variety Clark's Early Special, formerly Bonny Best) every Thursday. On Mondays, we moved his check plants to our greenhouse when the lesions were just 4 days old from day of inoculation. At that time, the lesions contained no stalks. We put the plants in clear plastic bags (to maintain humidity) in continuous light for 4 more days. By that time, the lesions bore numerous stalks but no spores. The leaflets that bore stalks were then picked and placed on wet filter paper in petri dishes in the dark to form spores overnight.

In the morning, they were examined under the low power of the microscope. The stalks and spores were either counted directly or estimated by grading into one to five categories: 0 = none, 1 = 1 to 10 per field, 2 = 10 to 50 per field, 3 = 50 to 100 per field, and 4 = over 100 per field. We calculated the mean number of each per field and the mean percentage sporulation.

When we are hacking a path through the forest rather than engineering a highway, the direction is more important than the grade. Or, in making a synopsis that runs, it is more important that the experiments be pertinent

than that they be precise. Nevertheless, the reader will want to know how reproducible our observations are, and examples are presented here.

First we examined the reproducibility of stalk production in cultures grown on paper in plates. Eight cultures were grown for 3 days, and then the stalks per field in ten microscopic fields per plate were counted. The means for the eight cultures ranged from 7.2 to 10.5 stalks per field.

Next we examined the spore production per stalk. The example is again taken from eight cultures treated alike until stalks were formed. After the stalks were formed, however, the plates were divided into two sets that were treated differently during sporulation. We are not interested in the treatment here, but we are very interested in whether the variability in sporulation within the two sets is small enough for the difference between the sets to be seen clearly. In fact, the means for the four cultures treated in one fashion ranged from 23 to 38, and the means for the other four ranged from 97 to 99 percent of the stalks with spores. There was no trouble in establishing the difference between the two sets!

Finally, the stalks and spores on leaves rather than on plates would also be counted. When ten microscopic fields on each of five leaflets were examined and graded into five categories according to number of stalks and to number of spores, we obtained the following data. The first three leaflets yielded an average of 50, the last two leaflets an average of 47 stalks per field. Since another set of five leaflets that had been treated differently from the first five yielded an average of 11 stalks per field, the variability of 50 to 47 within the first set is certainly small enough to permit a difference between two sets of leaflets to be firmly established.

In the case of spores, the first three leaflets referred to above had 96, and the remaining two leaflets treated the same had 92 percent of the stalks with spores. This variability was certainly small enough to permit us to distinguish the difference between the set of five leaflets treated alike and the other set of five where the mean was 18 percent of the stalks with spores.

With these experimental methods adequate to our task, we now turn to the results, beginning with the effect of environment on stalk formation.

### B. Stalk Formation

The technical term for a stalk is "conidiophore," but stalk is just as lucid, and it fits our language better. The literature is pretty quiet on the factors in stalk formation of any fungus. Stalk formation is usually lumped with spore formation. But to form a stalk is a distinct phase in the life cycle of *Alternaria solani* and, therefore, it can and does play a role in epidemiology. Perhaps, we were forced into separating stalk formation from spore formation by Lukens' (1960) discovery that stalks of *Alternaria* are formed primarily in the light and spores in the dark. This characteristic of *Alternaria solani* gives the weather factors another opportunity to accelerate or decelerate the life cycle, and, hence, the epidemic. Our computer program, EPIDEM, could scarcely recapitulate the life cycle of *Alternaria* if we did not separate stalk from spore formation.

*Elongation of stalks:* The height of a stalk is important in the cycle of life of *Alternaria solani*. The stalk must be 100 microns tall, more or less, if it is to hold the spore above the lamina of still air that envelopes the leaf and expose it to the turbulent air above. Then the spore can fly to another leaf.

Three experiments were run to measure the rate at which stalks add cells and height at 23 C in the light. The results are exemplified by the outcome shown in Fig. 1. Clearly, the stalks grow rapidly in the light for about 3 days, and then growth slackens. If 100  $\mu$  be the magic number for the height that a stalk requires to thrust its spore up into the turbulent air, then this height is reached in about 32 hours.

These data were obtained from stalks growing in continuous light, but the data could be irrelevant because no summer day runs to 32 hours. What role does darkness play in stalk formation?

*Effect of light and dark:* Although stalks are produced primarily in the light, a few do form in the dark. It is important in programming the computer to know what are the relative numbers that are produced in the light and in the dark. In one test at 23 C, stalks were counted after 24

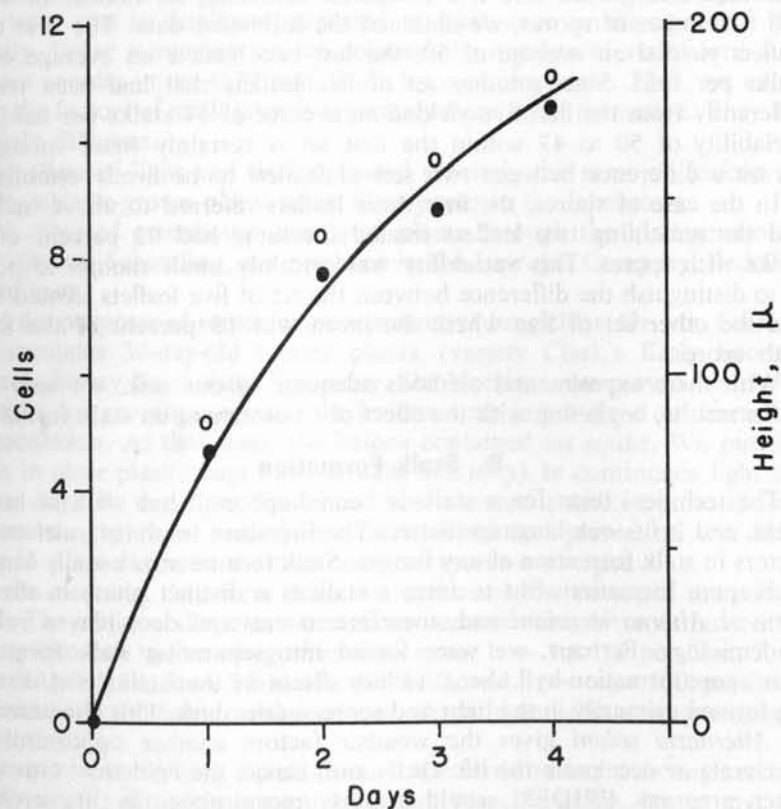


Figure 1. Elongation of stalks (8/19/68). Height (○) and number of cells (●).

hours. We found 11.2 stalks per low-power field in the light and only 5.4 stalks per field in the dark at the same temperature. In a second experiment a day later, we found 11.3 stalks per field in the light and 3.4 stalks in the dark. This indicates that 3 or 4 times as many stalks are formed in continuous light as in continuous dark. Thus, Lukens' results are confirmed, but these results also may not be germane in the open field where the fungus is exposed to alternate light and dark.

To get out of this box, we need to know (a) whether once initiated a stalk grows as rapidly in the dark as in the light, and (b) whether light merely triggers the stalk initiation.

Four experiments bearing on the first point are shown in Table 1. The stalks were allowed to develop during light and dark regimes more or less comparable to summer conditions. Within the limits of these experiments, the duration of darkness had little to do with the total stalk development during 48 to 72 hours. The intrusion of night into the regime did not slow down the long-term stalk development.

Table 1. Effect of light on stalks and spores

Date 1968	Light regime, hours of light (L) and dark (D)	Total time hrs.	Stalks per field	Stalks with spores, %
8/27	15 L	15	3	0
	15 L - 9 D	24	9	0
	15 L - 9 D - 15 L	39	16	0
	15 L - 9 D - 15 L - 9 D	48	14	8
2/20	7 L - 17 D - 7 L - 17 D	48	17	51
	10 L - 14 D - 7 L - 17 D	48	32	75
	31 L - 17 D	48	26	90
	12 L - 12 D - 12 L - 12 D	48	35	25
9/11	31 L - 17 D	48	13	98
	15 L - 9 D - 7 L - 17 D	48	14	98
9/19	31 L - 17 D	48	12	100
	15 L - 9 D - 15 L - 9 D	48	13	30
	15 L - 9 D - 15 L - 9 D - 15 L - 9 D	72	18	54

In all the cases, however, the stalks were given considerable time to start in the light before being moved to the dark. This leaves question (b) dangling. Is the light merely necessary for starting the growth and not for maintaining it? We get some evidence on this from an experiment on temperature, Table 2. We observed stalk and spore production at intervals in the dark. At each interval, the plates that had been examined were returned to darkness. It required about 10 minutes to unwrap a pair of plates, observe them, and return them to darkness. Hence, we had plates that had been exposed for 10 minutes, once, twice, and thrice in 48 hours. If once, the exposure was at 15 hours; if twice, at 15 and 24, and if thrice, at 15, 24, and 39 hours.

The data are clear. The number of stalks increased with the number of brief exposures to light, irrespective of temperature.

We may consider the 48 hour reading for 23 C, for example, since this

is the standard test temperature. In continuous light, the fungus produced 11.3 stalks. With three 10-minute exposures to light, it produced 7.4 stalks; at 2 exposures, 6.1 stalks; at 1 exposure, only 3.6 stalks; and with no exposure (i.e. continuous dark), 3.4 stalks.

These data suggest that a few minutes of illumination triggers stalk formation and that the stalks grow afterwards as well in the dark as in the light. Leach (1965) thinks that a "sporogenic" chemical is formed in the light. It might be more accurate if less elegant to call it a "stalkogenic substance."

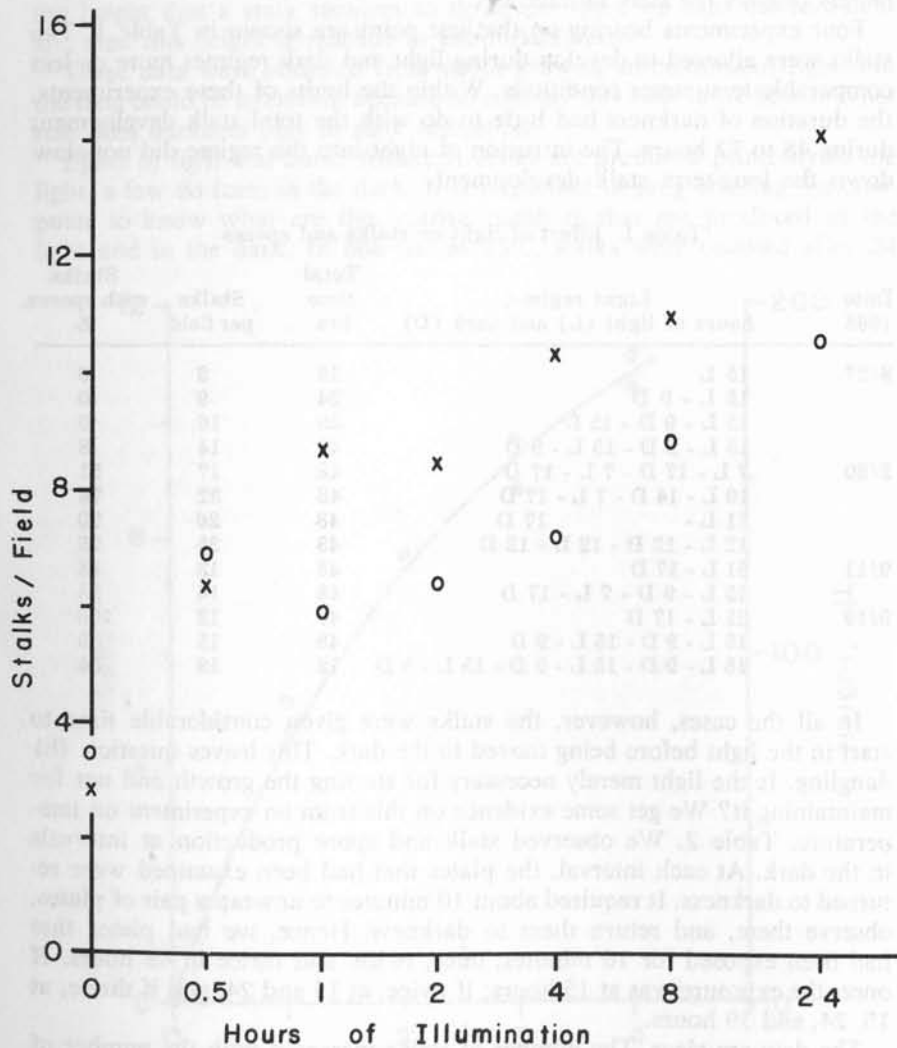


Figure 2. Triggering of stalks by initial exposure to light. Inoculation in ordinary laboratory (X) or red (O) light.

Table 2. Effect of temperature and light on stalks per field and percentage of stalks with spores after 15, 24, 39, and 48 hours of growth, 2/28/68

Temperature C	Light exposures	Elapsed hours							
		15		24		39		48	
		Stalk	Spore	Stalk	Spore	Stalk	Spore	Stalk	Spore
15	Continuous	0.9	0	3.4	21	9.4	79	11.4	85
	One	—	—	.7	33	1.6	34	3.7	62
	Two	—	—	—	—	1.8	49	3.0	56
	Three	—	—	—	—	—	—	1.4	25
	None	0.4	13	0.7	43	0.8	47	1.6	52
23	Continuous	2.0	0	8.1	0	10.6	0	11.2	0
	One	—	—	1.4	24	6.6	33	7.4	44
	Two	—	—	—	—	5.2	7	6.1	8
	Three	—	—	—	—	—	—	3.6	30
27	Continuous	0.6	0	0.8	29	2.8	48	3.4	40
	One	—	—	1.6	0	9.0	0	9.6	0
	Two	—	—	—	—	3.8	0	2.3	0
	Three	—	—	—	—	—	—	1.8	0
	None	0.4	0	1.3	0	1.9	0	1.4	0

Other evidence for the triggering can be found in the three experiments shown in Table 3 and Figure 2 which show that the number of stalks increases with the duration of the initiating light. The theory that light triggers stalk formation runs into trouble, however, in Figure 2, which shows that the curve did not pass through zero stalks at zero light. Some stalks were formed in total darkness as already shown, of course, in Table 1. If the initiating theory is to hold, this must mean that the mycelial fragments growing in the light on the shaker are partially triggered before they are placed in the dark on the filter paper.

Accordingly, the triggering test was repeated three more times, but the mycelial fragments were grown in the dark, wrapped in aluminum foil, and the fungus was manipulated in the light from a 7.5-watt red bulb. Under these conditions, subsequent stalk formation was not appreciably different from earlier runs where the manipulations were done in white light.

Table 3. Triggering of stalk formation by initial exposure to light and total incubation of 24 hours at 23 C. Data are mean number of stalks per microscopic field

Manipulation in	Exposure to light, hrs.						
	0	0.5	1	2	4	8	24
White light <sup>a</sup>	3	6	9	8	10	11	14
Red light <sup>b</sup>	3	7	6	6	7	9	11

<sup>a</sup>In these experiments on September 10 and 24 and October 1, 1968 the flasks were inoculated in ordinary laboratory illumination.

<sup>b</sup>In these experiments on September 19 and 26 and November 13, 1968 the flasks were inoculated in red light.



This concludes our experiments on light and stalks. Clearly, darkness decreases but does not prevent stalk formation. The design for EPIDEM will force us to be specific, and we shall say that darkness decreases the rate of stalk formation to a fourth of that in the light.

*Effect of temperature:* We turn now to the effect of temperature on stalk formation in light and dark. Pound (1951) showed that the optimum temperature for growth of hyphae of *Alternaria solani* in culture is about 28 C. Is the optimum temperature for the growth of stalks the same? On account of scarcity of incubators, we had to run several tests. In the first we observed stalk formation at three temperatures in continuous light, continuous dark, and intermittent light and dark, Table 2. "Intermittent" means that the plates were unwrapped and exposed to light for a few minutes while being counted at the time specified. The number of stalks per field in continuous light is shown in Fig. 3.

Clearly, stalks appear more slowly at 15 than at 27 C, but in the long pull more appear at a temperature much cooler than the 28 C optimum for hyphal growth.

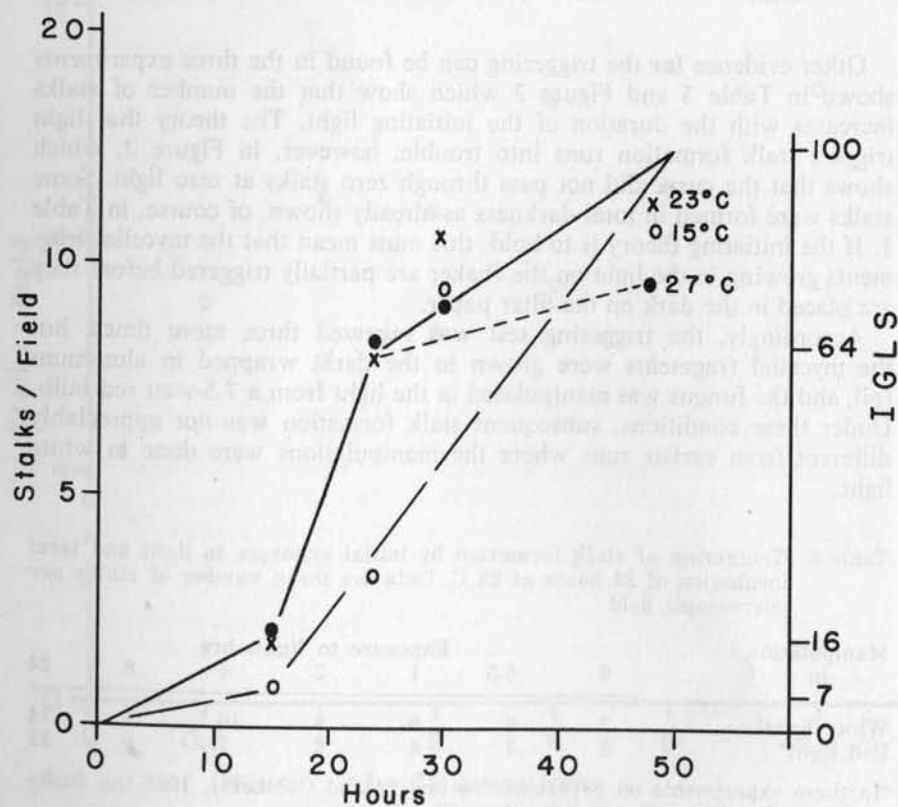


Figure 3. Formation of stalks during incubation in the light at three temperatures (2/28/68).

Table 4. Effect of cool temperatures on stalk and spore formation after 31 hours in light and then 17 more hours in the dark, 9/4/68

Temperature, C	31 Hours		17 More Hours	
	per field	with spores, %	per field	with spores, %
15	5.2	47	9.1	90
19	8.1	14	14.0	99
23	7.6	0	13.2	97
27	5.8	0	7.3	11

On that account, two other tests bracketing 23 C were set up. In the first, we tested 27, 23, 19, and 15 C as shown in Table 4. This test locates the long-term optimum between 19 and 23 C.

In the second experiment, we tested warmer temperatures, viz. 27, 32, and 37 C as shown in Table 5. The optimum temperature is obviously below 27 C. We are left with a conclusion that stalk formation does, indeed, have an optimum temperature 4 to 6 C below that for the growth of hyphae.

The data in Table 5 bring out a still different feature of *Alternaria solani*, and that is that most mycelial fragments at 32 C and 37 C failed to differentiate into stalks at all. They grew as mycelia. They were not killed by the high temperatures; they simply could not be triggered by light to initiate stalk formation. This is further and even more dramatic evidence that the fungus will grow at temperatures where it is unable to produce stalks, the first stage of reproduction. Later if the hot fungus is cooled to 23 C, it acts promptly as if it had always grown at 23 C. It puts on stalks in light and dark as it did in the tests reported above.

Thus, the fungus is not irreversibly inhibited by high temperatures as *Phytophthora infestans* is.

It should be noted that Aragaki *et al.* (1968) reported as this manuscript was nearly ready for the press, that *Alternaria tomato* in Hawaii also reverts to hyphal growth at temperatures above 24 C.

The temperature relations revealed in these experiments are a great

Table 5. Effect of 24 hours of warm temperature followed by 24 hours of 23 C. Incubation in either light or dark. Data are stalks per field or percentage of stalks with spores, 3/12/68

Temperature, C	After 24 hours at stated temperatures				After 24 additional hours at 23 C			
	Light		Dark		Light		Dark	
	Stalks	Spores	Stalks	Spores	Stalks	Spores	Stalks	Spores
23	—	—	—	—	13	99	—	—
27	14	0	4*	0	12	98	4	87
32	0	0	0	0	7	92	4	61
37	0	0	0	0	4	93	4	94

\*Most stalks reverted to mycelia.

assistance in building EPIDEM. First, during many hours of late June, July, and early August, *Alternaria* cannot proceed to reproduce. This being so, we wonder why the old timers who named the disease called it early blight. The computer must be instructed to obey the injunction — no stalk growth above 32 C. But it must also be instructed that the fungus has not been eradicated, and that when the air has cooled, stalk formation can proceed as shown in Fig. 3.

*Effect of drying:* Since leaves are periodically moistened and dried during an epidemic, we had to know the effect of moisture. We had to bear in mind that a mycelium growing through a well-hydrated leaf with a dry surface is likely better watered than a mycelium on a thoroughly dry paper. Also, too much water as well as too little could be detrimental.

Several years ago in our laboratory we observed that stalks were produced more profusely on moist than on flooded paper. Rands (1917) reported a similar observation for stalks grown on agar.

We attempted to simulate this situation in both the laboratory and in the greenhouse. First, in the laboratory, the stalk-forming process was subjected to two sets of conditions: (a) the inoculated filter paper was placed as usual in petri dishes and kept wet. In this circumstance, not only was the foot of the stalk wet, but the stalk itself was formed in very humid air. In treatment (b), the inoculated paper was put on a low rack in the dry laboratory air and kept moist by a wick that passed to a water reservoir a centimeter below. After 31 hours in the light, there were 25.2 stalks per field in the standard moist test in the dishes and 33.4 stalks per field in the drier test. A completely dry paper would produce no stalks. The test was repeated several months later with the same results. Thus, the preliminary observation was confirmed. Too much moisture at the foot reduced stalk growth. Stalks do grow in dry air if their feet are damp.

On the other hand, the laboratory test does not precisely duplicate the field. It does show that excessive wetness inhibits stalk formation. During a dry day in the field, however, the lesion, and, therefore, the foot of the stalk may get drier than a mycelium in a wick. If so, does this inhibit stalk formation?

To provide some relevant data, we used greenhouse inoculated plants on four separate occasions. For each test, two plants were exposed on the greenhouse bench to dry, wintertime air, while two others were kept moist in clear plastic bags. All were continuously illuminated for 3 days to allow the stalks to form. All leaflets were incubated overnight in dark, moist plates before observation. The data are displayed in the first two lines of Table 6.

Clearly, more stalks grew after the moist than after the dry circumstance. The remaining experiments of Table 6 show that a moist environment at night is surprisingly effective compared to a continuously moist one. Added to the "wick experiment" above, the greenhouse experiments show either the extreme of a flooded paper or an arid leaf produce fewer stalks than a merely moist environment — and nighttime moistness is adequate.

Before leaving moisture and going to the next subject, we must consider

Table 6. Effect of a moist chamber upon stalk formation on plants in the greenhouse and upon subsequent sporulation in a dark, moist environment, 4/19, 2/15, 2/22/68

	Dry	Moist continuously
Stalks/field	11	49
Spores/field	2	45
	Moist at night only	Moist continuously
Stalks/field	30	50
Spores/field	5	26
	Moist at night only	Moist continuously
Stalks/field	11	10
Spores/field	1	2

that an advanced early blight lesion may be more like a dry paper than a turgid leaf. We have observed that stalks tend to form around the periphery of lesions, in bags in the greenhouse, presumably because there is more water in the oasis of the margin than in the desert of the lesion. And in the open, dry greenhouse we have seen neither stalks nor spores.

We are now ready to rationalize some field observations and make a specification for EPIDEM. Rotem and Reichert (1964) found spores, and presumably stalks, but only an eighth as many on continuously dry plants as on plants wet nightly by dew. Rands (1917) observed much the same. Thus, we shall instruct EPIDEM that some stalks can form in the dry as Rands, Rotem and Reichert have seen, and many can form in the wet as both they and we have seen.

*Effect of nutrients:* Since the severity of some diseases is correlated with the sugar content of the host (Horsfall and Dimond, 1957), and the sugar content of leaves varies from about 1% of fresh weight at night to 3% during the hours of rapid photosynthesis (Miller, 1938), the weather may affect *Alternaria* by affecting photosynthesis. Thus, a cloudy day will decrease photosynthesis and, hence, sugar content, and this in turn may change stalk formation. But does nutrition affect stalk formation?

In the standard laboratory test, the fungus is severely starved. Probably the fungus can gain some carbon by hydrolyzing the cellulose in the filter paper, but such nutrient comes the hard way.

In an experiment on February 20, 1968, 1,000 ppm glucose in the moistening water nearly trebled the production of stalks from 26 per field to 69 per field. On the other hand, 100 ppm and less exerted no effect on stalk formation.

Orange juice is the nutrient suggested by McCallan and Wilcoxon (1936) to promote spore germination. Quadruplicate plates received three concentrations of fresh juice per 20 ml of the moistening water. The plates were incubated in normal light and dark of the month of May and observed 1, 2, and 3 days later. As with glucose, the highest concentration of orange juice increased stalk formation. On the other hand, we recall that Horsfall and Dimond (1957) found *Alternaria* attack severest in "low sugar" plants. Thus, being in a quandry, we shall not instruct the computer to vary stalk formation with photosynthesis, which presumably would be done by asking whether the sun is shining.

*Effect of rain:* To now we have been expanding stalks, but we must also consider their destruction. Does a beating rain destroy existing stalks?

Stalks without spores were grown upon plants under plastic bags in the greenhouse on March 15, 1968. The equivalent of 0.65 inch of rain was sprinkled onto 6 of 12 leaflets. The excess water was removed from the wet leaves, and all leaflets were placed in a dark, moist incubator. One day later, ten fields (under the microscope) on six leaves showed averages of 41 and 45 stalks/field on the check and sprinkled leaves. That is, the treated and check leaflets had about the same stalk production at the time of treatment. The average number of spores per field, however, was different: the check had an average of 29 and the sprinkled 19 spores per field. That is, a simulated rain of 2/3 inch had prevented subsequent sporulation upon 1/3 of these stalks that had not yet borne spores. This subject, part stalk and part spore, brings us to experiments in spore formation on established stalks.

### C. Spore Formation

The literature is as full of information on spore production as it is empty on stalk production. Unfortunately in most of the data, spore production is confounded with stalk production. It is the sum of the two factors. We are certain that the factors for the two problems differ, and so we have to take data in the literature of spore production with a grain of salt. We shall do our best to sort it out.

*Effect of stalk age:* If age is measured from the moment of inoculation, some hyphae will be less and some more than 24 hours old when they enter the "stalk" account named, e.g., in Figure 3. If the sporulation process can be initiated before the hyphae enter the stalk account, stalks that took longer to reach maturity will sporulate sooner than ones that arrived quickly.

Tables 1, 2, and 3 have already shown us that many stalks less than 24 hours old can already have spores. This mixes sporulation and stalk growth, however.

Stalk and spore formation are separated in the experiments of Fig. 4, on the other hand. In these experiments, stalks were kept infertile by growing them in continuous light, which we have seen prevents sporulation (Table 3). Then, to learn their fecundity at different ages, they were put in the dark. The course of sporulation was slower if the stalks were 1 day old rather than 2, 3, or 4 days old, Fig. 4. Since 1-day-old stalks are shorter than 100  $\mu$ , the results of Fig. 4 can be restated: stalks shorter than 100  $\mu$  produce spores more slowly than taller ones that are needed to reach into turbulent air.

To employ the preceding information on stalk age in EPIDEM, we must ask how fast EPIDEM specifies stalk formation to be. Since Fig. 3 sets the upper speed for stalk formation in EPIDEM, most stalks will consume more than 1 day in growing. Because we have just learned that stalks older than 1 day all have the same rapidity of sporulation (Fig. 4), stalk age will be ignored. Further, we can now profitably explore the effects of light and

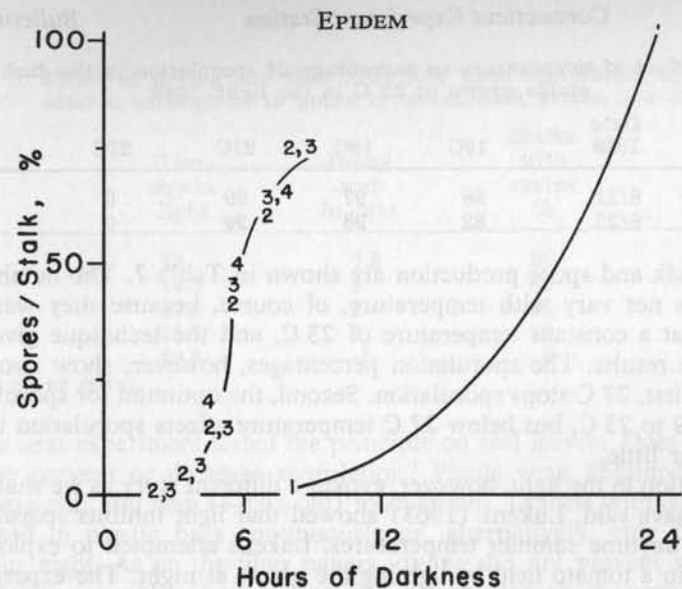


Figure 4. Course of spore formation on stalks 1, 2, 3, and 4 days old. January and February, 1967.

warmth with older stalks because we know that the age of stalks will not confuse us.

*Effect of light and dark:* As we have seen, light encourages the formation of stalks. On the other hand, Lukens (1963) showed several years ago that light inhibits the formation of spores on the very stalks that are stimulated by light. Since darkness encourages spore formation, how much night is required for spore formation on a fully grown stalk?

Lukens (1963) published a curve from an experiment on variable length of darkness. Interpolation on his curve shows that about 10 hours of darkness is required for 50% sporulation. In two separate tests (February 22 and March 14, 1968), we got comparable values of 10.2 and 11.4 hours, respectively. This is a somewhat slower rate than observed in 1967 (Fig. 4), but the slower rate has been observed more often and is employed in EPIDEM.

That is to say that 50% of the stalks freely formed in the light will produce spores during 10 hours of darkness. It is interesting that this is about all the darkness available in mid-summer in Connecticut. Thus, the reaction of the fungus in producing spores is simple if the question of light and dark be simplified by asking the effect of darkness on preformed stalks. Thus, we have a clear specification for EPIDEM.

*Effect of temperature:* The optimum temperature for growth of mycelium is about 28 C and that for growth of stalks is about 23 C. The question now is whether spore formation has a still different optimum.

Two separate experiments on temperature were run on different days. The stalks were grown in the usual way for 31 hours in the light at 23 C and then distributed in pairs at 15, 19, 23, and 27 C in the dark. The

Table 7. Effect of temperature on percentage of sporulation in the dark upon stalks grown at 23 C in the light, 1968

Date 1968	15C	19C	23C	27C
8/21	86	97	99	0
8/22	82	98	99	0

data on stalk and spore production are shown in Table 7. The number of stalks does not vary with temperature, of course, because they were all produced at a constant temperature of 23 C, and the technique gives reproducible results. The sporulation percentages, however, show two phenomena. First, 27 C stops sporulation. Second, the optimum for sporulation is about 19 to 23 C, but below 27 C temperature affects sporulation in the dark rather little.

Sporulation in the light, however, evokes a different story as we shall see.

As we have said, Lukens (1963) showed that light inhibits sporulation at normal daytime summer temperatures. Lukens attempted to exploit his discovery in a tomato field by lighting the plants at night. The experiment failed, but no explanation was at first apparent.

Miss Wooding discovered the reason one winter's day when the laboratory radiator was accidentally turned off, and the temperature fell sharply. On that day, many spores appeared on stalks in the light. Obviously, the inhibiting effect of light is quenched by low temperature (Lukens, 1966). This is shown clearly in Tables 2 and 4. The stalks at 23 and 27 C in both experiments followed the Lukens pattern and produced no spores. At 15 C, however, 85% of the stalks in Table 2 and 47% of the stalks in Table 4 formed spores in the light.

One could state these results that light inhibits sporulation at room temperature, but that cool temperature quenches the light inhibition. These results confirm those of Aragaki (1961) on *Alternaria tomato*. They will provide us with three guides when we compose EPIDEM. In the dark, sporulation is stopped by hot but not by moderate temperatures. In the light, all temperatures are very important to sporulation.

*Effect of drying:* We have shown that drying decreases but does not stop stalk production provided the foot of the stalk is moist. The question now is what is the effect of drying the stalk on spore production? Clearly, the stalk in Nature gets dry during a hot dry period. Can it produce spores?

First, can mature stalks on a dry mycelium, as in a desiccated lesion, form spores? In the first laboratory test, stalk formation proceeded for 56 hours in humid air in the light. The filter papers bearing crops of stalks were all allowed to dry overnight in the light to simulate the desiccation of a lesion. Then in the morning, duplicates were rewet at intervals and kept in the light to allow the stalks to rehydrate. All were put in the dark at the end of the day to allow spores to form on the stalks. The data are given in Table 8. Clearly, spores will not form on stalks when the substrate is dry as in the last line of Table 8. Further, there seems to be a delay in sporulation, a time for recovery, if the stalks have been dry.

Table 8. Effect of drying and then rewetting upon sporulation upon leaflets after a subsequent 16 hours in moist, dark plates, 2/9/68

Hours dry in light	Hours wet in light	Stalks with spores %
12	7.5	86
14.5	5	80
17.5	2	55
19.5	0	19
19.5	—*	0

\*Plate never rewet.

The next experiment tested the principle on real leaves: Does a dry leaf surface prevent or decrease sporulation? Plants were obtained with old (11-days-old) and new (4-days-old) inoculations. Leaflets with lesions were enclosed in plastic bags continuously or, alternatively, only during the 16-hour night. As on the filter papers, drying did not prevent subsequent sporulation, on old or new lesions, but the percentage of sporulation was only about half as great after interrupted as after continuous wetness, Table 9. The same outcome is seen in Table 6.

The next experiment demonstrates not only how many but how fast spores form on once-dry versus continuously wet stalks. Stalks were allowed to form for 36 hours in the usual way in humid air and in the light. Then half of the petri dishes were opened and allowed to dry for 16 hours, all still in the light. Then they were moistened again and allowed to stand for 6 more hours in the light. At that point, they were all put in the dark for different lengths of time to allow spores to form. The data are given in Table 10.

Even though the stalks and their feet in the paper were dried for 16 hours, they lost little ability to produce spores later. They rehydrated when they received water and began to form spores, slowly at first but soon equaling the rate of the continuously moist stalks.

For these reasons the specifications for EPIDEM will permit sporulation of only a very few stalks if the leaf is not wet; this follows Rands (1917) and Rotem and Reichert (1964). On the other hand, if a leaf has just become wet, sporulation will proceed slowly, and if it has been wet for a long time, sporulation will proceed rapidly toward 100% as in Table 10.

*Effect of nutrients:* Earlier we examined the effect of nutrition upon stalk formation to determine whether the varying photosynthesis of the host in varying weather would change the stalk population. Abundant nutrient

Table 9. Effect of 8-hours drying during the day upon the spores per stalk on old and new lesions, 2/29/68

Lesions	Continuously wet	8-hours drying
Old	74	42
New	33	16

increased the number of stalks, but we noticed that the stalks fed with glucose or orange juice produced fewer spores than stalks not fed. We had more stalks per field, but a smaller percentage of them bore spores. Apparently a luxury diet of glucose or orange juice discourages a stalk from sporulating. Thus, Klebs' law seems to stand for sporulation per stalk, which is enhanced by starvation, but not for stalk formation. The net effect is somewhat more spores per field when the mycelium is starved.

Since these two phenomena seem to counterbalance and since the literature will suggest that nutrition affects disease via the penetration — not fructification — of the pathogen, EPIDEM will receive no instructions about photosynthesis and spores.

*Succeeding crops of spores:* Before leaving spore formation to study their take-off, we need to know whether that departure destroys the stalks or permits another crop on them.

By observing marked lesions in the field, Rands (1917) noted that three or four crops of spores will form on the same stalks. We confirmed this in the laboratory. Spores produced in the standard way can be dislodged easily by blowing on them or by dropping the plastic petri dish that contains them. In a preliminary test, we observed that stalks so freed of spores will produce a new crop. A more complete test in quadruplicate is shown in Table 11. Stalks and spores were counted after 2 days in the standard test. The data show the usual number per field. Then the spores were blown off, stalks put back in the dark, and a new crop of about 1/3 as many spores as before were formed.

In an earlier section "Effect of rain (on stalks)," we found that 2/3 inch of rain falling upon stalks that had not yet sporulated put 1/3 out of the game. In this section, we see that spore formation and removal puts 2/3 of the stalks out of the game. Now we can go on to the way the spores, once formed, leave for a new host.

#### D. Departure

The take-off of spores into the wind must be related to wind speed, but we were not equipped for studying this. On the other hand, we could perform some simple tests of removal by rain.

The numbers of spores per field were counted on leaflets. Water was permitted to pass through perforations in a bottle cap and drop onto the leaflets. The number of remaining spores per field was observed. The equivalent of 1/4 inch of water removed about 99% of the spores, Fig. 5.

#### E. Survival of Germinated Spores

*Alternaria* spores germinate quickly in water or humid air. Can they survive subsequent drying?

In the first experiment, spores were germinated in water. They were then dried for 10 minutes and rewet. The germ tubes did not grow further. Neither did new tubes grow later in wet weather.

Later, spores were germinated in humid air. They were moved into arid air to dry. Later, after returning to humid air, the germ tubes grew.

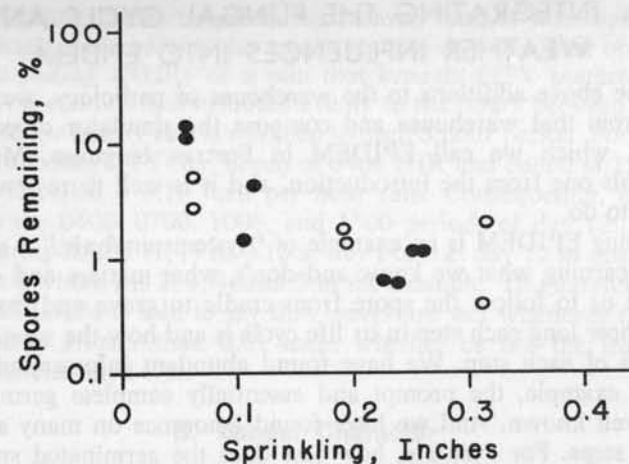


Figure 5. Removal of spores from leaflets by sprinkling with water. Separate experiments are represented by open and closed circles.

The conclusion from these experiments as incorporated in EPIDEM is: spores that germinate in liquid water die in arid air and those that germinate in humid air survive in arid air.

#### F. Penetration and Enlargement

Since drying kills spores that germinate in liquid water, we can stop penetration at different times and learn what proportion of the spores have penetrated to the leaf interior. This way, the rapidity of penetration can be learned.

The following experiment was generously performed for us by Dr. B. von Schmeling in the Uniroyal Laboratory, Bethany. Using aqueous spore suspensions, he inoculated tomato plants in a moist chamber and removed plants after 3, 6, 9, 12, and 24 hours. Subsequently, the percentage of infection was respectively, 0, 13, 74, 100, and 100% of the infection after 24 hours in the moist chamber. This experiment will permit the speed of infection to be specified in EPIDEM.

After an infection becomes visible as a small lesion, it enlarges. In our greenhouse, we have found that lesions do not enlarge in the dry leaves, but remain as small spots. If, however, the leaf is moistened by enclosure in a plastic bag, the lesion enlarges rapidly and greatly. This experiment requires that leaf wetness be specified in writing EPIDEM, which we are now ready to undertake.

## II. INTEGRATING THE FUNGAL CYCLE AND WEATHER INFLUENCES INTO EPIDEM

With the above additions to the warehouse of pathology, we are ready to draw from that warehouse and compose the simulator of early blight epidemics, which we call EPIDEM in Fortran language. Many pages separate this one from the introduction, and it is well to review what we are about to do.

Composing EPIDEM is an example of "systems analysis," a stern discipline for learning what we know and don't, what matters and doesn't. It has forced us to follow the spore from cradle to grave and made us say definitely how long each step in its life cycle is and how the weather affects the success of each step. We have found abundant information on some steps. For example, the prompt and essentially complete germination in water is well known. And we have found ignorance on many simple but important steps. For example, how fast does the germinated spore reach into the oasis of the leaf and no longer care whether dew dries? Or how many spores are washed away by a quarter inch of rain and how many of these are caught by healthy leaves?

As the reader peers into the construction of EPIDEM, he will be forced, as we were, into many corners of the life of *Alternaria* that he had not seen before. He may find citations to investigations that illuminate that corner. He may learn that we had to make the experiments of the preceding section. Or he may see some "educated guesses."

When the reader will have followed us through the course, we hope that he will enjoy the complete simulator — not empirical, but logical; not statistical, but biological; not hit-or-miss, but whole. He can be assured that EPIDEM has run through at least five seasons as *Alternaria* did, and that EPIDEM has run numerical experiments that show how weather that might have been would alter *Alternaria*. He can also anticipate an explanation of whether *Alternaria* likes wet, dry, or mixed weather.

### A. Reading the Weather Reports

First, EPIDEM reads the weather, and then it modulates the life of the fungus model in accordance with the weather.

Beginning on June 1, EPIDEM reads from a card the temperature, relative humidity, wind speed, sunniness, and wetness for each 3 hours of each day that follows June 1. It reads the temperature in °F, the humidity in percent, the wind in mph, and sunniness and wetness as true or false. The weather records came from observations made at the Lockwood Farm, Mt. Carmel, Connecticut. In the few cases when instruments had failed, observations were estimated from Hartford data taken 30 miles north of Lockwood Farm. The sunniness was measured by a sunlight indicator set on the ridgepole of the barn. We guessed from rain, dew, sky, wind, and humidity records whether leaves were wet. The 3-hour periods were numbered as follows: 1, 0100h; 2, 0400h; 3, 0700h; 4, 1000h; 5, 1300h; 6, 1600h; 7, 1900 h; 8, 2200h.

After EPIDEM reads the preceding factors, rainfall information is assimilated. Each card contains the month and the day and hour of initiation (IHR) and ending (NHR) of a rain that brought QTY hundredths inch of water. This rainfall is distributed evenly to the hours between initiation and end, and the hourly rate is assigned to each 3-hour period. For example, a rain of 0.9 inches QTY that began at 0400 IHR and ended at 1200 NHR on day 12 is called a 0.10 inch per hour rain. Consequently, an 0.10 is assigned to the 0400, 0700, 1000, and 1300 periods of day 12. This provides a quantity RAIN (I, J) of 0.10 at day I or, i.e. day 12 in this example, and periods J where J is 2, 3, 4, and 5 in the example. To guarantee against oversight, EPIDEM is told to say that leaves are wet whenever the hourly rainfall rate is greater than 0.01 inch, whether or not the leaves have already been classified wet.

### B. Fungal Character

After acquiring a set of weather data, EPIDEM can perform several experiments on that set. The several experimental conditions or fungal characters as expressed usually in mnemonic terms are:

F	Fraction of spores that survives a 3-hour period.
TSTK	The hot temperature that stops stalk growth.
C <sub>u1</sub>	Determines the release of spores into the wind.
C <sub>u2</sub>	Incorporates the effects of field size and maximum LAI upon the catching of air-borne spores by leaves.
UPOW	Incorporates the effect of wind speed upon the catching of air-borne spores by leaves.
IBEAT	Determines destruction of stalks by beating rain.
RM	Determines the washing of spores by rain.
RP	Fraction of spores awash in 0.01 rain and caught by leaves.
WASP	Percentage of spores washed and caught that are infective.
NUSTK	If NUSTK is true, spore removal makes 1/3 of denuded stalks available for a new crop of spores.
FECT	Determines the course of infection as time passes.
CL	Modifies infection as midday cloudiness changes.
NOJGH	If NOJGH is true, no effect upon susceptibility by fruit load.
DFECT	Infection in dry leaves as a fraction of wet.
WVNV	If WVNV is true, lesions enlarge only in the wet.
PD	Modifies enlargement of lesions according to temperatures.
VDV	Number of periods to reach maximum lesion size.
ICBT	Number of days from infection to lesion appearance.
XSIZE	Maximum number of stalks per lesion.

All but three of these parameters are quantities, e.g. XSIZE is usually 1000 stalks per lesion. On the other hand, the parameters NUSTK, NOJGH, and WVNV are logical variables that might be either true or false. For example, if NUSTK is given as false, the dissemination of 100 spores will leave 100 stalks sterile and out of the game; while if NUSTK is given as true, the dissemination of 100 spores will cause 33 stalks to re-enter the

game and grow new spores just as if they were newly grown stalks. The meaning of all these parameters will be explained as we go through the fungal cycle. An alphabetical list of all symbols is found in Section VIII, page 77.

### C. The First Day

The first day with I equal to 1 is now entered and the daily calculation of disease progress begins. Several indices associated with each day must be at zero. They are:

- IDLS (I) Index for stalk formation during wet weather.
- IGLS (I) Index for stalk formation during all weather.
- OPTY (I) Opportunities for stalk formation that are opened on day I.
- SIZE (I) Attained size of lesions that appeared on day I.

On the first occasion, EPIDEM must learn some history. It reads a card that tells the number and size of lesions at hand, the number of ungerminated and germinated spores lying on new infection sites, and some past weather conditions. Since the number of lesions at any later time will be proportional to the number on day 1, we transmit via the card the information that the initial lesion number is one and that no spores are lying about. We also transmit the observed weather of the past. EPIDEM assumes that, at the beginning, there are no infections that have not formed lesions.

At the beginning of each day, first or not, the number of infections on that day must be set at zero. The stage is now set for the new day I and EPIDEM examines the weather data for period 1 of that day, which is at 0100 hours.

The calculations and decisions for each period are divided into eight sections: stalk formation and the beating of those stalks by the rain, sporulation, washing of spores in the rain and catching them on leaves, spread of spores in the wind and catching them on leaves, germination of spores, invasion of the host, calculation of the index for involvement or growth of the lesions, and opening new opportunities for stalk growth. We begin with our most difficult task: calculation of stalk formation.

### D. Stalks Are Formed

The first step in stalk formation, however, is easy. The experiment in Table 5 shows that stalks are not formed at 32 C. On the other hand, the hot temperature did not sterilize or destroy the stalks present. Therefore, if the temperature is greater than TSTK, which was set at 32 C, EPIDEM simply by-passes the stalk calculations, leaving stalk numbers exactly as they were. Usually, however, the temperature is below 32 C and more stalks will be produced.

There are two sets of four accounts each for stalk formation. One set is GSTK; this is for stalks formed on wet or dry lesions. The use of GSTK is justified because Rands (1917) and Rotem and Reichert (1964) found a few spores and, hence, stalks on lesions that were sheltered from rain

and dew. The mnemonic reason for the expression GSTK is that these few stalks may be formed on the green margins of the lesions.

The second set of stalk accounts, DSTK, is employed only when the leaves are wet, whereas GSTK was employed whether leaves were wet or dry. Observers mentioned above found many more spores and, hence, stalks where leaves were wet, and Table 6 certainly emphasizes the importance of moisture in stalk formation. Thus, EPIDEM must form more abundant stalks when leaves are wet. The mnemonic reason for the expression DSTK is that these abundant stalks may be formed on a desiccated lesion that is re-wet by rain or dew.

The age of the stalks will be needed later, and accounts are kept by age of stalk. The first accounts GSTK(1) and DSTK(1) contain the numbers of stalks on hand in the present period. Accounts number 2 contain the number of stalks present 3 hours and 1 period ago, and so forth. The GSTK account for any period will always be lower than the DSTK account. Since the calculation will be an accumulation from the disease lesions (DLSN) appearing in all past dates, GSTK(1) and DSTK(1) are first set at zero.

Since much the same performance is required for both green and dry lesions, the calculation is made by calling upon a subroutine STALK, see Fig. 6. In the first call, which is made in all periods regardless of leaf wetness, GSTK is the subject.

The opportunities for stalk formation, called OPTY(K), are opened by the enlargement of lesions on day K in the past. Later, the calculation of OPTY(K) will be explained. For now, however, please accept that EPIDEM has learned how many OPTY(K) or opportunities for stalks appeared on day K past, and we need only calculate their filling.

As an example, we say the fifty-seventh day has been reached. Calculation proceeds from the present day, 57, backwards into history. If no OPTY(56) for green stalks is open at day 56, OPTY(56) is zero, and we go to day 55. This step is shown in the first diamond in Fig. 6.

Now suppose OPTY(55) is not zero because opportunities were opened on day 55. The index of maturity, IGLS, for GSTK will tell whether they have been filled. IGLS(55) was zero when the OPTY(55) were first opened and will reach 100 when all opportunities are filled. Thus, the second diamond in Fig. 6 asks whether IGLS(55) has reached 100. If it has, all OPTY(55) are filled. If OPTY(55) is filled, then older opportunities or sockets from days 54, 53, . . . , 1 are necessarily also filled, and Fig. 6 shows a return to the main program because calculation of GSTK is at an end.

In fact, however, the OPTY(55) cannot be filled completely in less than 2 days. IGLS(56) will not be 100, and the next step will be to the table in the center of Fig. 6. From this table, an increment in IGLS(55) will be selected that will make the filling of OPTY(55) proceed as the observation of Fig. 3. The IGLS are shown in the margin of Fig. 3. Stalk growth begins slowly, especially when cool. Formation then speeds up, and finally slows down if it is warm. Thus, at 23 C, the increment in

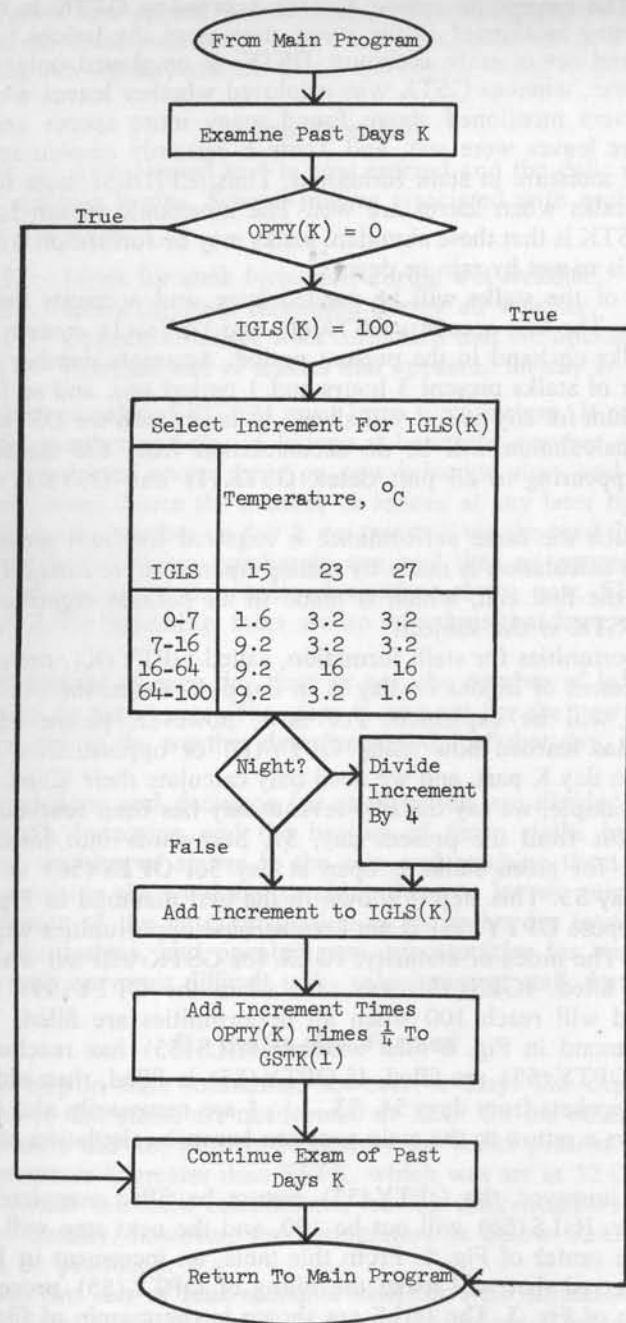


Figure 6. The subroutine STALK.

IGLS(55) is 3.2% per 3-hour period at first. It then rises to 16% and later slows to 3.2% per period. Nineteen of these periods or 57 hours would, therefore, bring IGLS(55) to 100 and fill all OPTY(55).

Stalk formation is only about one-fourth as great in the dark as in the light, Table 5. Hence, after the increment is selected from the table in Fig. 6, it is divided by 4 if night has fallen.

The two processes that we have anticipated can now be completed. First, IGLS(55) is brought up to date. Second, the supply of green stalks GSTK(1) available in the present period in day 57 is increased. Since the number of green stalks found on a recently dry lesion was only one-fourth the number formed if the lesions were wet in Table 6, the increment in GSTK(1) is multiplied by  $\frac{1}{4}$ .

The calculation now goes to the next day in the past, day 54, and adds the contribution of OPTY(54) to GSTK(1) according to the increment in IGLS(54). The calculation is repeated until an IGLS(K) of 100 is reached, indicating all OPTY(K) are filled, and no more stalks can be made for that day or days longer past.

After the contribution of past days to the present stalk crop GSTK(1) has been calculated, EPIDEM turns its attention to DSTK(1). Unlike the few GSTK(1) that are formed whether the lesions are wet or dry, DSTK(1) are formed abundantly, but only when the lesions are wet. Hence EPIDEM asks whether leaves are wet, and if the answer is "yes," returns to the calculation procedure of Fig. 6. This time IDLS(K) rather than IGLS(K) is consulted, and the increment is added to DSTK(1). Further, in the last calculation of Fig. 6, the increment is not multiplied by  $\frac{1}{4}$ , the adjustment for the few stalks GSTK on dry leaves. Since Table 6 shows half as many stalks on leaves occasionally wet as on leaves continuously wet, the increment in IDLS is multiplied by  $\frac{1}{2}$  if they are wet in the present but not in the past period and by 1 if the lesions have been wet in the past as well as in the present.

The stalks, once formed, can survive dry weather and later sporulate as Table 8 demonstrated. Surprisingly, however, a beating rain deteriorates the stalks. In the experiment of March 15, 1968, section IB, 0.7 inch of artificial rain destroyed the sporulation capacity of  $\frac{1}{3}$  of the stalks. This observation is incorporated in EPIDEM by multiplying the number of stalks by

$$\frac{2}{2 + 3 \text{ Rain}} = \frac{1}{1 + \text{Rain}/\text{IBEAT}}$$

"Rain" is the rainfall rate in inches/hour. The numbers in this expression were set by setting the parameter IBEAT equal to  $\frac{2}{3}$ . This completes the calculations regarding stalks and sets the stage for spore production on these stalks.

### E. Spores Appear

Once again, the first step of a process is easy: If the critical temperature is exceeded, spores are not formed. Lukens (1966) found this temperature was 27 C, and Table 7 confirms his observation.



Table 10. Effect of drying for 16 hours and rewetting for 6 hours in the light upon the subsequent sporulation rate in moist darkness. Data are percentages of stalks with spores, 3/14/68

	6*	9	12	18
Wet	0	19	86	94
Dried	—	6	83	81

\*Six-hour observation made in experiment of 2/22/68

The following course of spore formation in the dark on continuously wet stalks has been derived from Table 10: After 6 hours, no spores have appeared; after 9 hours, 1/5 of the stalks have spores; and in 12 hours, all have spores. Since each period for EPIDEM is 3 hours long, the present plus two past periods makes the 9 hours for 1/5 sporulation. (The experiments of Fig. 4 showed somewhat more rapid sporulation, but we have employed the rates of Table 10 for they include formerly dry as well as continuously wet conditions and agree with the results of Lukens (1963).) Now we must consider the modification of this course by water and temperature.

First, let us take GSTK, the stalks formed regardless of leaf wetness. Since Rands (1917) and Rotem and Reichert (1964) found a few spores on lesions beneath rain and dew shelters, we assume that the GSTK's can form spores, GSPOR, regardless of leaf wetness, and EPIDEM simply need not question leaf condition. Further, if it has been dark for some time, as at 0100 and 0400 hours, EPIDEM need not ask the temperature because Tables 2 and 4 show sporulation is roughly the same at any temperature below 27 C. Thus at 0100 and 0400 hours, when the GSTK have been in the dark for two previous periods, we are justified in calculating the number of GSPOR of spores on them as simply 1/5 of GSTK present two periods before or roughly 9 hours earlier. The sporulation requires, of course, an equal reduction in the GSTK available for sporulation later.

During the other hours of the day, the sporulation process in GSTK is illuminated for at least part of the time. This requires that EPIDEM look at the temperature because Lukens (1966) has found sporulation in the light is sharply decreased by warmth. His observation of the decrease in sporulation with rising temperature can be represented accurately by the cumulative Normal curve with mean of 21 C and standard deviation of 2.5 C. Therefore, if the time is not 0100 or 0400 hours, EPIDEM calculates a factor from the mean temperature of the current and three preceding periods and multiplies GSPOR by this factor. This adjustment, for example, decreases daytime sporulation to half that in the dark if the temperature is 21 C.

The calculation of the crop DSPOR upon DSTK follows the same rule about hour or darkness and about temperature. Further, it requires EPIDEM to examine leaf wetness. If the leaves have been continuously wet for the present and past three periods or about 12 hours, and if the temperature or darkness are suitable, every DSTK present three periods

ago can now bear a DSPOR. A fifth of any DSTK that appeared two periods ago can also bear DSPOR.

If wetness has only continued for the present and two, not three past periods, sporulation is less abundant. Table 10 indicates that about 1/10, not 1/5, of the stalks bore spores in 9 hours if the stalks had been dry just prior to the sporulation process. Hence, if wetness has persisted for only two past periods, EPIDEM calculates DSPOR as 1/10 of DSTK.

After the effects of wetness upon the formation of DSPOR have been considered, the effects of illumination and temperature and the reduction in the available DSTK are handled as they were for GSPOR.

*Alternaria* spores are robust, but McCallan and Wellman (1943) did report that viability was halved in 12 days. This is accomplished in EPIDEM by multiplying the spore crop on stalks and lying on new hosts by 0.993 at each 3 hour period. The 0.993 is F, a factor read into EPIDEM earlier.

#### F. Spores Are Washed Off by Rain and Caught by Leaves

Washing, as by rain, may also eliminate spores from the game. Figure 5 shows 99% of the spores were washed from rigidly supported leaves by a quarter inch of sprinkling. This clearly indicates that natural rain will wash spores from stalks, but the quantity is uncertain. For the present, we assume that 0.04 inch of natural rain per hour measured on a leaf area basis will in a 3-hour period remove half the spores from leaves supported on petioles in the field.

The preceding statement reveals that the leaf area index, LAI, or acres of leaves per acre of land must be known to EPIDEM. Watson (1952) observed that the LAI of a potato crop increased from about 1 in June to 3 in mid-August and then declined. We have, therefore, informed EPIDEM that the LAI of the tomato crop is represented by a parabola that rises from 1.1 on June 1 to a maximum of 3 eighty-four days later. The LAI then declines at the same rate that it rose.

The washing of spores and the role of the leaf area index have been combined in EPIDEM. Spores that are on stalks and that are caught on new hosts may be washed away. The percentage washed away is calculated as:

$$\frac{\text{Rain/LAI}}{0.4 + \text{Rain/LAI}} \times 100$$

The 0.04 was set earlier by reading RM equals .04. RM is the rain per hour that removes half the spores.

The stalks that lost their spores are likely sites for new spore formation. We have already found in an experiment concerning succeeding crops of spores that 1/3 of the stalks from which spores were removed formed new spores in the usual time for that process. Thus, EPIDEM restores to the active stalk account 1/3 of the stalks that have been washed clean of spores unless NUSTK were read "false" at the beginning.

Now, what happens to the spores washed from stalks? When spores are

washed to the ground, they will surely be lost. But common sense tells us that rain will also spread spores from stalks to new infection sites on the same and on nearby leaves. The account for spores caught on new infection sites is called CATCH, and it is increased by the number of spores washed from stalks and multiplied by the factor

$$RP^{100 \text{ Rain}}$$

RP is simply the fraction of the spores washed from stalks that is caught each period when .01 inch of rain falls. We have chosen an RP of 0.9 for the present, making the fraction caught

$$0.9^1, 0.9^2, 0.9^3, \dots, 0.9^n$$

when 1, 2, 3, . . . , n hundredths inch of rain falls per hour. The fraction caught has not been made a function of LAI because two phenomena seem counteracting: While the rainfall rate per leaf area is decreased, the area of traps for catching spores awash is increased by an increasing LAI.

Try as we may to make EPIDEM logical, we must introduce some empiricism. Here we admit that we do not know the proportion of washed and caught spores that will be infective. Hence, we introduce a fraction, WASP, that recognizes that less than 100% of the spores will be infective, and have EPIDEM multiply the rain catch by WASP, one of the parameters read by EPIDEM, at the beginning.

At this point, a review of progress is offered. Stalks have been formed according to the number and enlargement of lesions, to the state of maturity of the stalk crop, and to the temperature and wetness of leaves. Rain may have beaten some of the stalks into infertility. Spores have formed on the stalks according to the temperature, illumination, and wetness. This sporulation has, of course, decreased the number of stalks available for further sporulation. A small proportion of the spores are destroyed each period by old age. If it rains, however, many spores are washed away, some going into the group caught on new hosts and some falling from the game. Part of the stalks washed clean of spores is restored to the stalks that can form a spore crop. We now turn our attention from the occasional washing to the frequent blowing of spores.

### G. Spores Are Blown by Wind and Caught by Leaves

Since spores of *Alternaria* do not appear in the air if the leaves are wet (Rotem, 1964; Meredith, 1966), EPIDEM passes right by the following section if the leaves are wet. Often, however, the leaves are dry, and if we knew the shearing stress by the wind on the multiple layers of leaves, the flight of spores could be estimated.

Evidence that shearing stress is the appropriate function of the wind can be seen in Rotem's (1964) observations. Shearing stress at the surface is often proportional to the square of wind velocity. On the other hand, the spore load of the air is diluted more as wind speed increases. Consequently, one expects that the concentration in the air will vary with the square of wind speed divided by wind speed, or concentration will simply vary with wind speed. In fact, when leaves are dry and spores on leaves are abundant, that is exactly what happens (Rotem, 1964).

As the leaf area of the crop increases, the mean stress upon all leaves for a given wind above the crop will decrease. Ventilation in a corn crop decreases exponentially, from 100% in the top leaf area to 50% in the second and 25% in the third (Brown and Covey, 1966). This rule and the LAI already calculated for the tomato crop are employed by EPIDEM to obtain the mean shearing stress from the wind speed.

The blowing of additional spores will become increasingly difficult as the wind rises. The proportion of spores blown away will not, therefore, increase indefinitely with shearing stress. Rather a function of the familiar form

$$\frac{\text{Mean stress}}{200 + \text{Mean stress}}$$

is employed for the proportion of spores blown from stalks in EPIDEM. This rule simply says that half the spores are blown away at a mean wind speed in the canopy of (200)<sup>1/2</sup> or about 14 mph. The 200 was set by reading  $C_{u1}$  as 200.

Earlier we learned that blowing spores from stalks had permitted 1/3 of the stalks to grow new spores, Table 11. Hence, EPIDEM rehabilitates 1/3 of the stalks that lose their spores to the wind unless NOSTK were read "false" by EPIDEM at the beginning.

How many of these air-borne spores will enter the CATCH account on new infection sites is most important for the course of the disease. Common sense suggests that the proportion caught will decrease with LAI, and EPIDEM multiplies the proportion blown by the ratio of attained LAI to maximum LAI.

The proportion caught within our field will increase with increasing field size. Gregory (1945) has provided a theory for the deposition of spores, indicating that the proportion of spores caught would increase by 30 to 100% if the field size increased from 10 to 100 m radius. Put another way, the air reaching a plant will be richer in spores if it has blown a long way over the diseased field.

The effect of LAI and field size have been incorporated into the following expression that is multiplied by the number of air-borne spores to obtain the number caught:

$$C_{u2} * LAI$$

The factor  $C_{u2}$  includes the maximum LAI. It also includes those factors that decrease the effectiveness of the caught spores; thus,  $C_{u2}$  plays a role in wind dispersal like WASP plays in dispersal by washing. Finally,  $C_{u2}$  increases with field size, and increases of 50% are logical for great changes in field size.

In addition to these factors, the upward diffusion and loss of spores and the trapping efficiency of a unit of leaf may be functions of wind speed. Gregory (1961) could not, however, discern any clear relation between trapping and wind speed. Although we have not yet done so, we may take into account these last two effects of wind upon catching by dividing the proportion caught by the wind speed raised to some fractional power,

Table 11. Regrowth of spores on wind-denuded stalks. Data are numbers of stalks and spores per field, 5/2/68

Spores removed	Before		After	
	Stalks	Spores	Stalks	Spores
No	7.7	7.6	8.7	8.5
Yes	8.3	8.1	8.9	2.8

UPOW. This concludes consideration of spread of spores to new sites and brings us to the matter of their germination that must precede infection.

#### H. Spores Germinate

If the leaves are wet and the temperature is not abnormal, *Alternaria* spores germinate in less than one of our 3-hour periods (Rands, 1917). Thus, if EPIDEM finds the leaves wet, it simply transfers all spores in the CATCH account into the GERM(1) account, a non-cumulative tally of the number of spores germinated in the present period. This completely erases CATCH.

If the air is humid, some germination is possible even when the leaves are dry. Munnecke, *et al.* (1959) found that germination was prompt in humid air. Their observations of germination at various relative humidities can be summarized by a cumulative Normal curve with mean at 92% relative humidity and a standard deviation of 4%; this rule is incorporated in EPIDEM.

The germinated spores are more susceptible to drying than when they are dormant. In the experiments of section IE, spores germinated in humid air persisted in dry air, but spores germinated in water were promptly killed if the liquid water around them were withdrawn. Therefore, EPIDEM destroys all germinated spores when leaves change from wet to dry. This step brings us to the end of the germination process, and we proceed to the essential process of infection.

#### I. Germinated Spores Invade Leaves

When leaves are dry, a small rate of infection is possible as shown in Rotem and Reichert's (1964) observation of infection under a dew shield. If the parameter DFECT in EPIDEM is set at some value other than zero, infection proceeds at that rate while the leaves are dry. On the other hand, if the leaves are wet, the rate is set at 100%. For the present, DFECT has been made 1%, permitting a little infection when the leaves are dry and permitting the full rate when they are wet.

The quantity of infection increases with temperature between 12 and 25 C (Moore, 1942; Pound, 1951). The observed increase is summarized in the relation:

$$\frac{2 \text{ Temperature}}{30 + \text{Temperature}}$$

where temperature is in degrees Celsius, i.e. C.

The load of fruit upon tomato plants also changes the amount of disease. This phenomenon is associated with the infection step because sterile tomatoes standing among diseased plants and receiving great quantities of inoculum do not become diseased (Horsfall and Heuberger, 1942b). The factor for increased susceptibility with increasing fruit load is taken from the relation between defoliation of tomatoes by *Alternaria* and amount of fruit. Since defoliation is proportional to disease index (Horsfall and Heuberger, 1942a), "defoliation" may be translated as "number of infections." Defoliation increased from about 50 to 100% as the number of fruits per plant increased from 0 to 50 (Horsfall and Heuberger, 1942b). The number of fruit increased as the cumulative Normal curve with mean 83 days after June 1 and standard deviation 17 days, Fig. 7. Hence, the fruit load factor for susceptibility is simply 50% plus 50% of the cumulative Normal ordinate for the preceding factors and the number of days after June 1. If NOJGH were read "false," the fruit load factor would remain constantly 50%.

The susceptibility of plants also increases in the shade (Rowell, 1953). We may attribute the effect of shade to a decrease in photosynthesis as would occur if the sun did not shine at 1000 and 1300 hours. Thus, infection can be modified in EPIDEM by a factor CL(IC). IC is 1 if both

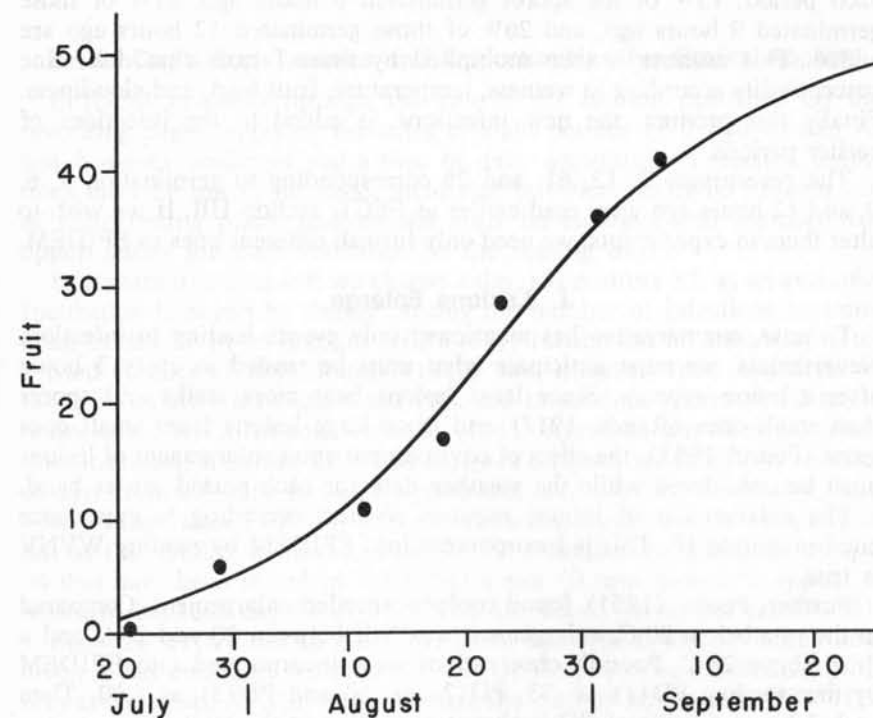


Figure 7. Increase in number of half-grown fruit on tomato plants as observed in 1941 (●) and as estimated by the cumulative Normal curve.

midday hours are sunny, 2 if one is sunny, and 3 if neither is sunny. So far all three CL (IC) have been set at 1, but in the future we may experiment with different values.

The preceding paragraphs concern susceptibility, and in each 3-hour period, the final step in calculating infection is examining how many spores were germinated in past periods and what fraction of those spores could infect in the time since their germination.

In the experiment described in section IF, von Schmeling observed the percentages of infection after tomatoes had remained for different periods in a moist chamber.

After 3 hours, no leaves were infected, but after 6, 9, and 12 hours the percentages infected rose to 13, 74, and 100%. That is 3 hours after germinating, spores will cause no infection. After 6 hours, however, 13% of the inoculations will be successful. At the end of 9 hours, another (74-13) or 61% will be successful. Finally, at the end of 12 hours, another 26% will be successful, bringing infection from that lot of spores to 100%.

In EPIDEM, however, the problem is calculating the number of infections at a given time, not from a given lot of spores. This is easily done from von Schmeling's data, nevertheless. EPIDEM has carried an account for spores germinated 6, 9, and 12 hours ago. As the calculations reach each period, 13% of the spores germinated 6 hours ago, 61% of those germinated 9 hours ago, and 26% of those germinated 12 hours ago are added. This number is then multiplied by those factors that determine susceptibility according to wetness, temperature, fruit load, and cloudiness. Finally this product, the new infections, is added to the infections of earlier periods.

The percentages 0, 12, 61, and 26 corresponding to germination 3, 6, 9, and 12 hours ago were read earlier as FECT, section IIB. If we wish to alter them in experiments, we need only furnish different ones to EPIDEM.

#### J. Lesions Enlarge

To now, our narrative has mentioned only events leading to infection. Nevertheless, we must anticipate what must be tended to every 3 hours after a lesion appears. Since large lesions bear more stalks and spores than small ones (Rands, 1917) and since large lesions from small ones grow (Pound, 1951), the effect of environment upon enlargement of lesions must be considered while the weather data for each period are at hand.

The enlargement of lesions requires wetness according to experience cited in section IF. This is incorporated into EPIDEM by reading WNVV is true.

Further, Pound (1951) found coolness speeded enlargement. Compared to the rate below 20 C, enlargement was half between 20 and 25 C and a third above 25 C. Pound's observations were incorporated into EPIDEM by first reading PD(1) as .33, PD(2) as .50 and PD(3) as 1.00. Then each 3 hours a value of PD is chosen according to the temperature.

We have assumed that 50 3-hour periods or about a week of cool temperature and PD equal to 1.00 and of wet leaves would permit full

enlargement of a lesion. This is accomplished in EPIDEM by reading the factor VDV as 50 and calculating a 3-hourly enlargement index as  $PD/VDV$ .

At the end of the narrative about one of the eight 3-hour periods in a day, we pause to review what has been done. The crop of stalks has been modified according to the number of opportunities opened by lesion enlargement on past days and to the temperature and state of maturity of the crop on those opportunities. Some of these stalks, GSTK, are grown under wet or dry, but the stalks DSTK are grown in greater numbers when the leaves are wet. Next spores are grown on the stalks according to the age of the stalks, to the wetness of the leaves, to the temperature and to the illumination. The spores are then carried away by the washing of rain or the stress of the wind, and part of the stalks are made fertile again. Some of the spores carried away are caught on new infection sites, especially in a light rain or in a large field with many leaves. Spores caught on new leaves will germinate in water or in humid air, but if spores germinate in liquid water, they are killed if the wet leaves dry. Infection follows germination after a few hours, and susceptibility is greater when fruit loads the plants, temperatures are warm, and skies are cloudy. Finally, an index for the enlargement of lesions is calculated from the temperature.

#### K. At Day's End, Lesions and Opportunities for Stalks Appear

EPIDEM proceeds through the day in the fashion described on the preceding pages, applying the rules to eight periods of 3 hours each. At last, however, midnight and a time of daily accounting is reached. Infections must be put to incubate, incubated infections must be brought out of their resting place, and lesions must be enlarged and searched for opportunities for stalk formation in the coming day.

Explanation is clearer if we choose a day, say number 57, as an example. Incubation is begun by simply placing the number of infections accumulated in day 57 in an account NCBT(57). Incubation is terminated after a fixed number of days. Rands (1917) said incipient spots appeared 48 to 72 hours after incubation and enlarged to produce spores in 72 to 96 hours more. McCallan and Wellman (1943) found lesions 40 to 60 hours after inoculation. Earlier EPIDEM accepted a parameter ICBT, the number of days from infection to lesion appearance, and we have set it at 4 days. Thus, 4 days after EPIDEM puts infection into incubation, it brings them out as the number of new lesions. In the example, 10 infections on day 54 that have been stored in ICBT(54) cause 10 new lesions to appear at midnight between day 57 and 58. The 10 lesions are called DLSN(58).

Each DLSN(K) has an index SIZE(K) associated with it, telling how much it has enlarged. At midnight, EPIDEM sorts over the SIZE(K). If they are less than XSIZE, the maximum, the index of enlargement  $PD/VDV$  calculated each period is employed. Rands (1917) observed the maximum size or number of spores per lesion at 1 to 2 thousand, and we have set XSIZE at 1000.  $PD/VDV$  was determined according to the observations

of Pound (1951) and summed up over the preceding day. If all periods of day 57 have been wet and cool, the index of enlargement will be 8/50. Thus, the increment in lesion size for day 57 will be 8/50 times XSIZE times the DLSN (57). The 8/50 will also be added to all other SIZE (K) where K is less than 57 and SIZE (K) is less than XSIZE.

The reader will recall that opportunities for stalk formation were employed in calculating the stalk crop. These opportunities OPTY (57) opened at the end of day 57 are the increments in lesion size made on day 57 in the lesions of day 57, as described in the preceding paragraph, plus the increments on day 57 in lesions that appeared on earlier days but had not yet reached maximum XSIZE.

Having established the number of infections incubating, the number of lesions that have appeared and the number of opportunities open for stalk formation, EPIDEM is ready for the first of the eight periods in the new day 58. It continues in this fashion, period after period, and day after day, from June 1 to the end of the season of disease observation. At last it writes the number of lesions newly appearing on each day, the accumulated number of lesions and their logarithm for each day, and a graph of the rise in logarithm of accumulated lesions. All of these data are "per 1 initial lesion."

The next section, "What EPIDEM Did," tells how it all turned out when the computer was faced with the weather data of five seasons and expected to recapitulate the courses of the epidemics in those years.

### III. WHAT EPIDEM DID WHEN IT SAW ACTUAL WEATHER

For over a decade, Horsfall and his colleagues observed the surges of tomato early blight near New Haven. When EPIDEM was being planned, we chose five years that would give a range of weather and disease severity. The five years are: 1941, 1943, 1944, 1950, and 1951. Among the first three years, 1943 had most, 1941 had less, and 1944 had still less blight. We employed these three years both to establish the value of some arbitrary parameters — as WASP and  $C_{u2}$  — in EPIDEM and to observe whether EPIDEM produces realistic but synthetic epidemics. Then we used 1950 and 1951 as an independent test of EPIDEM'S realism.

The weather of the five seasons is summarized in Table 12. In 1941 Horsfall observed the increase of disease in a large field of Scarlet Dawn tomatoes at the Nuttle farm in North Haven, about 5 miles east of the weather observatory at the Lockwood Farm (Table 12). Defoliation or disease was estimated by a four-class method (Horsfall and Heuberger, 1942b). In 1943 Horsfall observed disease at a single time in a small plot of John Baer (similar to Scarlet Dawn) tomatoes at the Lockwood Farm. Severe defoliation was seen and was estimated by an 11-class system (Horsfall and Barratt, 1945). In 1944, disease was observed at several times in the same plots and variety and by the same method as employed in 1943. Defoliation was less severe in 1944 than in either 1941 or 1943.

The plants of 1950 and 1951 were of a determinate variety grown in a different fashion and are not comparable to those of 1941, 1943, and 1944. Hence, we shall first see how EPIDEM behaves with the weather of the 40's and later offer it the 1950 and 1951 weather.

Defoliation is proportional to a "disease index" which is in turn proportional to the number of diseased leaves (Horsfall and Heuberger, 1942a). The number of diseased leaves, on the other hand, does not increase linearly with the number of infections. Rather, as the percentage of diseased leaves increases, more and more infections are required to involve the diminishing number of healthy leaves. This problem is recognized and corrected in the so-called Thompson transformation of percentage of leaves diseased into number of lesions per 100 leaflets (Gregory, 1945). Table 13 shows the observations of defoliation transformed in this fashion into numbers, log T, that logically should be linearly related to the logarithm of the number of infections calculated by EPIDEM for 1 initial lesion.

Before the observations can be compared with the output of EPIDEM, we must remember that EPIDEM shows a lesion on the day of its appearance, while defoliation will not occur until several lesions have appeared, and have enlarged considerably. Therefore, we can expect that the observations of defoliation may need comparing with earlier lesions in EPIDEM. For example, EPIDEM lesions for August 20 may correspond to observed defoliation on August 30.

If a candidate simulator contains many parameters whose values are not established by observations made prior to the test of the candidate, the test is scarcely critical. By adjusting these empirical parameters, the manipulator can make the simulator fit the data, and we are left wondering whether the simulation is valid or the manipulator of parameters is artful.

In constructing EPIDEM, we have striven to avoid this pitfall by using parameters estimated in laboratories *a priori*. For example, the values of the enlargement index, PD, are taken from Pound's (1951) observations. Nevertheless, we have been unable to estimate all parameters *a priori*, and  $C_{u2}$  and WASP are left unknown.  $C_{u2}$  determines the fraction of infective air-borne spores caught on leaves. WASP determines the fractions of spores washed onto leaves and infective.

Table 12. Weather at Mt. Carmel Lockwood Farm by 10-day intervals from June 1

First Day	Rain, inches					Humidity %					Wind, mph				
	1941	43	44	50	51	1941	43	44	50	51	1941	43	44	50	51
1	3.3	2.2	.9	2.1	.3	71	82	70	74	71	7	5	4	9	7
11	.9	2.2	.6	.8	1.0	76	78	77	77	74	4	5	5	7	8
21	0	.9	.3	1.0	1.3	72	77	80	74	80	6	5	4	7	7
31	2.1	1.1	.2	2.6	.8	79	81	70	76	71	5	5	4	5	8
41	1.2	.1	.2	2.1	1.4	82	76	75	82	77	5	5	5	6	6
51	1.1	1.6	.6	.6	.8	75	78	73	73	75	4	4	4	5	6
61	0.8	.3	.5	1.1	.3	70	77	76	67	75	2	5	3	5	6
71	1.8	1.4	1.1	3.3	1.2	67	81	73	65	84	7	3	4	6	5
81	2.1	.3	.1	1.9	.6	72	77	68	80	79	5	4	5	6	6

Table 13. Percentage defoliation (Defol.) in tomatoes and log T, the logarithm of the Thompson transformation of those percentages. Observations by: 1941 and 1943, Horsfall; 1944, R. W. Barratt; 1950 and 1951, S. Rich

1941				
Date	July 21	Aug. 11	Sept. 2	Sept. 11
Defol.	15.0	34.3	95.0	96.3
log T	1.20	1.62	2.48	2.52
1944				
Date	Aug. 8	Aug. 30	Sept. 20	Sept. 25
Defol.	6.5	25.0	73.0	83.5
log T	0.83	1.46	2.12	2.26
1943				
Date	Sept. 20			
Defol.	97.0			
log T	2.54			
1950				
Date	Sept. 7			
Defol.	59.0			
log T	1.95			
1951				
Date	Sept. 5			
Defol.	28.0			
log T	1.52			

The two unknown parameters were set by three criteria. First, early 1941 had much rain, and the year had much disease relative to 1944. Hence, WASP, the fraction of spores washed from stalks, caught and effective, can be high relative to  $C_{u2}$ . Second,  $C_{u2}$  may logically be larger for larger fields as 1941 and smaller for smaller fields as in the remaining years. Third, since the output of EPIDEM is the number of lesions per initial lesion, between 10 thousand and 1 million lesions (log lesions equal 4 to 6) at season's end is a reasonable amount. Values of 5% for WASP, 3% for  $C_{u2}$  in 1941 and 2% for  $C_{u2}$  in 1943 were established.

Now we return to the critical question of the comparison of EPIDEM's behavior to field observation. The values of WASP and  $C_{u2}$  were chosen with the abundance of disease in September 1941 and its scarcity in September 1944 in mind. Thus, making the two unknown parameters meet criteria 1 and 2, prejudices the comparison of 1941 versus 1944 somewhat. It is not entirely prejudiced, however, for a logical reason exists for making  $C_{2u}$  larger in larger fields. Further, criterion 3 and the differing characteristics of "per initial lesion" and "per 100 leaflets" invalidates the comparison of absolute EPIDEM lesions with absolute defoliation data. On the other hand, simulation by EPIDEM of the actual course of disease within a year or the variation from 1943 to 1944 is valid evidence of the faithfulness of EPIDEM to the real thing.

The real thing, observations of defoliation transformed into "log T" (Table 13), should logically be linearly proportional to the number of

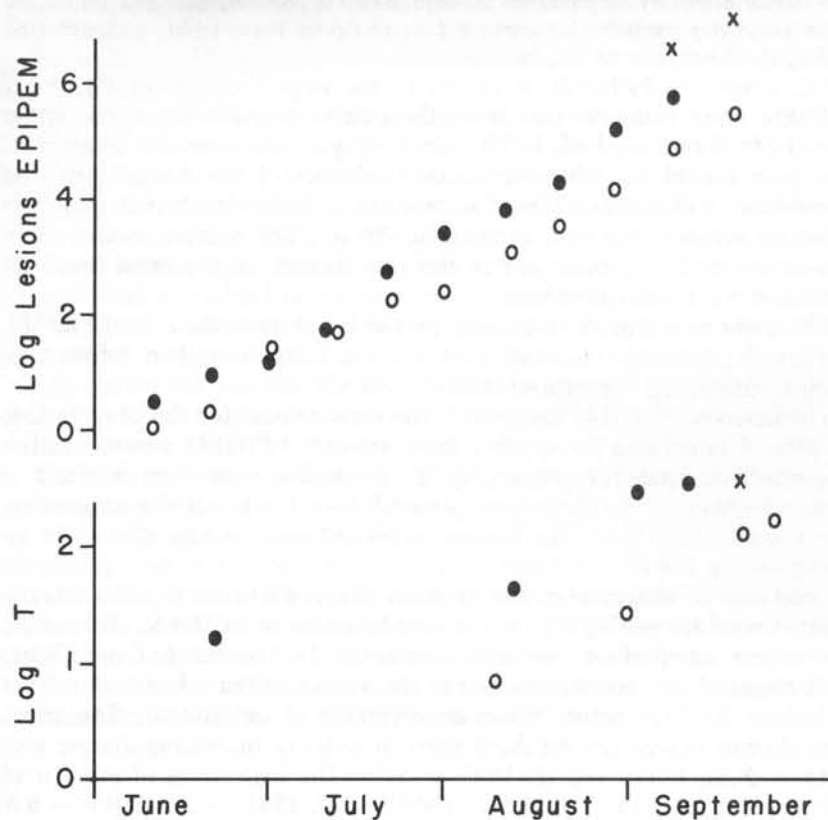


Figure 8. The courses of observed (log T) and calculated (log lesions EPIDEM) disease for three years. Log T is the logarithm of the number of lesions per 100 leaves obtained from observations of defoliation. Log lesions EPIDEM is the logarithm of the number of lesions per initial lesion as calculated by EPIDEM. 1941 (●), 1943 (X), 1944 (○).

lesions. The log T for 1941, 1943, and 1944 are shown in the lower part of Fig. 8 above the date of observation.

In 1941, abundant disease was seen early, disease increased somewhat slowly during July, and a rapid increase in August brought the quantity of disease to a high level in September. In 1943, only a single observation was made, but this revealed abundant disease.

Although the 1944 growing season was remarkably dry, considerable disease appeared. The numerical estimates of Fig. 8 are supplemented by the following quotation from R. W. Barratt's notebook for 1944: On August 1, he wrote, "Defoliation is showing up in the field now." On September 1, he wrote, "The season has been exceptionally dry and little defoliation is present." The subsequent disease readings, however, showed

74% defoliation by September 20 and 84% by September 25. Thus, we know from the records that disease leaped up in July, 1944, was arrested in August, and rose in September.

The output of EPIDEM is shown in the upper portion of Fig. 8. If EPIDEM is an authentic simulator, the synthetic epidemics of the upper part of Fig. 8 that are built by the computer program from the weather of each year should resemble the actual epidemics of the lower part. The resemblance will not, as we have written above, be in the absolute numbers of lesions because they have been arbitrarily set. The relative severity from year-to-year and the course within the year should, on the other hand, be mimicked by a valid simulator.

The early appearance of disease in 1941 was mimicked by EPIDEM. Further, the synthetic epidemic grew more quickly after than before mid-August, mimicking the real epidemic.

The outcome of 1944, however, is the most critical for the observations are more detailed and the weather more unusual. EPIDEM was successful. The synthetic epidemic, upper Fig. 8, showed a slow start in June, a surge — observed by Barratt — around July 1 and then a stagnation. Nevertheless, EPIDEM, like Nature, produced considerable disease in remarkably dry 1944.

Only a single observation was made in 1943, and hence the 1943 datum is only useful for testing the year-to-year behavior of EPIDEM. To make a year-to-year comparison, we have employed the transformed defoliation percentages of the last observations of the years and the calculated number of lesions 10 days before those observations of defoliation. The transformed observations for the three years in order of increasing disease are: 1944 — 2.26, 1941 — 2.52, 1943 — 2.54. The logarithms of number of lesions according to EPIDEM are: 1944 — 5.0, 1941 — 5.3, 1943 — 6.8. That is, the correspondence between observation and simulation is not a proportionality, but both observation and simulation identify 1943 as most severe and 1944 as least severe.

We are now ready to test EPIDEM upon the 1950 and 1951 weather and disease observations. In 1950 and 1951, Chatham tomatoes were grown in the small plots at the Lockwood Farm. These determinate plants were supported within individual wire fences. The change in variety plus the fences decreased the average amount of disease from the previous years and invalidated a comparison of the 40's and 50's. On the other hand, EPIDEM should predict more disease in 1950 than in 1951, the fact observed by Saul Rich using the 11-class Horsfall-Barratt scale of defoliation (Table 13). Since the values of WASP and  $C_{u2}$  will be maintained the same as 1943 and 1944, expecting EPIDEM to predict more lesions in 1950 than in 1951 is a test unprejudiced by the adjustment of parameters.

The increase in disease in 1950 according to EPIDEM was regular, and the logarithm of lesion number reached 6.1 ten days before the observation of Table 13. On the other hand, early June in 1951 was dry and the disease increased slowly. By late June, however, a regular increase began and continued until September. Nevertheless, the logarithm of lesion number

reached only 4.3 ten days before the observation of Table 13. Thus, EPIDEM's accuracy as a simulator of the effect of weather upon *Alternaria solani* is again verified by its simulation of the greater disease in 1950 and less in 1951.

This completes the tests of EPIDEM that we have been able to perform and leaves us reasonably confident that EPIDEM is a simulator of early blight epidemics. First, we shall review the tests that the simulator has passed, and then we shall exploit some of the virtues claimed for simulators.

The first test passed by EPIDEM was not pointed out during the passing. This was simply that when a logical set of characteristics of a fungus and disease were assembled no inconsistencies or missing pieces were evident, and the output looked like a disease in its ten thousand to million-fold increase of a single lesion.

The second test was the mimicking of the courses of disease within 1941 and 1944. The rises and levelings documented in data or remarks in a notebook were simulated.

The third test was the mimicking of the year-to-year variation of the final observation of disease in a trio of years in the 40's. This test was prejudiced by our choosing the values of parameters WASP and  $C_{u2}$ , and it is not surprising that 1941 and 1944 arranged themselves in the proper order. On the other hand, 1943 observations were not employed in choosing the values for the two parameters, and it is to EPIDEM's credit that it calculated abundant disease for 1943 as was observed in the field.

The final test was the mimicking of the abundance of disease in 1950 and scarcity of disease in 1951. This was well done.

#### IV. ADEQUACY OF OUR KNOWLEDGE OF EARLY BLIGHT

Now that EPIDEM has received passing marks in its simulation of early blight, some of the advantages of a simulator that were advertised in the Introduction should now be reaped.

The first advantage is the discipline of constructing a complete and consistent structure. We have been forced into the drudgery of digging cellar holes as well as the excitement of erecting the steeple. This advantage of the simulator has already been reaped in section I where we described the numerous simple experiments required for constructing EPIDEM. Although they were both simple and required for understanding early blight, they were not performed until the present system analysis led us to them. And although they resemble the countless exercises in student dissertations that have been often ridiculed, they are lent importance here because their relevance is clear.

Von Schmeling's experiment on the time needed for penetration, section IF, exemplifies this advantage of simulator construction. This experiment required no elaborate equipment and only a little time. But until its results were known, the effect of different durations of dew could not be evaluated. And, as we hope would often be the case, its performance had a happy bonus outside EPIDEM: the experimenter learned that 12 hours produced as much disease as 24 hours in the moist chamber and thus increased the capacity of his system for fungicide assay.

The second advantage of the simulator is testing the adequacy of our knowledge. Since EPIDEM passed the tests that we put it to, we conclude that our knowledge is passable, and we entitle the present section for this significant achievement. Since the knowledge is passable, it is worth displaying in unequivocal Fortran IV in the final section. Nevertheless, we have also learned that some very weak links endanger our knowledge of early blight, and unfortunately of many other diseases, too.

The reader will already have discovered these weak links as he went through the construction of EPIDEM in section II. They are concentrated in our knowledge or lack of it concerning the washing, blowing, and catching of spores. This problem has broad importance because these matters are of concern in most other diseases. And the weakness is grave because, as we shall see in the following section, the values of the parameters that concern washing, blowing, and catching can profoundly affect the course of the epidemic. The next section, where the efficacy of different parameters is demonstrated, will be postponed, however, until a riddle is solved.

The riddle is whether early blight is favored by wet or by dry weather. In the Introduction, the puzzling conflict of statements about the favoring of this disease by both wet and dry weather was presented. Since EPIDEM embodies a workable knowledge of early blight, it should explain this paradox.

The explanation seems to be that *Alternaria* profits from wet, but not always, and from dry, but not always. As EPIDEM shows, it is a lucky cycle of things that benefits *Alternaria* most. Thus, moisture is needed for abundant stalk and spore production, dryness for spore travel on the wind, humid air followed by uninterrupted wetness for spore germination and penetration, and any sort of weather for incubation. Persistent wetness would prevent flight to a new host, and wetness followed quickly by dryness would kill the spores before they could escape to the oasis of the leaf interior.

The cause of the surprisingly similar observed disease in wet 1941 and dry 1944 can be seen in the structure of EPIDEM and the hourly weather. Although 1941 had much rain and wet weather, it did have two long, untimely dry periods that caused the hesitations already mentioned. And although 1944 had little rain, it had some timely wet periods at 4-day intervals that germinated the abundant air-borne spores and caused the surge about July 1. It also had many dry days for spore travel followed by evenings with high relative humidities that germinated spores and then mornings of timely dew that permitted infection.

Solving this paradox of the dual character of *Alternaria* demonstrates the power that we have gained in giving our common sense free play in writing a computer program and reveals how disabled we were when we tried to embody epidemiology in either a single mathematical equation or in a forecasting rule that employed averages of the weather. Solving the paradox also brings us to the discussion of two remaining advantages of the simulator: exploring the efficacy of characteristics embodied in EPIDEM and experimenting with the weather. These two subjects are sufficiently important to be given separate sections.

## V. EXPERIMENTS WITH THE CHARACTER OF PATHOGEN AND HOST

EPIDEM contains many characteristics of the fungus and host. Most have been determined by experiment, some by judgment and some empirically. If we vary these and observe the effect upon the ensuing synthetic epidemic, we can judge which are important and effective and which are trivial. Some do not warrant our attention, some merit more exact investigation, and some offer opportunities for disease control.

The experimenter in the outdoors soon learns that one year's results are not to be extrapolated to a century. Nature rolls the climatic dice each season and seemingly at random produces a new sample of the weather. The outcome of a control attempt or a change in the fungus may be a success in one year, a failure in the next. This tedious waiting on a weather sample to be drawn and displayed is, of course, both the frustration and the fund devourer of practical testing.

Shortening and economizing on this testing is a reward held out to the simulator or EPIDEM builder. We cannot have the outdoor experimenter's knowledge that his results are real for EPIDEM undoubtedly contains unnatural things, faults of construction or parameters. On the other hand, our results are more realistic than laboratory experiments, and we need not err because our results pertain to a single season. The numerical experiments that follow have been performed in wet 1941 and dry 1944.

### A. How the Pathogen is Blown and Caught

The parameter  $C_{u1}$  determines the take-off of wind-blown propagules. To now  $C_{u1}$  has been 200, indicating that a wind of  $(200)^{1/4}$  or about 14 mph would carry away half the spores on stalks. If  $C_{u1}$  were halved, a 10 mph wind would carry away half. EPIDEM shows that halving  $C_{u1}$  increases the number of lesions on August 20, 1944 by 78%.



The generality of this result is tested by performing it in a windier season, 1941. Whereas 80 days in 1944 had only 36 periods in 640 with wind faster than 9 mph, the 80 days in 1941 had fully 93. Nevertheless, more easily blown spores and a smaller  $C_{u1}$  would have increased the number of lesions on August 20, 1941 by 26%.

The other parameter concerning wind is  $C_{u2}$ . It incorporates the maximum LAI and, more important, is increased by bigger fields and greater viability of air-borne spores. We have already seen Gregory's (1945) investigations indicate  $C_{u2}$  may increase by half when the field becomes bigger, bringing a greater abundance of spores from down wind. When  $C_{u2}$  was increased from the standard 0.02 of the small plots to 0.03, the number of lesions calculated for August 20, 1944 increased fully three-fold. In windier 1941, the change was nearly as great.

The remaining characteristic of wind dispersal is UPOW. Gregory (1961) in his Tables XI and XII shows that the relation between deposition coefficient and wind speed outdoors is uncertain. We have to now assumed the relation is nil. From Gregory's Tables, one could, by neglecting some data, conclude that the coefficient is inversely proportional to the square root of wind speed. This can be entered in EPIDEM by making the caught proportion of the air-borne spores equal to

$$\frac{C_{u2} \times LAI}{U^{1/2}}$$

The exponent  $1/2$  is UPOW.

This escaping of wind-borne spores was particularly important in dry 1944 when aerial dispersal was particularly important. Then it decreased the predicted number of lesions on August 20 to only one-fifth. Even in wet 1941, however, it decreased the number to a third.

The foregoing paragraphs on wind dispersal of *Alternaria* have demonstrated two things. First, the character of wind dispersal is influential in the course of disease. Second, our knowledge is incomplete. We have been forced to set  $C_{u1}$ ,  $C_{u2}$ , and UPOW with little knowledge. The next subject, washing of spores, presents the same picture.

### B. How the Pathogen is Washed and Caught

The parameter RM is the inches of rain per hour that will in each period remove half the spores from both stalks and the CATCH account. We have used a value of .04 inch, but Fig. 5 would support a value of .02 or even less. The easier washing of spores implied by an RM of .02 would increase the predicted number of lesions on August 20 by about half in either rainy 1941 or drier 1944.

Some spores may be washed onto new infection places and others may be lost from the game. The fraction caught is controlled by the parameter RP, the fraction of the spores washed from stalks that is caught by leaves during a period with .01 inch rain per hour. We have been employing an RP of nine-tenths, catching many spores awash. If RP is decreased to

seven-tenths, the number of lesions is decreased by a third on August 20, 1944 and, following heavy rains, by 80% in 1941.

The final parameter regarding rain is WASP, the proportion of washed and caught spores that is effective. If it is increased from the .05 that we have been using to .07, the number of lesions on August 20 is predicted to more than double in 1941 and increase by two-thirds in 1944.

As we said when we began these paragraphs on the washing of spores, the phenomena are influential, and we are uncertain of our facts. We know that the spores are easily washed, but the exact quantities washed, caught, and effective are unknown.

Since Table 11 showed that spore removal permits a third of the stalks to grow new spores, EPIDEM does too. As an experiment, however, we can ask how important this phenomenon is. If stalks lost this facility, the predicted number of lesions on August 20, 1941 or 1944 would be only about half as great.

At this point in our writing, one wonders why no variables concerning stalk growth and spore formation and germination appear in the list read into EPIDEM before each calculation. Clearly, the lack of variables testifies to greater certainty. And this certainty comes from the laboratory. Sporulation and germination are conveniently watched in the laboratory, and Miss Wooding and countless others have eradicated a lot of ignorance.

### C. Susceptibility Changes with Fruit and Sun

The infection process is neither as well characterized as sporulation nor as vaguely known as dispersal. The susceptibility of plants has been correlated with their sugar content. Susceptibility rises as the load of fruit rises and—presumably—sugar declines (Horsfall and Heuberger, 1942b). If we delete the rule that calls for susceptibility to rise from half to one as fruit accumulates, the predicted number of lesions on August 20 is decreased by about one-fifth in 1941 or 1944. Stated another way, a plant without fruit is expected to have one-fifth fewer lesions than one with a normal fruit load on August 20, and the difference will become greater in September.

Cloudy weather might decrease photosynthesis, thus decrease sugar content and thus, in turn, make the plants more susceptible. We have no clear information on this point; we only know that shaded plants are more abundantly infected than sunlit ones (Rowell, 1953). If we say that susceptibility is only 80% if the sun shines at both 1000 and 1300 hours, is full if it shines at one of those times, and is 120% if the sun shines at neither time, then the predicted amount of disease on August 20, 1941 or 1944 is decreased to about half of the standard case with susceptibility independent of sun.

Accepting this result as evidence of the importance of sunshine is superficial, however, for our arbitrary scale of susceptibility, not Nature, has increased abundance. We should, instead, examine whether such a rule will change the year-to-year relations. In fact, it does not when it encounters the small difference in sun between 1941 and 1944.

The difference in sunny periods between cloudy but dry 1951 and rainy but sunny 1950 is more than two-fold. (The 50's cannot be compared to the 40's because Hartford cloudiness rather than Mt. Carmel sunniness was employed in the 50's.) When the susceptibility depended upon cloudiness, the abundance of lesions on June 30 was scarcely changed in cloudy 1951 but decreased by half in sunny 1950. Clearly, if rapid photosynthesis and rich sugar change susceptibility as much as half, year-to-year differences in sun in the temperate zone can influence the course of disease importantly.

#### D. Speed of Invasion, The Escape from Weather

The speed of the spores seeking the oasis of the mesophyll and escaping the desert of the surface may be critical. Now we speed the fungus and leave the weather of 1944 as it was. To now, 13% of the spores that germinated 6 hours or 2 periods ago successfully infected leaves, while 61% of those germinated 9 hours past infected leaves, and 27% of those germinated 12 hours past infected the new host. These percentages are the increments in infection observed by von Schmeling in an experiment described earlier, and they are the 4 numbers read as FECT. In our present experiment, we advance the process 3 hours or 1 period, permitting 13% to infect in the first 3-hour period after germination. These courses of infection or FECT, and an additional, slow course are shown further in a tabulation:

Hours since germination	3	6	9	12
Percent infection				
Standard Course	0	13	61	26
Fast	13	61	26	0
Slow	0	0	13	87

An increase in the amount of disease from a faster infection seems obvious *a priori* for dry 1944. Surprisingly, however, the increase is even greater in wet 1941. The predicted abundance of lesions was increased by half on August 20 in the dry year but by 90% in the wet year. Although the rainfall was greater in 1941 than in 1944, the alternation of wet and dry in the wet 1941 fit the fast course particularly well.

The outcome of a slow infection course was also surprising. In 1941, the slow course fit the chances of the weather as well as the standard. And in 1944, the slow course actually caused a 15% increase in predicted disease. When the day-to-day progress of the 1944 course is examined, we find that the slow course gained its small margin of advantage when it moved infection into warmer morning hours.

The conclusion from these experiments with the infection course is that very speedy escape into the humid interior is generally advantageous and, sometimes, a slower course may benefit the pathogen by fitting the weather and moving infection into warmer hours.

#### E. Speed of Enlargement and Incubation, Two Long Processes

The opportunities for stalk growth are opened by the enlargement of

lesions. EPIDEM enlarges the lesions only when the leaves are wet (section IF), more rapidly in cool weather (Pound, 1951), and completely after 50 periods.

Pound's observations clearly show that lesion enlargement is favored by cool weather. Would a mutation or new strain whose lesion enlargement is favored by warm weather, flourish in the Connecticut climate? We examined this question by inverting Pound's rule in EPIDEM, making *Alternaria* lesions expand more rapidly in warm weather. EPIDEM answered: "Your hypothetical mutation would have produced only about a tenth as much disease as the normal *Alternaria* observed by Pound."

In the second experiment, the minimum endurance of enlargement is changed from 50 to 40 periods. Clearly, this factor has been limiting EPIDEM, especially in a wet year. The abundance of lesions predicted for August 20 is about doubled in both 1941 and 1944 by this change.

The incubation period is the greatest user of time and has, therefore, been singled out by van der Plank (1963) as the important slower of epidemics. In a disease limited by the weather, as potato late blight, the epidemic is often timed by the weather, however, and incubation duration is not important (Waggoner, 1968). *Alternaria* lies between these two extremes.

An incubation period of 4 days has been used. If a day is added for the remainder of the fungal cycle, 16 cycles should be completed in 81 days. If the epidemic course is idealized as 16 m-fold multiplications in 81 days, then it has multiplied about 1.7 times in each cycle to reach the 10 thousand lesions predicted for August 20.

Ideally, doubling the incubation time and making the fungus cycle every 9 days or nine times in 81 days should decrease the abundance of lesions to only 2% or about 200 lesions on August 20. In fact, weather as well as fungal cycling speed was limiting in EPIDEM — as it would a natural *Alternaria*. Hence, the abundance of lesions according to EPIDEM is decreased to about a fourth, not 2%, by a doubling of incubation time. This example of EPIDEM'S responding to the realities of the weather every 3 hours according to the physiology of an actual fungus exemplifies the progress made since the simple, pioneering models of epidemics.

For several years we have been looking for a workable antisporeulant to reduce the rate of spore production and hopefully to aid disease control (Horsfall and Lukens, 1968). This is the analogue of "chemosterilants" in insect control.

During the work we labored under a vague anxiety that even if we found one, it would not be very effective in the field because fungi are so fecund. The worst part was that we would not know until we had found a compound that would survive all the hazards of the field — sun, rain erosion, photodecomposition, and all the rest.

EPIDEM gives us an opportunity to test the odds for success or failure in the computer rather than in the field. EPIDEM could answer the question: how great a decrease in disease at season's end can be affected by changing sporulation?

Two means of changing sporulation were tried in EPIDEM. In the first, sporulation increments were halved. In the second, half the stalks were sterilized. The results were dramatically different.

The reader will recall that additions are made to the spore accounts each period. The addition is calculated as a weather-dependent fraction of the stalk population. This additional quantity must be subtracted from the stalk population because a stalk can bear only one spore. In the first experiment, the rate of spore formation was halved by halving the fraction of the stalk population that added spores in each period. Thus both the increase in spores and depletion of stalks was slowed.

In moist 1941 the amount of disease on August 20 would have been fully 57% as much even though the rate of sporulation was halved. The result was nearly identical in dry 1944. Clearly taking twice as long to grow spores on the same number of stalks has only a modest effect upon the epidemic.

Sterilizing the stalks has a more profound effect. Sterilization was accomplished within the STALK subroutine outlined in Fig. 6. Near the conclusion of the subroutine an increment is added to both the index of stalk development (IGLS or IDLS) and to the stalk population (GSTK or DSTK). In the present experiment the increment added to the index is unchanged, and the limit of complete occupation of stalk opportunities is reached as soon as before. In the experiment, however, the increment added to stalks is halved. The effect, therefore, is of forming stalks and then sterilizing half of them.

This process decreases the amount of disease on August 20 to only 6% in wet 1941 and 8% in dry 1944. The result predicts a profitable result from stalk sterilizing in a field that receives little foreign inoculum.

On the other hand, the decrease is not as dramatic as would have been predicted by simply calculating the relative disease in the partially sterile situation as  $(\frac{1}{2})^n$  where  $n$  is the number of generations. In the eighty days between June 1 and August 20 the 4 day incubation period of *Alternaria* could have been repeated 10 times with plenty of days left for the other stages of multiplication. Multiplying  $\frac{1}{2}$  by itself 10 times gives, of course, a tenth of a percent, not the 6 or 7 percent calculated by EPIDEM. This disparity between the simple mathematics of  $(\frac{1}{2})^n$  and EPIDEM is caused by the many limiting factors entering EPIDEM. The disparity illustrates the realism of EPIDEM compared to the simple formula and gives us confidence in the prediction that sterilizing half the stalks would decrease disease in an isolated field to 5 to 10%.

And it gives us confidence that research on antisporeulation might be stymied by inefficient chemicals to sterilize stalks but probably not by the mathematics of the matter. This brings our experiments in fungal character to an end, and we go on to changing the weather.

Before describing the experiments with weather modification, however, a summary of the present section is required. EPIDEM'S realism in five years gave a confidence that justified experimenting with it as a proxy for *Alternaria*. Outdoors the real *Alternaria* is expensive to experiment with,

requires years of waiting while Nature draws random samples of weather with changes in rain confounded with changes in humidity, and can never reveal the effects in past, exemplary years that might have been if the fungus had been different. EPIDEM, the artificial *Alternaria*, makes cheap and quick experiments in classic years with all conceivable changes. We tried a few.

Increasing the ease of take-off or the proportion of catch of airborne spores both markedly change the course of infection, especially in a dry year. And in a wet year, making the spores more easily washed and then caught greatly increases infection. Clearly, these characteristics of spore spread, by wind and rain, which are poorly known because they must be investigated outdoors, deserve our attention.

The characteristics of susceptibility and infection were also tested by the artificial *Alternaria*. The well-known effect of fruit load upon susceptibility was, of course, only moderately important by mid-August and was consistent from year to year. If sunshine decreases susceptibility, its effect could be important early and could alter the year-to-year change of severity of epidemics. If infection is greatly hastened, the germinated fungus is safer from untimely desiccation, and infection is markedly greater. If infection is slowed 3 hours, however, the fungus may not be decimated because it may infect during more favorable hours.

Opportunities for spore stalks are opened by lesion enlargement that is favored by cool, wet weather. A strain of *Alternaria* that is favored by warmer weather would produce a smaller epidemic in Connecticut. On the other hand, a strain that would produce faster enlargement toward its maximum lesion size would favor bigger epidemics.

Finally, we learned that lengthening the incubation period will not decrease infection as much as we might hope because the tempo of the disease is controlled by the weather as well as the parasite. And sterilizing half the stalks, not slowing their growth, would decimate disease.

## VI. WEATHER CHANGES THAT SLOW OR SPEED THE RISE OF ALTERNARIA

A simulator is a comprehensive means of predicting how a change in the environment would change an outcome, and EPIDEM should tell us whether *Alternaria* would be a curse or only a curiosity if a crop were moved to a new region and climate or if the weather were modified by mechanics and meteorologists. We begin by speeding the wind, go on to desiccate the air and conclude by drying leaves or by wetting them with irrigation or dew.

### A. The Wind that Carries Spores

Wind carries the dry spores from old host to new and also dissipates them into the upper air. During June 1 to August 20, 1944, the mean wind speed at the top of the crop was 6 mph. If the leaf area index was 2, the mean wind on the leaves was 4.5. The rule

$$\frac{\text{Mean stress}}{200 + \text{Mean stress}}$$

for the proportion of spores blown from stalks makes 1/11 of the spores take off in a 4.5 mph wind.

As an experiment, the wind speeds of 1944 were doubled. The effect was startling: the predicted number of lesions on August 20 was tripled! Clearly, given the rules of EPIDEM and weather of 1944, the wind is limiting aerial spread and spread is limiting disease.

Observations of actual aerial dispersal confirm that it is limited by the slowness of winds. For example, the concentration of *Alternaria* spores in the air increased as the wind speed increased to fully 10 miles per hour (Rotem, 1964). Further, this was not merely a burst unsustained by an adequate supply of spores in reserve: Rotem found that an extraordinary wind storm, 9 hours of more than 25 miles per hour, was required to deplete the spore reserve. Thus, the general features of aerial dispersal seem correctly incorporated into EPIDEM, although the phenomena described by  $C_{u1}$ ,  $C_{u2}$ , and UPOW must be better measured before the details of EPIDEM are secure.

### B. Humidity of the Air that Permits Germination

Relative humidity can profoundly affect the increase of *Alternaria*. Humidities above 83% permit germination, and these unwet spores are not killed by dry air. If spores are germinated in humid air in the evening and then a few hours of leaf wetness follow, the infection cycle can be completed before drying kills the germinated spores. The same hours of wetness without prior moist air might not permit infection, only germination, desiccation and death.

This effect of high humidity can be shown in 1944, which had little

rain, only 255 wet periods between June 1 and August 21, but a surprising amount of disease. As an experiment, all relative humidities greater than 85% were decreased to 85%, the typical nighttime humidity in the Negev (Rotem, 1964). (We shall speak again of the climate of the Negev desert.)

The rule that no relative humidities exceed 85% meant a decrease in humidity in 312 periods of the 648 periods of June 1 to August 20, 1944. The consequent decrease in disease was great: when the maximum relative humidity never exceeded 85%, the predicted lesions on August 20 were only 42% as numerous as when the natural humidities were given to EPIDEM. This testifies to the importance of the germination in humid air — but on dry leaves — that Munnecke *et al.* (1959) observed and illustrates the culling of significant from insignificant phenomena by a system analysis, EPIDEM.

### C. Dew and Irrigation that Wet the Leaves

The prosperity of *Alternaria* is improved by water in most phases of its life cycle. On the other hand, the fungus is unaffected by drought during its incubation and actually aided by drought during dissemination. Thus, the effect of wetness will depend not only upon whether the weather is predominantly wet but also upon the timing of wet and dry.

Since germination requires a little time and infection requires a great deal of time, all wet, while drying wipes out the entire sequence from spore to infection, 12 hours of wet are obviously more dangerous to the host than are four 3-hour periods separated by dry. That is, the timing of drying is most important, as we shall demonstrate with the 1944 weather.

In dry 1944, drying the first wet period in 79 runs of wet periods between June 1 and August 20 decreased the predicted abundance of lesions to only one-fourth the number calculated from the actual weather. But this shortening of runs, rather than drying a wet period here and there, left the runs intact.

If, on the other hand, 60 periods were dried, here and there through the same period, only 9% as many lesions were predicted as for actual weather. The scattered drying caused only a third as many lesions as shortening of runs of wet periods; this emphasizes the importance to fungal prosperity of the natural persistence in the weather; if one period is wet, the next is likely to be wet.

From June 1 through mid-August 1944, little rain fell at the Lockwood Farm, and we can test the effect of irrigation in this weather. EPIDEM was told to keep a budget of evaporation and rain. The balance began at zero on June 1. Then EPIDEM was told to add the rainfall and subtract evaporation during the four daytime periods at the rate of an inch per week or 1/28 inch per period. When the deficit reached an inch and the time was 1300 hours, EPIDEM was told to sprinkle an inch of irrigation water in 6 hours.

The simulated overhead irrigation affected the spores in two ways. First, it wet the leaves. Second, it washed spores about. With the parameter

RM equal to 0.04 and a leaf area index of 2, the washing of spores by 1 inch of irrigation in 6 hours or 1/6 inch per hour was

$$(1/6)/2$$

$$0.04 + (1/6)/2$$

or about 2/3 in each of the two periods. This depleted both the CATCH and the DSPOR and GSPOR on stalks. Only a fraction of the spores washed from stalks entered CATCH:

$$RP^{100 \text{ RAIN}} \text{ or } 0.9^{16.5} \text{ or } 1/6$$

During the 81 days from June 1 through August 20, 1944, the irrigation rule required sprinkling eight times at fairly even intervals. Four times the leaves dried after irrigation, and spores were desiccated and killed. In the other four cases, spores were not desiccated, but the supply of spores was depleted by washing. The predicted consequence of the irrigation was a 30% decrease in the number of lesions on August 20.

We turn now to the matter of dew and the astonishing assertion of Rotem and Reichert (1964) that early blight develops to epidemic proportions in the Negev desert of Israel and that irrigation by overhead sprinkling does not increase disease over that of furrow irrigation. Rotem and Reichart (1964) ascribe the epidemic to the effect of dew.

Unlike irrigation, dew comes mainly at night, often after spores have germinated in the moist evening air. Dew may contribute little to the water supply of vegetation and it does not deplete the spore account by washing, but it can provide many hours favorable for infection. The Bible land is the classic place of dewfall. In the Negev, little rain falls, and the humidity measured in a shelter rises to only about 80% even at night. Still, dew is present for 15 hours on a typical night.

In his Figure 2, Rotem (1964) shows the weather of a typical Negev day: temperature rises from 8 to 22 C; humidity ranges from 85% at night to 50% by day; wind rises from 8 km/hr at dawn to a maximum of 18 at midday, and dew persists from 1800 to 0900 hours.

A hundred days of Negev weather were offered to EPIDEM. The outcome was a riotous epidemic of early blight. The logarithm of the number of lesions reached 8.8 as compared with 6.8, the highest of the 5 years in humid Connecticut. This was a hundredfold more.

Thus, Rotem's observation is matched by EPIDEM; the nightly dews of the Negev, alternating with dry, windy days provide an almost ideal environment as specified by EPIDEM for both the growth of *Alternaria* and its spread.

These results point up an important hiatus, however. Epidemics in the desert of Idaho (Guthrie, 1958) must have a different origin from those in the desert of Israel. In both, overhead irrigation encourages the disease, but furrow irrigation produces disease only in Israel.

Since it is the dews in Israel that encourage disease, we concluded that dews must be essentially absent in Idaho. Whereupon, we wrote Guthrie in Idaho, "Do you generally have dew at night; do you have any significant

amount of rainfall; and does this tend to occur during the day or during the night?" Guthrie replied "... dew is really rather rare during the summer season . . . and rainfall might be 0.2 to 0.4 inch per month . . . [occurring] as late afternoon thundershowers and [depositing] an insignificant quantity of water."

The hiatus was resolved. The difference is due to dew.

It may well be that the puzzlement expressed by Harrison *et al.* (1965) about severe disease in a dry season in arid Colorado is to be explained also by the occurrence of dew.

The course has now been run, the English is at an end, and EPIDEM itself will be the summary, written in explicit but concise Fortran IV. Along the way we have not just reviewed the literature, but have analyzed how *Alternaria* works, have been forced into some corners, and have lighted a few with experiments. Because the analysis produced an authentic epidemimetic model, we went on to experiment with fungal characteristics.

Finally, experiments with modified weather have been performed. They showed that increasing spore-bearing wind would increase disease. Or, decreasing the humidity of the air would slow disease development because germination in humid air on dry leaves provides germinated spores that survive dry periods and that are ready to infect when water arrives. Shortening the wet periods also decreases disease, but interrupting runs of wet periods with dry periods decimates disease. And irrigation by sprinkling turned out to be a bugaboo, while dew, as in Israel, would make an explosive epidemic.

This concluding, dew experiment brings us again to the paradox of *Alternaria* and the weather. Here is a pathogen adapted to the alternation of wet and dry, and it cares more for the timing of the changes than for the average weather. Thus, *Alternaria* has been an ideal subject for exemplifying the common sense of putting epidemiology into a simulator like EPIDEM and then doing a lifetime of experiments, in weather modification — all in one afternoon.

## VII. THE SUMMARY, EPIDEM AS WRITTEN IN FORTRAN

On the following pages is the computer program that we call EPIDEM. It is written in IBM 7090/7094 Fortran IV language, which is described in IBM's document C28-6390. The program has been employed in the Yale University Direct Coupled Operating System and used the Purdue University Fast Fortran Translator.

In addition to the main program, EPIDEM includes four subroutines. The subroutine CENSUS gives a frequent inventory of several indices, stalk, spore, catch, germination, and infection accounts if the variable DETAIL is true. The subroutine STALK is outlined in Fig. 6. The function subprogram GAUSS provides the integral of the cumulative Gaussian or Normal distribution. Finally, subroutine GRAF draws a summary of the rise of *Alternaria* during the season.

\*\*\*\* EPIDEM, A PROGRAM FOR THE 7094-7040, WRITTEN IN FORTRAN IV\*\*\*\*

```

$PUFFT          NOCHK
C IDENTIFY INTEGER, REAL AND LOGICAL VARIABLES AND RESERVE SPACE.
  INTEGER DY(7),IHR(7), NHR(8)
  REAL END,T(150,8),RH( 150,8),U(150,8),PH(3),CL(3),TP(4),DLSN(150),
  INCBT(150),IGLS(150),IDLS(150),GSTK(4),DSTK(4),GERM(5),FECT(4)
  2*   ,NFECT          ,SIZE(150),TITLE(16),RAIN(150,8),QTY(7)
  3,IBEAT,LUKT,JGH,WXTIT(16),OPTY(150)
  LOGICAL S(150,8),W(150,8),WP(4),SUNP(4),DETAIL,WVNV,NUSTK,NOJGH
  COMMON DLSN,OPTY,IDLS,IGLS,GSTK,DSTK      ,CATCH,GERM,NFECT,VNV,I,J
  1,GSPOR,DSPOR
  DATA END/1HZ      /,F/.993/,IBLNK/1H /,TSTK/32./,IBEAT/.67/,DETAIL/.
  1TRUE./,DFECT,XSIZE,VDV/U.,1000.,50./,WVNV,NUSTK/.TRUE.,.TRUE./
  2,   START,STOKK,BEAT,SPORS,SPRED,GRM,INFCT, VOLV,MDT/5HSTART,
  15HSTALK,4HBEAT,5HSPORS,5HSPRED,4HGERM,6HINFECT,4HVOLV,3HMDT/
  4,BLNK/1H /,REPEAT/5HREPEA/
C F DECAYS SPOR, TSTK MAX TEMP FOR STALK, IBEAT STALK IN RAIN, DETAIL PRINTS CEN
C SUS,DFECT 0 FOR NO DRY INFECT, XSIZE MAX STALKS PER DRY LESION, VDV SETS MAX
C RATE INVOLV OR INCREASE IN LESION SIZE. RP PROPORTION RAIN SPRED.
C WVNV REQUIRES WET FOR GROW LSN SIZE, NUSTK PUTS NEW SPOR ON DENUDED STALK.
101 READ(5,1) WXTIT
  IF(WXTIT(1).EQ.REPEAT) GO TO 107
  IF(WXTIT(1).EQ.END) STOP
  WRITE(6,2) WXTIT
  WRITE (6,6) F, TSTK, IBEAT, DFECT, XSIZE, VDV, DETAIL,WVNV,NUSTK
  6 FORMAT(-OF,TSTK,IBEAT,DEECT,XSIZE,VDV,DETAIL,WVNV,NUSTK-,6F10.3,3L
  12)

```

```

C READ DAILY TEMP,RH,WIND,SUN,WET CARD ENDED WITH Z CARD. START JUNE 1.
  DO 3 I = 1,150
  READ(5,4)FIN,(T(I,J),RH(I,J),U(I,J),S(I,J),W(I,J),J=1,8)
  4 FORMAT(A1,2X,3(1X, 3F2.0,2L1),5(2X,3F2.0,2L1))
  IF(FIN.EQ.END) GO TO 5
C CHECK THE WX DATA READ IN.
  IF(I.EQ.1.OR.I.EQ.20.OR.I.EQ.100) WRITE (6,8)I,T(I,4),RH(I,4),U(I,
  14) ,S(I,4),W(I,4)
  3 CONTINUE
  5 I=I-1
  IEND=I
C NUMBER OF DAYS READ IN IS COUNTED AND CALLED IEND.
  WRITE(6,8) I,T(I,8),RH(I,8),U(I,8),S(I,8),W(I,8)
  8 FORMAT(- DAY-,I3,-CHECK T,RH,U,S,W-, 3F5.0,2L1)
C CONVERT WX BUREAU-S F DEGREES TO CELSIUS.
  DO 10 I=1,IEND
  DO 10 J=1,8
  T(I,J)=(T(I,J)-32.)*.5555
  10 RAIN(I,J)=0.0
C AFTER ZEROING ALL RAIN, READ ONLY OCCASIONS OF RAIN. READING ENDS WITH BLANK.
C QTY IN HDRDS INCH BETWEEN IHR AND NHR ON DAY L OF MONTH MO. RAIN=PPT/HR.
  DO 11 K=1,150
  READ(5,12) MO,(DY(L),IHR(L),NHR(L),QTY(L),L=1,7)
  12 FORMAT(T3,I2,7(1X,3I2 ,F3.2))
  IF(QTY(1).EQ.0.0) GO TO 14
  WRITE(6,73)MO,(DY(L),IHR(L),NHR(L),QTY(L),L=1,7)
  73 FORMAT(T3,I2,7(1X,3I2 ,F5.2))

```

```

C CONVERT MONTH NUMBER TO NUMBER THAT CAN BE ADDED TO DATE FOR DAYS AFTER JUNE 1
MO=(MO-6)*30
IF(MO.GT.30) MO = MO+1
IF(MO.GT.61) MO=MO+1
DO 13 L=1,7
IF(QTY(L).EQ.0.0) GO TO 11
I=MO+DY(L)
JB=IHR(L)/3+1
JE=NHR(L)/3+1
IF(JE.GT.8)JE=8
TEMP=NHR(L)-IHR(L)+1
TEMP=QTY(L)/TEMP
DO 13 J=JB,JE
RAIN(I,J)=TEMP
13 CONTINUE
WRITE(6,72)I,JB,JE,TEMP,RAIN(I,JB),RAIN(I,JE)
72 FORMAT(-,3I3,3F10.3)
C SECOND ESTIMATE OF RAIN REPLACES FIRST.
C AFTER 7 DAYS OR RAIN PERIODS REACH STATEMENT 11 AND READ NEW CARD.
11 CONTINUE
14 WRITE(6,15)I,JB,RAIN(I,JB)
15 FORMAT(-OLAST RAIN-,2I3, F6.3)
C FOR CONSTANT SYNTHETIC CLIMATE READ ONE TEMP CARD AND ONE RAIN CARD.
C THIS EXEMPLARY DAY IS SPREAD THRU 30 DAYS HERE AT 587.
IF(IEND.GT.1) GO TO 588
IEND=30
DO 587 I=1,IEND
DO 587 J=1,8
T(I,J)=T(1,J)

```

```

RH(I,J)=RH(1,J)
U(I,J)=U(1,J)
S(I,J)=S(1,J)
RAIN(I,J)=RAIN(1,J)
587 W(I,J)=W(1,J)
C ASSURE WET LEAVES DURING RAIN.
588 DO 16 I=1,IEND
DO 16 J=1,8
IF(RAIN(I,J).GT..01) W(I,J)=.TRUE.
16 CONTINUE
C PREPARE TABULATION OF HIGH EVE RH AND OF RAIN IN THSDTHS INCHES.
DO 500 I=1,IEND
IRH=0
IIRH=0
IF(RH(I,7).GT.83.) IRH=RH(I,7)
IF(RH(I,8).GT.83.)IIRH=RH(I,8)
DO 568 J=1,8
568 NHR(J)=RAIN(I,J)*1000.
500 WRITE(6,509) I,(W(I,J),J=1,8),NHR,IRH,IIRH
509 FORMAT(-,I3,8L1,10I4)
C READ TITLE FOR EACH OF ONE TO SEVERAL EXPERIMENTS IN FUNGAL CHARACTERS UNDER
C SAME WEATHER CONDITIONS. THIS STATEMENT IS REACHED WITHOUT READING SECOND SET
C OF WEATHER IF WXTIT CARD IS REPLACED BY -REPEAT-.
107 READ(5,1) TITLE
1 FORMAT (16A5)
WRITE (6,2) TITLE
2 FORMAT (-1-,T25,16A5)
C READ EXPERIMENTAL CHARACTERS

```

```

      READ(5,9)UCON,UCON2,RM,UPOW,(FECT(J),J=1,4),(PD(J),J=1,3),(CL(J),J
      1=1,3),      ICBT,NOJGH,NUSTK,VDV,DFECT,RP, WASP
      9 FORMAT(2F5.0, 2F3.2,10F3.2,3X,      I3,2L1,0P4F3.0)
C UCON AND UCON2 ARE C SUB U1 AND C SUB U2 IN MANUSCRIPT AND CONCERN WIND SPREAD
C RM AND UPOW CONCERN RAIN AND SPORES.
C FECT(J) IS INCREMENT IN INFECTION FROM SPORES GERMINATED J PERIODS AGO.
C PD IS EFFECT OF TEMPERATURE ON LESION ENLARGEMENT.
C CL IS EFFECT OF CLOUDINESS AT MIDDAY ON SUSCEPTIBILITY.
C ICBT IS THE INCUBATION TIME IN DAYS.
C IF NOJGH IS TRUE, SUSCEPTIBILITY DOES NOT CHANGE WITH THE CHANGE IN FRUIT LOAD
C IF NUSTK IS TRUE, A PORTION OF STALKS IS RESTORED WHEN DENUDED OF SPORES.
C LESIONS ENLARGE TO MAX LESION SIZE IN VDV FAVORABLE PERIODS.
C DFECT IS RATIO OF INFECTION IN DRY TO INFECTION IN WET PERIODS.
C RP AND WASP CONCERN CATCHING OF SPORES AWASH IN RAIN.
      WRITE(6,7)UCON,UCON2,RM,UPOW,(FECT(J),J=1,4),(PD(J),J=1,3),(CL(J),
      1J=1,3),      ICBT,NOJGH,NUSTK,VDV,DFECT,RP, WASP
      7 FORMAT(-OUCONS-,2E10.3,- RM-,E10.3,- UPOW-,E10.3/-FECT-, 4E10.3,-
      1PD-,3E10.3/- CL-, 3E10.3,- ICBT-,      , I2,- NOJGH, NUSTK-,2
      1L2,- VDV-,F4.0,- DFECT-,F5.2,- RP-,F5.2,- WASP-, F5.2)
C J IS HR, I IS ATTAINED DATE AND K IS PAST DATES.
COMMENCE BY READ LESION NO. AND SIZE, PAST TEMP, SPORE CATCH AND GERM, PAST WET
C AND SUN. IC IS CODE FOR CLOUDINESS OF PAST MIDDAY.
C *****
C START A NEW DAY I HERE.
      DO 99 I=1,IEND
C FOLLOWING CARD STOPS CENSUS WRITING. REMOVE IF DETAIL WANTED.
      DETAIL=.FALSE.
C SKIP TO STATEMENT 20 EXCEPT ON FIRST PERIOD OF FIRST DAY.
      IF(I.NE.1) GO TO 20

```

```

C ZERO CUMULATIVE ACCOUNTS
      DO 17 J=1,IEND
      IDLS(J)=0.0
      IGLS(J)=0.0
      SIZE(J)=0.0
      OPTY(J)=0.0
      17 CONTINUE
      GSPOR=0.0
      DSPOR=0.0
      DO 27 J=1,4
      DSTK(J)=0.0
      27 GSTK(J)=0.0
C STATUS AND HISTORY REQUIRED TO START.
      READ(5,21)DLSN(1),SIZE(1),(TP(J),J=1,3),CATCH,(GERM(J),J=1,4),(WP(
      1J),J=1,4),(SUNP(J),J=1,4),IC
      21 FORMAT(      10F5.0,8L1, I1)
      DO 24 J=1,3
      24 TP(J)=(TP(J)-32.)*.55
      WRITE(6,22)TP,WP,SUNP,DLSN(1),SIZE(1)
      22 FORMAT(- TP-,4F5.0,- WP-,4L1,- SUNP-,4L1,- DLSN,SIZE(1)-,2F5.0)
      CALL CENSUS(START)
      20 NFECT=0.0
C CALCULATE LAI FROM WATSON RULE AND FROM LAI CALCULATE RL THAT WASHES HALF OF
C OF SPORES.
      XI=I
      ELAI=3.-.0003*( XI-80.)**2
      RL=ELAI*RM
C CALCULATE JGH TO MODIFY SUSCEPTIBILITY ACCORDING TO FRUIT LOAD IMPLICIT IN DAY

```



```

JGH=0.5
IF(I.LE.44.OR.NOJGH) GO TO 75
JGH=0.5*GAUSS(XI,84.,17.,.01 )+0.5
C *****
C START A PERIOD J HERE.
  75 DO 98 J=1,8
    IF(DETAIL)
      1WRITE(6,74) I,J,T(I,J),RH(I,J),U(I,J),RAIN(I,J),S(I,J),W(I,J)
      2,DLSN(I),SIZE(I)
      74 FORMAT(-0TIME-,2I3/- T,RH,U,RAIN,S,W-, 3F5.0,F6.3,2L2,- DLSN-,E10.
      12,- SIZE-,F10.2/ T10,-IDLS-,T30,-IGLS-,T50,-DSTK-, T90,
      2-GSTK- /T10,-DSPR-,T20,-GSPR-, T30,-CATCH-,T40,-GERM-,T90,-NFECT
      2-)
C TEMPERATURE OF TSTK OR HOTTER PREVENTS STALK FORMATION BUT DOESN'T ERASE STALK
  IF(T(I,J).GE.TSTK) GO TO 30
C STALK FORMATION IMPOSSIBLE ON DAY 1 BECAUSE NO OPTY OPEN. SKIP FORMATION .
  IF(I.EQ.1) GO TO 30
C GSTK FORMATION ON FIRST STALK CALL IN ALL WEATHER.
  CALL STALK(1,T,WP)
C DSTK FORMATION ON SECOND STALK CALL ONLY IF LEAVES WET.
  IF(W(I,J)) CALL STALK(2,T,WP)
  30 IF(DETAIL) CALL CENSUS (STOKK)
C IF IBEAT IS 2/3, 2/3 INCHES OF RAIN DESTROYS 1/3 OF STALKS.
  IF (RAIN(I,J).EQ.0.) GO TO 31
  GSTK(1)=GSTK(1)* IBEAT/(IBEAT+RAIN(I,J))
  DSTK(1)=DSTK(1)* IBEAT/(IBEAT+RAIN(I,J))
  IF (DETAIL) CALL CENSUS (BEAT)
C FORM SPOR ON GSTK(K) IF DRY, SAME PLUS ON DSTK(K) IF WET.
C ACCUMULATE SPORES IN DSPOR AND GSPOR ACCOUNTS

```

```

C NO SPORES AT 27C.
  31 IF (T(I,J).GE.27.) GO TO 40
C SUBSCRIPT IW WILL TELL HOW LONG LEAVES HAVE BEEN WET.
C   W   WP1   WP2   WP3   WP4
C 3HR  6     9    12    15
C IW  1     2     3     3
  IW=1
  IF(.NOT.W(I,J).OR..NOT.WP(1).OR..NOT.WP(2)) GO TO 37
  IF(.NOT.WP(3)) IW=2
  IF(.NOT.WP(3)) GO TO 37
  IW=3
C LUKT EMBODIES OBSERVATION OF TEMPERATURE AND SPORULATION IN LIGHT.
  37 LUKT=1.
C SINCE TEMPERATURE HAS NO EFFECT AT 4 AM AND IS ONLY EFFECTIVE AT 1 AM IF
C IW IS LESS THAN 3, LUKT IS OFTEN LEFT AT 1.
  IF(J.EQ.2.OR.J.EQ.1.AND.IW.LT.3) GO TO 36
C CALCULATE A 12-HR MEAN TEMPERATURE CALLED TBAR.
  TBAR=T(I,J)
  DO 44 K=1,3
  44 TBAR=TBAR+TP(K)
  TBAR=TBAR/4.
  LUKT=1.-GAUSS(TBAR,21.,2.5,.01)
  36 TEMPA=0.0
  TEMPB=0.0
  GO TO (33,34,35),IW
  35 TEMPA=DSTK(4)*LUKT
C REMEMBER DSTK(1) AND DSTK(4) ARE STALKS PRESENT IN PRESENT AND 3 PERIODS AGO.
CUT SPORING STALKS FROM 3 PERIODS BEFORE AND YOUNGER ACCOUNTS.

```

```

DO 38 K=1,4
38 DSTK(K)=DSTK(K)-TEMPA
   TEMPB=(DSTK(3)-DSTK(4))*LUKT/5.
C IF WET 3 PRIOR PERIODS, 20 PCT SPOR ON NEW STALKS ONLY.
  GO TO 33
34 TEMPB=DSTK(3)*LUKT/10.
C IF WET ONLY 2 PRIOR PERIODS, 10 PCT SPOR ON ALL STALKS AT DSTK(3).
C ALWAYS 20 PCT SPOR ON GSTK(3) AT 2 PERIODS PRIOR.
33 TEMPG=GSTK(3)*LUKT/5.
CUT SPORING STALKS FROM 2 PERIODS BEFORE AND YOUNGER ACCOUNTS.
  DO 39 K=1,3
  DSTK(K)=DSTK(K)-TEMPB
39 GSTK(K)=GSTK(K)-TEMPG
  DSPOR=DSPOR+TEMPA+TEMPB
  GSPOR=GSPOR+TEMPG
C SINCE DISPERSAL INSTANT, NO PAST SPOR ACCOUNTS NEEDED.
  IF (DETAIL.AND.1.EQ.2)
    1 WRITE(6,41) DSPOR, GSPOR, TBAR, LUKT, TEMPA, TEMPB, TEMPG
41 FORMAT(- SPOR, TBAR, LUKT, TEMPS - , 8E10.3)
  IF (DETAIL) CALL CENSUS (SPORS)
C CURRENT SPORE ACCOUNTS DECAY BY FRACTION F.
40 GSPOR=GSPOR*F
  DSPOR=DSPOR*F
  CATCH=CATCH*F
  IF (RAIN(I,J).EQ.0.0) GO TO 59
C RL INCHES OF RAIN WASH HALF OF SPORES - NOT GERMINATED - AWAY.
  WASH=1.-RAIN(I,J)/(RL+RAIN(I,J))
  AWASH=(1.-WASH)
C RESTORE 1/3 OF DENUED STALKS TO ACTIVE ACCOUNT.

```

```

  IF (.NOT. NUSTK) GO TO 45
  DSTK(1)=DSTK(1)+DSPOR*AWASH/3.
  GSTK(1)=GSTK(1)+GSPOR*AWASH/3.
45 CATCH=CATCH*WASH
C FRACTION RP OF SPORES AWASH IS CAUGHT IN .01 INCH RAIN.
C FRACTION WASP OF WASHED AND CAUGHT SPORES IS EFFECTIVE.
  IF (RP.EQ.0.0) GO TO 51
  RPOW=RAIN(I,J)*100.
  CATCH=CATCH+(GSPOR+DSPOR)*AWASH*(RP**RPOW*WASP)
C FINALLY REDUCE DSPOR AND GSPOR ACCOUNTS.
51 GSPOR=GSPOR*WASH
  DSPOR=DSPOR*WASH
59 IF (DETAIL) CALL CENSUS (SPORS)
C WET LEAVES PREVENT SPREAD BY WIND.
  IF (W(I,J).OR.U(I,J).LT.1.) GO TO 60
C CALCULATE WIND ON EACH LEAF AREA UNIT ACCORDING TO LN(U/U TOP)=0.7*ACCUM-
C ULATED LEAF AREA.
  UBAR=U(I,J)/ELAI*(AMIN1(1.,ELAI)+AMIN1(1.,ELAI-1.)/2.+AMIN1(1.,ELA
  1I-2.)/4.)
CUT SPOR CROP BY STRESS TAU . UCON IS SQ OF MPH THAT REMOVES HALF SPORS.
  TAU=UBAR**2
C UCON IS CALLED C SUB U1, UCON2 IS CALLED C SUB U2 IN MANUSCRIPT.
  BLO=TAU/(TAU+UCON)
C UCON2 INVERSELY PROPORTIONAL TO MAX LAI. MORE ELAI, MORE FIELD, MORE TRAPPING.
C UPOW RELATES TRAPPING TO WIND U.
  COT=UCON2*BLO/(UBAR **UPOW) *ELAI
  IF (DETAIL) WRITE(6,57) COT, BLO
57 FORMAT(- COT-, E10.3, - BLO-, E10.3)

```

```

CATCH=COT*(GSPOR+DSPOR)+CATCH
C IF MUSTK IS TRUE, RESTORE 1/3 OF DENUDED STALKS TO ACTIVE ACCOUNT.
  IF(MUSTK)DSTK(1)=DSTK(1)+DSPOR*BLO/3.
  IF(MUSTK)GSTK(1)=GSTK(1)+GSPOR*BLO/3.
  GSPOR=GSPOR*(1.-BLO)
  DSPOR=DSPOR*(1.-BLO)
  IF (DETAIL) CALL CENSUS(SPRED)
C GERM(K) NOT CUMULATE. EVENT OF KTH PERIOD.
  60 GERM(1)=0.0
  IF(.NOT.W(I,J).AND.WP(1)) GO TO 61
  IF(.NOT.W(I,J)) GO TO 65
C ALL SPORES GERMINATE IN 1 PERIOD OF WET LEAVES.
  GERM(1)=CATCH
  CATCH=0.0
  GO TO 70
C STATEMENT REACHED IF WET LEAVES DRY, KILLING GERMINATED SPORES BY DESICCATION
  61 DO 63 K=2,5
  63 GERM(K)=0.0
C 65 REACHED DIRECT IF CONTINUOUS DRY. REACHED VIA 61 IF WET THEN DRY.
  65 IF(RH(I,J).LT.83.) GO TO 70
C MOIST AIR GERMINATES SOME SPORES ON DRY LEAVES ACCORDING TO MUNNECKE.
  GERM(1)=CATCH*GAUSS(RH(I,J),92.,4.,.01)
  CATCH=CATCH-GERM(1)
  70 IF (DETAIL) CALL CENSUS(GRM)
C FECT INCREMENT IN INFECTION/3HR FROM GERM SPOR. TEMP EFFECT OF MOORE. DFECT IF
C DRY. INCREASE FROM HALF TO FULL EFFECTIVE WITH JGH AS HORSFALL BULLETIN.
C MORE INFECTION IF CLOUDY PREVIOUS MIDDAY AND IC IS 2 OR 3.
  TEMP=DFECT
  IF(W(I,J)) TEMP=1.

```

```

  IF(TEMP.EQ.0.0) GO TO 79
  DO 71 K=2,5
  71 NFECT=NFECT+GERM(K)*2.*TP(K-1)/(30.+TP(K-1))*FECT(K-1)*TEMP*JGH
  1 *CL(IC)
  IF (DETAIL) CALL CENSUS(INFCT)
CALCULATE VNV TO MAKE LESION GROW .
C WET REQUIRED FOR LESION GROWTH IF WVNTRUE.
  79 IF(WVN.AND..NOT.W(I,J)) GO TO 25
  IP=1
  IF (T(I,J).LT.25.) IP=2
  IF(T(I,J).LT.20.) IP=3
C PD IS EFFECT OF TEMP ON VOLV. POUND SAYS COOL SPEEDS.
  VNV=VNV+PD(IP) /VDV *TEMP
C VDV IS PORTION OF FULL EXPANSION POSSIBLE/PERIOD. SUGGEST 8 DAYS OR. VDV=50.
  IF(DETAIL)WRITE(6,76)IP,IC,VNV ,WVN,W(I,J)
  76 FORMAT(- ,T10,-IP-,I3,T20,-IC-,I3,T30,-VNV-,T40,E10.2,2L2)
C MOVE ACCOUNTS OF PAST PERIODS
  25 DO 23 KK=1,3
  K=4-KK
  DSTK(K+1)=DSTK(K)
  GSTK(K+1)=GSTK(K)
  WP(K+1)=WP(K)
  TP(K+1)=TP(K)
  SUNP(K+1)=SUNP(K)
  23 GERM(K+1)=GERM(K)
  GERM(5)=GERM(4)
  WP(1)=W(I,J)
  TP(1)=T(I,J)

```

```

      SUNP(1)=S(I,J)
    98 CONTINUE
C 98 IS END OF EACH OF 8 PERIODS(J).
C *****
C AT MDT SET NCBT AND OPTY FOR DAY ENDING AND IC AND DLSN FOR DAY COMING.
C NCBT(I) IS FROM INFECTION DAY I ONLY
      NCBT(I)=NFECT
C DLSN(I+1) IS NOT CUMULATE. NEW LESIONS ONLY.
C ICBT DAYS FROM NFECT TO DLSN. NO TEMP EFFECT. NO DLSN FOR I=2 TO ICBT.
      ITT=I- ICBT + 1
      IF(ITT .LT.1) DLSN(I+1)=0.0
      IF(ITT.GE.1) DLSN(I+1)=NCBT(ITT)
COUNT BACKWARDS TO GET OPTY(I) OPENED DURING DAY ENDING. OPTY(I) IS OPPORTUNITY
C FOR STALKS TO BE GROWN BY SUBROUTINE STALK UP TO XSIZE. XSIZE ABOUT 1000
CORDING TO RAND.
      DO 81 KM=1,I
      K=I-KM+1
CEASE SEARCH OF PAST DAYS IF LESIONS ENDED
      IF(SIZE(K).GE.XSIZE) GO TO 82
CONTINUE TO NEXT PAST DAY IF NO DLSN ON THIS DAY.
      IF(DLSN(K).EQ.0.0) GO TO 81
C DSIZE CANNOT MAKE SIZE GT XSIZE.
      TEMPA=VNV*XSIZE
      TEMPB=XSIZE-SIZE(K)
      DSIZE=AMIN1(TEMPA,TEMPB)
      OPTY(I)=OPTY(I)+DSIZE*DLSN(K)
      SIZE(K)=SIZE(K)+DSIZE
      IF(DETAIL)
1WRITE (6,501) SIZE(K),VNV      ,TEMPA,TEMPB,DSIZE,OPTY(I), K

```

```

501 FORMAT(- SIZE,VNV,TEMPA,TEMPB,DSIZE,OPTY,K-, 6E10.3,I5)
81 CONTINUE
82 VNV=0.0
C IF 10 AND 13 HOURS HAVE BEEN CLOUDY, MAKE IC 3 FOR NEXT DAY.
      IC=3
      IF(S(I,4).OR.S(I,5))IC=2
      IF(S(I,4).AND.S(I,5))IC=1
      IF(DETAIL)
1CALL CENSUS (MDT)
      IF (DETAIL) WRITE(6,77)
77 FORMAT(-1-)
99 CONTINUE
C 99 IS END OF A DAY.
C *****
C SUMMARY OF NEW LESIONS ON EACH DAY IS WRITTEN AT SEASON-S END.
      WRITE(6,100)TITLE
100 FORMAT(-1-,T25,16A5/ T55,-NEW LESIONS BY DAYS-)
      WRITE(6,103)(K,K=1,10),(DLSN(K),K=1,IEND)
103 FORMAT(- ,T4,I1,9I10/3(10E10.3/)/3(10E10.3/) E10.3//3(10E10.3/)E1
10.3//4(10E10.3/))
C CONVERT NEW LESIONS TO ACCUMULATED LESIONS.
      WRITE(6,102)
102 FORMAT(- ,T55, -ACCUMULATED LESIONS-)
      DO 104 K=2,IEND
104 DLSN(K)=DLSN(K-1)+DLSN(K)
      WRITE(6,103)(K,K=1,10),(DLSN(K),K=1,IEND)
C CONVERT ACCUMULATED LESIONS TO LOGARITHMS.
      IF(DLSN(1).LT.1.) DLSN(1)=1.

```

```

DLSN(1)=ALOG10(DLSN(1))
DO 106 K=2,IEND
106 DLSN(K)=ALOG10(DLSN(K)) - DLSN(1)
WRITE(6,108)
108 FORMAT(- ,T55,-LOG ACCUMULATED LESIONS-)
WRITE(6,103)(K,K=1,10),(DLSN(K),K=1,IEND)
CALL GRAF(DLSN,IEND,TITLE,2)
GO TO 101
C DECK IS WXTITLE, WX, Z, RIIN, BLANK, SPORE CHARACTERS, INITIAL, WXTITLE, ETC.
C IF WX TITLE SAYS REPEAT, WX AND RAIN CARDS SKIPPED. IF WXTITLE Z, STOP.
END

```

```

SUBROUTINE CENSUS (TITLE)
C SUBROUTINE CENSUS PERIODICALLY SHOWS STATUS IF -DETAIL- IS TRUE.
REAL DLSN(150), OPTY(150), IDLS(150), IGLS(150), GSTK(4), DSTK(4), GE
1 RM(5), NFECT, MDT
COMMON DLSN,OPTY, IDLS, IGLS, GSTK, DSTK , CATCH, GERM, NFECT, VNV, I, J
1, GSPOR, DSPOR
DATA IJUN, IJUL, IAUG, ISEP/3HJUN,3HJUL,3HAUG,3HSEP/
M=IJUN
IF (I.GT.30) M=IJUL
IF (I.GT.61) M=IAUG
IF (I.GT.92) M=ISEP
IDAY=I
IF (M.EQ.IJUL) IDAY=I-30
IF (M.EQ.IAUG) IDAY=I-61
IF (M.EQ.ISEP) IDAY=I-92
IF (I.LE.2) GO TO 3
LL=I-2
K=I-1
GO TO 4
3 LL=1
K=2
4 WRITE(6,5) TITLE, M, IDAY
5 FORMAT(- ,A6,1X,A3,I3)
WRITE(6,2) (IDLS(L),L=LL,K),(IGLS(L),L=LL,K),DSTK,
1 GSTK,DSPOR,GSPOR,CATCH,GERM,NFECT
2 FORMAT(- ,T10,12E10.2/T10, 9E10.3)
RETURN
END

```

```

SUBROUTINE STALK(IST,T,WP)
C SUBROUTINE STALK CALCULATES GSTK IF IST=1, DSTK IF IST=2.
CALCULATE STALKS FROM ALL PAST LESIONS FOR EACH 3 HR PERIOD(J)
C EG DSTK(1) ARE STALKS FORMED BY TIME(I,J) IN WET WX ON DLN(K),K=1,I-1 ACCORDI
C NG TO IDLS(K) ATTAINED IN DAYS SINCE DLN(K) APPEARED.IDLS(K) UPDATED
C EACH THREE HOURS. DSTK(2) WERE FORMED BY 3 HOURS AGO.DSTK(1)=DSTK(2) IF DRY.
  LOGICAL WP(4)
  REAL DLN(150), OPTY(150), IDLS(150), IGLS(150),GSTK(4),DSTK(4),GE
  1RM(5),T(150,8),NDXT,NITSTK
  COMMON DLN,OPTY,IDLS,IGLS,GSTK,DSTK      ,CATCH,GERM,NFECT,VNV,I,J
  1,GSPOR,DSPOR
  DATA      NITSTK,DGST/0.25,0.25/
  NK=I-1
  Y=0.0
C KK IS DEVICE FOR SEARCHING FROM RECENT TO OLD.
  DO 30 KK=1,NK
    K=NK-KK+1
  CONTINUE TO K+1 IF NO OPTY ON K.
    IF(OPTY(K).EQ.0.0) GO TO 30
C IST IS 1 FOR GSTK AND 2 FOR DSTK.
    IF(IST.EQ.2) GO TO 2
    X=IGLS(K)
    Z=DGST
    GO TO 3
    2 X=IDLS(K)
    Z=1.
C IF X=IDLS,IGLS=1, NO FURTHER STALKS POSSIBLE ON THAT OR OLDER OPTY.
  3 IF(X.GE.1.) GO TO 32
C NDXT AND IGLS OR IDLS EMBODY TABLE OF MANUSCRIPT FIGURE.

```

```

  IF(T(I,J).GT.19.) GO TO 35
  NDXT=.092
  IF(X.LT..073)NDXT=.016
  GO TO 36
  35 NDXT=.160
  IF(X.LT..161)NDXT=.032
  IF(X.GT..640.AND.T(I,J).LT.25.)NDXT=.032
  IF(X.GT..640.AND.T(I,J).GE.25.)NDXT=.016
C AT NIGHT, NITSTK AS MANY STALKS FORMED AS BY DAY.
  36 IF(J.LT.3.OR.J.GT.6)NDXT=NDXT*NITSTK
C DSTK FORMATION SLOWED IF LEAVES ONLY RECENTLY WETTED.
  IF(IST.EQ.2.AND..NOT.WP(1)) NDXT=NDXT/2.
C NDXT LIMITED BY X=IDLS,IGLS=1.
  TEMP=1.-X
  NDXT=AMIN1(TEMP,NDXT)
  X=X+NDXT
  IF(IST.EQ.1) IGLS(K)=X
  IF(IST.EQ.2) IDLS(K)=X
C Y WILL BE GSTK(1) OR DSTK(1).
  31 Y=Y+NDXT*Z*OPTY(K)
C OPTY SAME FOR GSTK AND DSTK, BUT ONLY DGSTK AS MANY ON GSTK.
C AS UNDER ROTEM-S DEW SHELTER.
  30 CONTINUE
  32 IF(IST.EQ.1) GSTK(1)=Y + GSTK(1)
  IF(IST.EQ.2) DSTK(1)=Y + DSTK(1)
CUMULATIVE GSTK(1),DSTK(1) REMEMBER INCREMENTS FROM OPTY,BEAT,SPRED,SPOR.
C Y OBTAINED FROM NDXT (NOT IDLS,IGLS) AND IS INCREMENT, NOT TOTAL.
  RETURN
END

```

```

FUNCTION GAUSS(X,BAR,SIG,TEST)
C CUMULATIVE NORMAL CURVE INTEGRAL REQUIRED FOR LAI, JGH, LUKT, GERM IN HUMIDITY
REAL DLSN(150), OPTY(150), IDLS(150), IGLS(150), GSTK(4), DSTK(4), GE
1RM(5), N
COMMON DLSN, OPTY, IDLS, IGLS, GSTK, DSTK      , CATCH, GERM, NFECT, VNV, I, J
1, GSPOR, DSPOR
N=9.0
IF(X.EQ.BAR) N=0.5
TEE=(X-BAR)/SIG
IF(TEE.LT.-3.5) N=0.0
IF(TEE.GT.3.5) N=1.0
IF(N.LT.9.0) GO TO 99
ATE=ABS(TEE)
Z=ATE/1.414214
Y=Z
FACT=1.0
DO 5 K=1,30
EN=K
FACT=FACT*EN
DEL=(-1.0)**K*Z**((2*K+1)/(FACT*(2.*EN+1.)))
Y=Y+DEL
ADEL=ABS(DEL)
IF(ADEL.LT.TEST) GO TO 98
5 CONTINUE
C IF SERIES FAILS TEST AT K=30, N=9.0.
GO TO 99
98 Y=Y*1.1273792
N=0.5*(1.0+SIGN(Y,TEE))
99 GAUSS=N
RETURN
END

```

```

SUBROUTINE GRAF(DLSN, IEND, TITLE, LOG)
C GRAF SUBROUTINE PROVIDES GRAPHICAL SUMMARY OF SEASON-S EPIDEMIC.
INTEGER LINE(101)
REAL DLSN(150), SIZE(150), IDLS(150), IGLS(150), GSTK(4), DSTK(4), GE
1RM(5), N, TITLE(16)
LOGICAL DONE
COMMON DLSN, OPTY, IDLS, IGLS, GSTK, DSTK      , CATCH, GERM, NFECT, VNV, I, J
1, GSPOR, DSPOR
DATA IYE, IDOT, IBLANK, IEX/1HI, 1H., 1H , 1HX/
DONE=.FALSE.
DMAX=10.
IF(LOG.EQ.1)
1WRITE(6,2)TITLE, DMAX, (K, K=10, 90, 10)
2 FORMAT(-1-, T25, 16A5/T40, -ACCUMULATED NUMBER OF LESIONS AS PCT OF M
1AX-, E10.2//T9, -0 PCT-, T20, 9(I2, 8X), -100-)
IF(LOG.NE.1) WRITE(6,9)TITLE, DMAX, (K, K=10, 90, 10)
9 FORMAT(-1-, T25, 16A5/T40, -LOG ACCUMULATED NUMBER OF LESIONS RELATIV
1E TO DMAX-, F10.5//T9, -0-, T20, 9(I2, 8X), -100-)
11 LINE(1)=IYE
LINE(101)=IYE
DO 3 K=2, 100
3 LINE(K)=IDOT
WRITE(6,4) LINE
4 FORMAT(- -, T9, 101A1)
IF(DONE) GO TO 12
DO 5 I=1, IEND, 3
J=100.*DLSN(I)/DMAX+1.
LINE(1)=IYE
LINE(101)=IYE

```

```

DO 7 K=2,100
LINE(K)=IBLANK
LINE(J)=IEX
IF(I.EQ.31.OR.I.EQ.64.OR.I.EQ.94) GO TO 8
M=I
IF(I.GT.30) M=I-30
IF(I.GT.61) M=I-61
IF(I.GT.92) M=I-92
WRITE(6,10)M,LINE
10 FORMAT(-,I2,T9,101A1)
GO TO 5
8 WRITE(6,6) LINE
6 FORMAT(- MONTH-,T9,101A1)
5 CONTINUE
DONE=.TRUE.
GO TO 11
12 RETURN
END

```

## VIII. SYMBOLS

(The symbols in subprograms GAUSS and GRAF that are peculiar to those subprograms are not listed here.)

- AWASH Proportion of spores awash in a rain.  
 BLO Proportion of spores blown from the leaves.  
 CATCH Number of ungerminated spores caught on leaves.  
 CENSUS A subroutine for printing details of disease development.  
 CL An array of 3 numbers that determines the effect upon susceptibility of clouds at no, 1 or 2 midday periods.  
 COT Proportion of spores that are air-borne and then caught.  
 C<sub>u1</sub> Determines the release of spores into the wind. C<sub>u1</sub> which is called UCON in EPIDEM is the square of the wind speed that carries away half of the spores.  
 C<sub>u2</sub> Determines the catching of air-borne spores by leaves. Field size and maximum LAI affect C<sub>u2</sub>, which is called UCON2 in EPIDEM.  
 DETAIL A "logical" variable. When true, details of disease development are printed frequently.  
 DFECT The susceptibility of dry relative to wet foliage to invasion or infection.  
 DLSN(I) Number of disease lesions that appear on day I.  
 DSIZE Increment in SIZE.  
 DSPOR Number of spores formed on DSTK.  
 DSTK Number of stalks formed on wet leaves. Mnemonic: formed on dead portion of lesions.  
 DY Date of rain.  
 ELAI Same as LAI.  
 EPIDEM Acronym for the simulator in section VII.  
 F Fraction of spores that survives a 3-hour period.  
 FECT An array of 4 numbers that determines the increment of infection 3, 6, 9 and 12 hours after spores germinate.  
 GAUSS The function subroutine that calculates the area under the cumulative Gaussian or Normal curve.  
 GERM(I) Number of spores germinated (I-1) periods past.  
 GSPOR Number of spores formed on GSTK.  
 GSTK Number of stalks formed on dry leaves. Mnemonic: formed on green margins of lesions.  
 IBEAT The rainfall, inches/hour, that destroys a third of the stalks.  
 IC Subscript for CL that indicates cloudiness at midday.  
 ICBT Number of days from infection to lesion appearance.  
 IHR Initiation hour of a rain.  
 IDLS(I) Index for stalk formation on opportunities opened on day I.  
 IGLS(I) Index for stalk formation on opportunities opened on day I.  
 IP Subscript for PD that indicates temperature.



LAI	The area of one side of the foliage per land area.
LUKT	Effect of temperature upon sporulation as shown by Lukens.
MO	Month number.
NCBT (I)	Incubating infections begun on day I.
NDXT	Increment in IDLS or IGLS.
NHR	End hour of a rain.
NITSTK	Stalk formation at night as a fraction of daytime rate.
NOJGH	A "logical" variable. When it is true, fruit load has no effect upon susceptibility.
NUSTK	A "logical" variable. When it is true, spore removal by wind or rain makes a third of the denuded stalks available for a new crop of spores.
OPTY (I)	Opportunities for stalk formation that are opened on day I.
PD	An array of 3 numbers embodying Pound's observations of temperature and lesion enlargement. The numbers pertain to the intervals: warmer than 25 C, 20 to 25 and cooler than 20.
QTY	Quantity of rainfall during a rain that began at IHR and ended at NHR.
RAIN	Rainfall rate, inches/hour, averaged over a 3-hour period.
RH	Relative humidity.
RM	Rain, inches/hour, that removes half the spores from stalks and from CATCH account.
RP	Fraction of spores awash in a 0.01 inch rain per hour.
RPOW	Exponent derived from rain rate to calculate number of spores awash and then caught.
S	A "logical" variable. If true the period was sunny.
SIZE (I)	Attained size, i.e. number of opportunities opened upon a lesion that appeared on day I.
STALK	The subroutine that calculates number of stalks.
SUNP (I)	A "logical" variable. If true, the period I past was sunny.
T	Temperature read in °F and converted to °C.
TAU	Shearing stress of the wind.
TBAR	Mean temperature of present and 3 past periods.
TEMP	A temporary variable of all work.
TP (I)	Temperature I periods past.
TSTK	Hot temperature that stops stalk growth. In °C.
U	Wind speed in mph.
UBAR	Mean wind speed among the leaves.
UCON	Same as $C_{u1}$ .
UCON2	Same as $C_{u2}$ .
UPOW	The trapping of spores on foliage may be decreased by dividing by the wind speed U raised to a fractional power, UPOW.
VDV	Minimum number of periods for a lesion to reach maximum enlargement, size or involvement.
W	A "logical" variable. If true, the leaves were wet.

WASH	Proportion of spores not washed away by a rain.
WASP	Proportion of spores washed onto new sites that is effective.
WVNV	A "logical" variable. If it is "true," lesions enlarge only when they are wet.
XSIZE	Maximum size reached by lesions expressed as the maximum number of stalks per lesion.

## Literature Cited

- ANON. 1954. Stations federales d'essais agricoles. Lausanne. Rapport d'activite 1953. Ann. Agric. Suisse N.S. 68: 775-913.
- ARAGAKI, M. 1961. Radiation and temperature interaction on sporulation of *Alternaria tomato*. Phytopathology 51: 803-805.
- ARAGAKI, M., J. W. HYLIN, AND KAREN MAEDA. 1968. Irreversible inhibition of spore formation in *Alternaria tomato* by dedifferentiation of conidiophores. Phytopathology 58: 1041.
- BROWN, K. W., AND W. COVEY. 1966. Energy budget evaluation of the micrometeorological transfer processes within a cornfield. Agr. Meteorol. 3: 73-96.
- CLINTON, G. P. 1916. Potato spraying experiments, third report. Conn. Agr. Exp. Station Ann. Rept. 1915: 470-487.
- COOK, H. T. 1949. Forecasting late blight epiphytotics of potatoes and tomatoes. J. Agr. Research 78: 545-563.
- CROSIER, W. 1934. Studies in the biology of *Phytophthora infestans* (Mont.) DeBary. N.Y. Agr. Exp. Sta. Mem. 155, 40 pp.
- GREGORY, P. H. 1945. The dispersion of air-borne spores. Trans. Brit. Mycol. Soc. 28: 26-72.
- GREGORY, P. H. 1961. Microbiology of the atmosphere. Leonard Hill, London, 251 pp.
- GUTHRIE, J. W. 1958. Early blight of potatoes in Southeastern Idaho. Plant Dis. Rept. 42: 246.
- HARRISON, M. D., C. H. LIVINGSTON, AND N. OSHIMA. 1965. Epidemiology of potato early blight in Colorado. I. Initial infection, disease development and the influence of environmental factors. Amer. Potato J. 42: 279-291.
- HORSFALL, J. G., AND R. W. BARRATT. 1945. An improved grading system for measuring plant diseases. Phytopathology 35: 655.
- HORSFALL, J. G., AND A. E. DIMOND. 1957. Interactions of tissue sugar, growth substances, and disease susceptibility. Zeitschr. f. Pflanzenkr. u. Pflanzensch. 64: 415-421.
- HORSFALL, J. G., AND J. W. HEUBERGER. 1942a. Measuring magnitude of a defoliation disease of tomatoes. Phytopathology 32: 226-232.
- HORSFALL, J. G., AND J. W. HEUBERGER. 1942a. Measuring magnitude and control of defoliation on tomatoes. Conn. Agr. Exp. Sta. Bull. 456: 183-225.
- JONES, L. R. 1892. The new potato disease or early blight. Vermont Agr. Exp. Sta. Report 6: 66-70.

- JONES, L. R. 1895. Potato blight and fungicides. Vermont. Agr. Exp. Sta. Bul. 49: 81-100.
- LEACH, C. M. 1965. Ultraviolet-absorbing substances associated with light-induced sporulation in fungi. Can. Jour. Bot. 43: 185-200.
- LUKENS, R. J. 1960. Conidial production from filter paper cultures of *Helminthosporium vagans* and *Alternaria solani*. Phytopathology 50: 867-868.
- LUKENS, R. J. 1963. Photo-inhibition of sporulation in *Alternaria solani*. Amer. J. Bot. 50: 720-724.
- LUKENS, R. J. 1966. Interference of low temperature with the control of tomato early blight through use of nocturnal illumination. Phytopathology 56: 1430-1431.
- LUTMAN, B. F. 1911. Potato diseases and the weather. Vermont Agr. Exp. Sta. Bul. 159: 248-296.
- McCALLAN, S. E. A., AND F. WILCOXON. 1936. The action of spores on Bordeaux mixture. Contr. Boyce Thompson Inst. 8: 151-165.
- McCALLAN, S. E. A., AND R. H. WELLMAN. 1943. A greenhouse method of evaluating fungicides by means of tomato foliage diseases. Contr. Boyce Thompson Inst. 13: 93-134.
- MEREDITH, D. S. 1966. Spore dispersal in *Alternaria porri* (Ellis) Neerg. on onions in Nebraska. Ann. App. Biol. 57: 67-73.
- MILLER, E. C. 1938. Plant Physiology. McGraw-Hill Book Co., Inc., N.Y. 1201 pp.
- MOORE, W. D. 1942. Some factors affecting the infection of tomato seedlings by *Alternaria solani*. Phytopathology 32: 399-403.
- MUNNECKE, D. E., R. A. LUDWIG, AND R. E. SAMPSON. 1959. The fungicidal activity of methyl bromide. Can. J. Bot. 37: 51-58.
- POUND, G. S. 1951. Effect of air temperature on incidence and development of the early blight disease of tomato. Phytopathology 41: 127-135.
- RANDS, R. D. 1917. Early blight of potato and related plants. Wisc. Agr. Exp. Sta. Res. Bul. 42: 1-48.
- ROTEM, J. 1964. Effect of weather on dispersal of *Alternaria* spores in a semi-arid region of Israel. Phytopathology 54: 628-632.
- ROTEM, J., AND I. REICHERT. 1964. Dew — a principal moisture factor enabling early blight epidemics in a semiarid region of Israel. Plant Dis. Rept. 48: 211-215.
- ROWELL, J. B. 1953. Leaf blight of tomato and potato plants. Rhode Island Agr. Exp. Station Bul. 320: 1-29.
- VAN DER PLANK, J. E. 1963. Plant diseases: epidemics and control. Academic Press, N.Y. 349 pp.
- WAGGONER, P. E. 1965. Microclimate and plant disease. Ann. Rev. Phytopathology 3: 103-126.
- WAGGONER, P. E. 1968. Weather, and the rise and fall of fungi. In W. P. Lowry (ed.) Biometeorology. Oregon State Univ. Press, Corvallis.
- WAGGONER, P. E., AND J. G. HORSFALL. 1968. Assessing an epidemic by computer. Nat. Acad. Sci. Proc. 61: 1157-1158.
- WATSON, D. J. 1952. Physiological basis of variation in yield. Adv. Agron. 4: 101-145.

*James L. Horsfield*  
Director

PUBLICATION  
Permit No. 1136

C CALCULATE JGH TO MODIFY SUSCEPTIBILITY ACCORDING TO

JGH=0.5

IF(I.LE.44.OR.NOJGH) GO TO 75

JGH=0.5\*GAUSS(XI,84.,17.,.01)+0.5

C \*\*\*\*\*

C START A PERIOD J HERE.

75 DO 98 J=1,8

IF(DETAIL)

1WRITE(6,74) I,J,T(I),RAIN(I,J)

2,DLSN(I),SIZE(I)

74 FORMAT(-OTIME-,2I3/- T, S,W-, 3F5.0,F6.3

12,- SIZE-,E10.2/ T10,-IDLS-,T30,-IGLS-,T50

2-GSTK- /T10,-DSPR-,T20,-GSPR-, T30,-CATCH-,T40,

2-)

C TEMPERATURE OF TSTK OR HOTTER PREVENTS STALK FORMATIO

IF(T(I,J).GE.TSTK) GO TO 30

C STALK FORMATION IMPOSSIBLE ON DAY 1 BECAUSE NO OPTY

IF(I.EQ.1) GO TO 30

