CHAPTER 8

Forecasting Epidemics

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I. Introduction 291
II. Primary Inoculum 292
III. The Dispersal of Inoculum 296
IV. The Transfer of Inoculum 298
V. The Trapping of Pathogens 300
VI. Infection 301
VII. The Incubation Period 303
VIII. Integration 305
IX. The Usefulness of Forecasting 306
X. Summary 309
References 310

I. INTRODUCTION

Man found his crops destroyed by rusts and smuts, mildews and blights long before he recognized the microscopic pathogens. Some men correlated disease with sinfulness; others, finding only a slight variation in the amount of sin and a large variation in the weather, obtained a better correlation—that between weather and disease. Consequently, they called the weather the cause of plant disease. In this imperfect state of knowledge they were able to forecast disease outbreaks before they were able to name the pathogenic fungi. Now, in our still imperfect state of knowledge, we too can forecast disease outbreaks from our science of the interaction of host, pathogen, and weather.

The forecasting of epidemics is a contribution to the forecasting of crop yields. Yield forecasts are useful if they arrive sufficiently early to permit adjustments in acreage or transportation or if remedies can be applied to prevent the prophesied disaster. An empirical relation between weather and yields can assist in adjustments. The relation becomes more logical and satisfying and is productive of remedies if it also includes a

291
knowledge of the contributions of soil fertility and of varieties to yield. Of primary interest here, the relation is more logical and fruitful if it includes a knowledge of the interaction of pathogens with weather, soil, and host; this is most fruitful if a remedy can be applied after the forecast is made.

Reviews of the forecasting of epidemics of plant disease have appeared in the past. Because the weather relations of diseases are often obvious, the practice is a venerable one, and the many examples over the world have been examined by Foister (1929) and by Miller and O'Brien (1952, 1957). These reviews provide complete coverage. Therefore, the subject will not be neglected if the present examination takes a different path: the etiology of plant diseases has been examined for opportunities for prognostication of disease and subsequent loss. Illustrative examples will be cited where possible.

The forecasting of epidemics is quantitative epidemiology applied with courage. The better to make it quantitative, a formal framework is proposed and employed as follows:

The number of spores reaching a host will double as the production is doubled or arrivals are proportional to $Q$, the number of propagules released. The arrivals also increase as the trapping efficiency $p$ increases; however, the relation is not linear because the disseminating “cloud” of pathogens is depleted by this trapping. Thus, arrivals are proportional to $pe^{-\text{constant} \cdot f(X)}$ where $f(X)$ is a function of distance $X$. The number of spores per volume of air or other medium decreases rapidly with distance $X$ or arrivals are proportional to $1/X^n$; since dissemination is generally three-dimensional, $n$ is about 2. Finally, the number of infections $D$ is related to arrivals or $D = \text{constant} \cdot [(Q/K)p/X^n]e^{-\text{constant} \cdot f(X)}$. The $K$ is the proportionality constant between arrivals and infection. For the important case of aerial dissemination, estimates of the parameters have been made: $p$ can be about $\frac{1}{20}$, $n$ about 2, the $f(X) = X^{1/3}$ (Gregory, 1945; Waggoner, 1952).

As the etiology is examined for possibilities for prognosis, these possibilities are evaluated in terms of the above model.

II. THE PRIMARY INOCULUM

Many factors will affect the magnitude of the explosion called an epidemic, but the spark that ignites, i.e., the primary inoculum, must be present. And, as the model shows, the greater the quantity $Q$, the greater the epidemic likely. Thus, the quantity of primary inoculum can be a criterion for forecasting, a criterion particularly useful because of its early appearance,
The diseases of crops grown in the temperate zone have been the objects of most forecasting schemes. Here the pathogen often must assume a resistant form, take shelter, become dormant, or be eliminated and renewed from the tropics. The forecaster can examine these survival mechanisms for his first hint of the new season's prospects.

An early indication of the amount of overwintering primary inoculum is the severity of disease in the previous season. Although many factors can modify the amount, a persistence in amount is seen from year to year in certain diseases due in part to the greater primary inoculum carried over after an epidemic year. For example, the persistence of the catastrophic severity of potato late blight from year to year increased the disastrous consequences of the appearance of Phytophthora infestans in Ireland in the "hungry forties." The appearance of the new Helminthosporium victoriae (Meehan and Murphy, 1946) led to the persistent decimation of the varieties derived from Victoria oats and necessitated the introduction of new varieties. Thus, the "grand cycle" of disease, the steady increase and decrease of severity from year to year, caused partially by the overwintering of inoculum, is an early straw in the wind indicating the prospects in a new season.

If an overwintering, resistant—often perfect—stage of the pathogen is known, the procedure is more satisfying than complete dependence upon the "grand cycle." Here the forecaster can search for the overwintering form itself and see the spark that may ignite the coming explosion. Many classic schemes for forecasting apple scab proceed by this means. The pathogen Venturia inaequalis overwinters in the perfect stage in fallen leaves where its maturity is dependent upon the winter and early spring weather (Wilson, 1928). Microscopic examination of the perithecia (Young and May, 1928), ripening in the warmth of the laboratory (Holz, 1939a), and considerations of winter weather (Holz, 1939b; Louw, 1947) have formed the bases for prediction of the first discharges of ascospores in the spring. Forecasts of infection then can be made from a knowledge of the stage of tree development, the response of growers to the spray warnings, and subsequent discharge and infection periods.

Brown rot of peaches, caused by Monilinia fructicola, is another ascomycetous pathogen that overwinters in the perfect stage although the imperfect stage is also functional. A search of orchards for the cankers and mummified fruit that harbor the pathogen reveals primary inoculum for the succeeding season, and could form the basis of a forecast.

Ergot of cereals, especially rye, is another classic disease that overwinters as an easily visible, perfect stage. The discovery of a multitude of the sclerotia of Claviceps purpurea in seed or even in a field can be
a warning of an epidemic in the field to be planted or in the field where sclerotia may have fallen.

A pathogen may take shelter during the cold season, and a forecasting scheme can be founded upon the amount sheltered. For example, *Bacterium stewartii*, the pathogen of bacterial wilt of sweet corn, survives the winter in the bodies of adult flea beetles. The survival of the sheltering beetles is encouraged by warm winters. Stevens (1934) found that severe epidemics of wilt followed warm winters, and, hence, founded a forecasting scheme employed successfully by him and Boewe in Illinois and by other workers in New Jersey and New York.

A pathogen can invade seed and be sheltered for the winter with the crop. *Phytophthora infestans* infects tubers in the autumn and overwinters in the storage bin. Here the inspector can estimate the amount of primary inoculum available for the following season. Wallin (1956) has done this with some success. Of equal importance when blighted tubers are culled from the storage and dumped, the sprouts on the cull piles are a fruitful source of inoculum (Bonde and Schultz, 1943) and an opportunity for the forecaster to take a census of primary inoculum (Hyre and Bonde, 1956).

The extent of virus infection can be accurately predicted by indexing potato seed, a practice generally followed.

Loose smut of wheat or barley derives from seed infected by *Ustilago tritici* or *Ustilago nuda* during the previous season. Thus the census of the infection in the seed can lead to a forecast of epidemics; the detection of infection can be made by germinating or by examining microscopically a sample of seed (Simmonds, 1946). A forecast can also be based upon an even earlier event, the weather at blossoming time in the preceding season, because this is the time of susceptibility (Dickson, 1947).

Some pathogens lie dormant awaiting the arrival of warm weather and a host. Their numbers are an index of epidemics to come. This is the case of many soil-borne pathogens—pathogens that spread relatively slowly. The extent of *Phymatotrichum omnivorum* and its depredations can be predicted almost to the foot from its extent in the previous year (Taubenhaus and Killough, 1923). Nematode infestation can be forecast because of the persistence of the worms or cysts. Whether or not a crop will be infected by *Verticillium albo-atrum* has been predicted from the response of an index plant, the tomato, grown in soil samples from the intended field (Wilhelm, 1950). If rotation decreases the population of a pathogen, severity of infection can be predicted from the intensity of management.

Pathogens can lie dormant in an overwintering crop. If the crop, like
winter wheat, is harvested in midsummer, the pathogen must race against
time if an epidemic is to occur. Hence, the overwintering fungus and its
early multiplication are critical. Thus, Chester (1946) found that
*Puccinia rubigo-vera* overwinters in Oklahoma in pustules of wheat leaf
rust; the level of infection on April 1 is determined by the weather in the
late winter; and this level of infection determines the extent of any
epidemic, because weather after that date is rarely limiting. Forecasts
by this method have been eminently successful, the only failure being
caused by the rare event of later weather limiting infection (Young and
Wadsworth, 1953).

A pathogen may be largely eradicated from a region by the winter,
and primary inoculum may be borne in on southerly winds. Following
the frequent observation of fungal spores in the upper atmosphere, much
attention has been devoted to this concept. For example, the annual
renewal of *Puccinia graminis* var. *tritici* and the production of epidemics
of stem rust of wheat has been attributed after extensive studies by
Stakman and co-workers to spores borne aloft in Mexico and showered
down upon the Great Plains (Christensen, 1942). Epidemics of tobacco
blue mold in Quebec have been associated with the production of
*Peronospora tabacina* in Kentucky and a forecasting scheme devised
accordingly (Stover and Koch, 1951). Two considerations should be kept
in mind in evaluating the foregoing. First, as spring progresses north­
ward, even diseases of local origin will appear to move northward.
Second, the rapid dilution by distance of spore clouds, as evidenced by
the steep gradients of infection about isolated sources (Gregory, 1945),
makes the probability extremely small that spores from continental dis­
tances will alight on a given field. The second consideration renders
spore traps of little use in forecasting; Rusakov found no spores upon
traps until 1% of the plants in the neighborhood had been infected, and
he suggested a local field inspection instead of dependence upon traps
(Chester, 1946).

The characteristics of stem rust make it more susceptible than many
diseases to a forecast based upon spore movement from the South. The
astronomical numbers of spores produced in the large acreages of wheat
in the South and the large acreages of hosts to the North somewhat
counteract the dilution by distance. The sturdiness of the *Puccinia* spores
assures that they will be viable when they arrive. The broad and nearly
continuous belt of wheat extending from Texas to Saskatchewan permits
*Puccinia* to leap, frog-like from county to county, never requiring it to
move continental distances at a single jump. Thus, a forecasting scheme
for stem rust can logically be based upon the systematic movement of
primary inoculum from the South. The sensitive spores of the downy
mildews, produced on limited acreages and seeking out limited acreages separated by miles deserted of hosts, presents a contrasting picture.

Thus, a survey of the inoculum available at the beginning of a new season provides a rational point of departure for a disease forecast. It has the advantage of earliness, with the consequent opportunities for remedial measures, such as selecting an alternate crop, roguing, or chemical control. It has the disadvantage of occurring so early that many factors can subsequently modify the outcome. Nevertheless, the forecaster courts disaster if he does not issue a word of warning when the inoculum potential is obviously high, or, on the other hand, if he forecasts an epidemic solely from weather data when the pathogen is absent.

III. THE DISPERSAL OF INOCULUM

When a given amount of primary infection is present, the successful pathogen must next produce units such as cells or spores, and have them detached. Garrett (in Chapter 2 of this volume) calls these units propagules. The product of the primary infection times the output of propagules per lesion comprises the source strength of $Q$ and the subsequent epidemic is proportional to $Q$. Hence, another opportunity for forecasting is presented.

Here, in considering the production and detachment of propagules such as spores, weather is met in all of its effectiveness. Many diseases, especially mildews, have long been associated with damp weather; the late blight forecasts of Martin (1923) and Cook (1949) were based upon average or accumulated rainfall and average temperatures. This is, however, an oversimplification. Crosier (1934), interpreting his own and Melhus’s studies of the biology of *Phytophthora infestans*, wrote, “It is not the total rainfall nor the average temperature, but the coexistence of moisture and low temperature (from 10 to 15° C.) for one-half hour or longer, that makes possible the formation of spores, and . . . infection follows promptly if the moisture persists.” Further, he emphasized, “No propagules can be formed, irrespective of the temperature and moisture, unless viable sporangia are present.” The present discussion, following the life cycles of pathogens, attempts to recognize these fundamentals.

Crosier, in the above study, found sporulation was most abundant in an atmosphere saturated with water and at a temperature of 18 to 22°; sporangia were abundant within 8 hours. Production was slower at lower temperatures, and sterile at temperatures 3 to 5° higher. Here is the necessary information for a description of an environment suitable for the multiplication of *Phytophthora* and the forecast of late blight epidemics.
Quantitative estimates of sporulation of this important pathogen have been made, permitting a more exact weighting of the forecast according to the production (Wallin, 1957). At 21° sporangia appeared in 6 hours, while 8 hours were required at 18°. If more time was permitted, most isolates produced more sporangia at 18 than at 21°. For example, a typical isolate produced about equal numbers of spores, \( N \), in 6 hours at 21° and 8 hours at 18°; in 12 hours at 18° it had produced about 20 \( N \) while at 21° it had produced only 3 \( N \). The forecaster should beware of environmental races, however: one isolate was able to produce between 1 and 2 \( N \) sporangia in 12 hours at the high temperature of 27°. Employing data of this type and a survey of primary infection one can estimate the production of spores from hygrothermograph records, and a forecast can be begun.

The final step in the estimation of \( Q \), the number of propagules dispersed, is an examination of the discharge of the units into the air. The units have been attached to the host for nutrition; now they must break this attachment, pass through the enveloping 100 microns of the laminar flow layer of air, and reach the turbulent air above. Many viruses are borne by insects, and their numbers at critical times in the host’s life can form the basis of a forecast of epidemics (Doncaster and Gregory, 1948). Some bacteria are borne in splattering raindrops; the arrival of rain might be employed in forecasting a bacterial epidemic.

Fungi have developed many clever devices for dispersing their spores—devices that have been studied by deBary, Buller, and Ingold. Among these are some that depend upon the weather and, hence, can be limiting and of interest to the forecaster. Tobacco blue mold is a case in point. DeBary observed how the sporangia of some Oomycetes are discharged as the sporangiophores dry and twirl; Pinckard (1942) found this phenomenon specifically in Peronospora tabacina. The disease tobacco blue mold does not increase during prolonged rains (Dixon et al., 1936); spores are found in the air as dew or rain dry, not while the lesions are wet (Waggoner and Taylor, 1958). From these observations the forecaster of blue mold can learn to look beyond rains and dews and consider the critical hours after the leaves have dried and the spores have flown (Waggoner and Taylor, 1958).

This completes the estimation of the number of spores released, the source strength \( Q \) to which the subsequent epidemic will be proportional if other things are equal. This early omen depends upon the quantity of primary inoculum and infection and upon conditions favorable for the production and release of the propagules. The omen appears to the forecaster early enough for chemical control to be initiated, probably not early enough for the selection of an alternate crop or for roguing. Many
hurdles must yet be taken by the pathogen before an epidemic occurs, but the presence or absence of spore production is a valuable, early clue.

IV. THE TRANSFER OF INOCULUM

The propagule, once separated from its parent, can be carried to an infection court on some object, in the soil or in water, or through the air. This transfer is generally not under the control of the pathogen, can be limiting, and, hence, is an opportunity for forecasting.

Many contaminated objects such as seed, soil, and machinery are borne by man. The speed and volume of commerce, the wide distribution of hosts—particularly economic species—and the prolific nature of pathogens causes the probability of permanent nonintroduction of new pests into a region to approach zero. A knowledge of sanitation and of quarantine measures, as well as the foregoing factors, permits the forecaster to estimate how soon the inevitable introduction and subsequent epidemic will come.

The annual reintroduction of pests can be forecast in the same way. For example, the coming incidence of potato ring rot, caused by Corynebacterium sepedonicum, can be anticipated from the liveliness of its transfer. Is seed inspected? Is contaminated equipment sterilized? Is whole seed used? If not, then an epidemic can be safely forecast whenever the inoculum was introduced into the seed-growing regions during the previous season.

Many viruses are transferred in insects, particularly aphids. As the number of aphids is decreased, transfer—as is dispersal—is decreased. This may be due to a northern climate, e.g., that of Maine or Scotland; the time of the year (Doncaster and Gregory, 1948); an exposed site (Waggoner and Kring, 1956); or sometimes an insecticide (Broadbent, 1957). Whatever drastically reduces the population of insect vectors reduces $Q$, and a lower incidence of infection can be forecast.

In many cases a sharp decrease in infection is observed at increasing distances from the source of aphid-borne viruses (e.g., Gregory and Read, 1949). In another case the sharp decrease observed by Waggoner and Kring (1956) became a broad distribution when the susceptible Green Mountain variety and extremely high insect populations were encountered (unpublished work). Nevertheless, under the usual field conditions of moderate populations of insects and some host resistance, the decrease with distance will be sharp, disease being proportional to $1/X^n$ where $n$ is about 2 (Gregory and Read, 1949). This is not surprising; Wolfenbarger (1946) has catalogued many insect dispersal patterns and found them similar. From this the forecaster can derive two useful
conclusions: disease severity will be slight at considerable distances from sources, especially in a single generation of the pathogen; and numerous widely scattered sources are necessary for an epidemic.

The spread of insect-borne fungi behaves in a manner similar to the spread of the viruses, providing similar bases for forecasting. For example, infection by *Ceratostomella ulmi*, the cause of Dutch elm disease, increases with the population of bark beetles (which can be limited by insecticides) and with propinquity to diseased trees (Zentmyer *et al*., 1944). Therefore, a forecast could be based upon a knowledge of the number of beetles and diseased elms in the neighborhood.

In undisturbed soil the spread of pathogens can take place through the contact or grafting of roots. The spread of *Phymatotrichum omnivorum* in cotton fields (Taubenhaus and Killough, 1923) and of *Endoconidiophora fagacearum* in oak forests (Beckman and Kuntz, 1951) can occur in this fashion. Because the span of root systems is relatively small, the forecaster should be able to draw an orderly prognostic map for these diseases and see it verified.

Plant pathogens can be carried by water: rain, irrigation, or spray. If these are the channels by which a pathogen travels, its distribution can be predicted to be localized. Faulwetter's (1917) classic study of the dissemination of bacteria by splashing rain demonstrated the short range of this type of distribution. Spores suspended in some fungicide or insecticide mixtures can infect plants (Dimock, 1951); unpublished experiments with *Phytophthora infestans* demonstrated that spray blasts do not increase its spread consequentially. Pathogens that spread in water evidently spread slowly.

Air-borne fungi have been classic subjects for studies in epidemiology as well as forecasting. Basing his analysis upon the statistical theory of the turbulent transfer of matter through air, Gregory (1945) has proposed a hypothesis for the transfer of inoculum; with slight modification this is the relation introduced in an early paragraph of this review. Gregory demonstrated the wide applicability of the hypothesis, infection generally being proportional to $1/X^n$, where $X$ is the distance from the source of inoculum and $n$ is about 2. Thus, one of the strongest clues available to the forecaster of these diseases is the nearness of inoculum: at half the distance, the probability of infection is fourfold. A concrete example can be seen in the map of an epidemic of tobacco blue mold: a few yards from the source of inoculum in an infected seedbed more than 100 lesions were present on each plant; at the far end of the 3-acre crop less than 5 lesions were present per plant; on a neighboring farm only 1 plant in 4 was infected (Waggoner and Taylor, 1955). With
the location of the source of inoculum in this neighborhood known, the course of the epidemic could be predicted for given weather and control practices.

A significant modification can be made in the average decrease with distance predicted by the inverse square relation. The spread of the pathogen downwind from the source is more rapid (Wilson and Baker, 1946; Waggoner and Taylor, 1955). Naturally, downwind refers to the direction of the wind during dissemination. Thus, the highest rate of infection would be forecast to the west of a pathogen that spread during rains.

The distribution of insect-, soil-, and air-borne pathogens all being commonly characterized by sharp decreases with distance from the source, van der Plank's (1949) analysis of the relative danger from field size is generally applicable. Thus, small fields and evenly distributed sources call for a forecast of a greater epidemic than do large and widely separated fields.

Two clues for forecasting have been pre-eminent in the discussion of transfer: the increased danger due to more vectors and that due to greater proximity to a source. These factors would have slight importance if the disease were permitted to run its course, but this it is rarely permitted among annual crops. Rather, the host and the pathogen race to the end of the season, and a winner is declared without a steady or equilibrium state ever becoming established. Thus, the number of vectors and the proximity of inoculum are important bases for the prediction of the damage sustained when the crop is harvested.

V. THE TRAPPING OF PROPAGULES

As the peripatetic plant pathogens pass over a unit area of the field, a proportion $p$ becomes attached to the soil and to plants. An increase in this attached proportion leads to an increase in the number of infections $D$. Increased trapping exerts another influence: it depletes the cloud of pathogens at a more rapid rate. Thus, $D$ is proportional to $pe^{-\text{constant } D(X)}$, and a knowledge of the rate of trapping $p$ should assist in forecasting the subsequent distribution of infection.

Unfortunately, little is known about the contribution of this factor. Logical conclusions can be drawn from the above hypothesis to supplement our meager knowledge. Contrast the case of a potato infected with Y virus situated among other potatoes attractive to *Myzus persicae* with the case of a source situated among plants unattractive to the aphid. In the first case, the danger to the adjacent plants is great, but the probability that this nonpersistent virus will be carried afar is slight;
in the second case, the danger to adjacent plants is decreased at the expense of more distant ones.

Now let us consider the spores of fungi—objects carried at the mercy of the winds. They vary in density, volume, and consequent settling velocity in the viscous air; presumably this might alter the proportion attached, but experience has shown the effect is inconsequential (Gregory, 1945). The ability of the spores to attach themselves to objects does, however, increase as spore size increases, leaf width decreases, or velocity increases; the small or slow-moving spores drift around a broad leaf (Gregory, 1951). From these considerations more infection nearby, less at a distance, has been forecast for large-spored pathogens in tall grass; and more infection afar, less nearby, for small-spored pathogens in low, broad-leaved plants (Waggoner, 1956). Verification is lacking, but the logic is compelling.

More than a forecast of distribution can be assisted by the foregoing. We have seen in preceding sections the necessity of a nearby source of propagules if infection and losses are to be consequential at harvest. From this it follows that widespread sources and subsequent epidemics should be frequent with the small spores pathogenic on broad leaves. This conclusion, too, is worth testing with a view to its eventual use in forecasting.

Rain is a well-known cleanser of the atmosphere, washing spores out of the air and onto foliage and soil. This effectively increases \( p \), the trapping efficiency. Rain has thus been an important factor in the consideration of long distance dissemination of spores: spores of, say, \textit{Puccinia graminis} are carried aloft and then northward in a maritime tropical air mass, eventually being washed to earth by precipitation (Stakman, 1942). The forecaster must bear in mind the dilution of the spore cloud with distance, but conceivably synoptic charts of the air currents at several levels could be useful in predicting the transfer of prolific fungi that infect large acreages.

VI. INFECTION

The pathogen has avoided many pitfalls before alighting, but it now has another crucial step to accomplish: it must infect a plant. In our hypothesis the number of spores deposited per successful infection is \( K \); infection increases as \( K \) decreases.

The first prerequisite is that the propagule be alive. The forecaster will have investigated the hardiness of the pathogen and entered this into his "rules." For example, he will be confident that the hardy rust spores or apple scab ascospores or the virus safe within an aphid are
alive, and that this step provides no opportunity for a forecast criterion. On the other hand, he knows that the spores of the downy mildews are susceptible to drought and that sunlight is a signal for a forecast of "no epidemic."

Germination is the second prerequisite for the success of a spore. This step is frequently susceptible to weather and has been a most fruitful source of forecasting methods. Satisfactory conditions for germination must arrive while the spore is viable. The requirement for moisture is common and has been widely applied in forecasting, e.g., the downy mildews. In contrast to this are the powdery mildews with their requirement for high humidity but not water (e.g., Delp, 1954); presumably, this could be employed in forecasting.

The temperature is also critical during germination. Not only can the temperature itself be limiting, but it determines the speed of germination, and hence, the number of hours of satisfactory moisture conditions required (e.g., Crosier, 1934). Thus, varying critical lengths of moist periods can be set for varying temperatures.

Next, the landing and germination must occur on a host. This success is improbable if few of the host species grow near the source or if the plants are small and cover little of the soil. In this case few of the spores will alight on a host, and many will fall on strange species or barren soil. Here, $K$ is large, since many spores fall and few infect; the forecaster may be conservative in his warnings.

Finally, the host that receives the pathogen must be susceptible. In the case of a heteroecious fungus, epidemics are most likely if the repeating stage is on the economic crop. Stakman (1942) has provided us with examples: Gymnosporangium juniperi-virginianae sporidia alone can infect apple, and no epidemic of rust would be forecast far from red cedars; Puccinia graminis var. tritici uredospores can infect wheat, and the pathogen can spread through a wheat belt by repeated, relatively short jumps with scattered sources appearing near many hosts.

In any case the strain of the pathogen must be capable of infecting the variety of the host. One of the forecaster's most important indicators is a survey of the various races present and the varieties being grown. Thus, the appearance of Race 56 of Puccinia graminis var. tritici and the large acreages of Ceres wheat foretold the elimination in the mid-thirties of that hitherto resistant variety.

The damage wrought by an infection could be the $D$ of our hypothesis. If this were our thinking, then the proportionality constant $K$ would be the number of propagules deposited per unit value destroyed. Then $K$ would fall, and the probability of damage would rise if we were concerned with a systemic disease, particularly of a large host (van der
8. FORECASTING EPIDEMICS

Plank, 1947). The effect is increased further if the individual plant is valuable. Consider how the probability of damage rises as we turn from the spots of apple scab to the systemic infection of Dutch elm disease or oak wilt of a prized shade tree.

In the preceding sections we have dealt with the several steps in the multiplication of an air- or insect-borne pathogen. The life of a soil-borne fungus may be less complicated, but an infection must be accomplished and the pathogen flourish within the host if an epidemic is to ensue. The separation of infection and incubation is incomplete in our knowledge but largely unimportant for this discussion. Seedling diseases are frequently associated with slow emergence and retarded early growth. Thus, the occurrence of damping-off of corn by *Pythmin* spp. can be forecast for cold, wet springs (Johann et al., 1928). The more specific, soil-borne wilt fungi also prosper best in certain environments: *Verticillium* wilt of tomatoes can be forecast for cool and *Fusarium* wilt for warm climates (Bewley, 1922; Clayton, 1923).

Infection phenomena are often susceptible to the weather and provide a wealth of opportunities for forecast criteria. Can the pathogen survive, germinate, and infect in the environment of the host? If the forecaster answers these in the affirmative, he knows that a frequent barrier to epidemics has been removed and that he had best beware.

VII. THE INCUBATION PERIOD

The rapidity of increase of a pathogen has already been mentioned as critical to the development of epidemics and consequential losses. This is so in large part because the pathogen and host rarely reach equilibrium during the life of an annual crop. Rather the pathogen is racing against the time when unfavorable weather will arrive. Therefore, what Chester (1950) has called "tempo" is critical.

The length of the cycles as well as the successful infections per cycle determine the tempo. The discharge, transfer, and trapping of inoculum and the infection of the host can, and often do, occur within a few hours. Incubation is generally a more extended process and considerable variation in its duration is frequent. Here, then, is an opportunity for alterations in the tempo, alterations critical to forecasting, alterations in the rapidity of reappearance of new sources and in their size Q.

With the fungus safely within the moist host tissues during incubation, temperature—not humidity—becomes the important factor. An example of the importance of temperature in the length of the incubation period is provided by *Phytophthora infestans* (Crosier, 1934). Decreasing the maximum and minimum temperatures from 23 and 15° C. to 20 and 10° C., increased the length of the period by one-fourth. This would
result in only 5 instead of 6 multiplications of the pathogen per month. Of course, raising the maximum and minimum temperatures to 35 and 25° C. destroyed the pathogen within the host.

A similar example of altered length of period is provided by *Uncinula necator* (Delp, 1954): the incubation period was halved by raising the temperature from 15 to 26° C.

*Peronospora tabacina* illustrates the disastrous effect upon the pathogen's prosperity of high temperature during incubation: hot weather causes "dry weather" blue mold lesions which are devoid of spores, and hence, ends the multiplication of the pathogen (Jenkins, 1952). Unquestionably many examples of accelerated multiplication by warm temperatures and truncated epidemics due to hot temperatures can be found among bacterial and viral as well as fungal incubations. If the forecaster is aware of these relations for his charges, he can estimate whether the tempo of multiplication is sufficiently rapid for an epidemic to develop within the season.

A second use for a knowledge of the length of incubation is in detecting synchrony of the cycles of weather and pathogen. Imagine that a period of weather unfavorable for sporulation and infection is followed by a day when infection does occur. If a second day of weather suitable for multiplication occurs before the end of the incubation, new infections will be added. If, instead, the second suitable day occurs at the end of the incubation, infections will be multiplied, not just added. Thus, favorable conditions alone are not enough; they must be meshed with the cycle of the pathogen, a cycle timed in large part by the temperature during incubation.

One large class of pathogens need not race with the host to a deadline at the end of the season. These are the pathogens of perennial plants, such as trees. Here ample time is allowed for an equilibrium to be established, and eradication and exclusion are relatively harmless to the pathogen over the long pull. The forecast will, therefore, be in terms of "when," not "if." The forecaster must guess the equilibrium rate from the best knowledge of the susceptibility of the host, the multiplication of both host and pathogen, and any deterrents to spread applied over the entire region concerned. As an example, among the American elms in the climate of Connecticut one can forecast with some confidence that in the neighborhood of 20% of the elms will become infected annually with Dutch elm disease if an insecticide is not applied, 3%, if it is (Dimond *et al.*, 1949).

The incubation period is lengthy, relative to the other periods of the pathogen's multiplication, and hence, provides a wealth of opportunities for the forecaster, who must estimate how the race between an annual
crop and its pest will end or at what level the equilibrium between a perennial host and its pest will be reached.

VIII. INTEGRATIONS

The large number of possible prediction criteria enumerated above are not only opportunities for improving forecasts, but are also opportunities for hopeless confusion because of their number. How can such complexity be resolved?

Fortunately a study of the biology of a particular pathogen will generally reveal a critical step to which attention can be directed. Chester's (1946) description of the forecasting of wheat leaf rust provides an excellent example. In Oklahoma, March is the critical month. If the weather during this period permits the first cycles of rust renewal, there is enough time during the ensuing season for the pathogen to reach epidemic proportions. After this month, the weather is rarely limiting. Therefore, the weather and rust behavior during this month can form the basis of a forecast of rust intensity 2 to 3 months later.

The well-known Dutch (van Everdingen, 1933; Beaumont, 1947) and Irish (Bourke, 1953) rules for forecasting potato late blight also are a simplification based upon the existence of a critical stage in the pathogen's life. In the maritime climates of northeastern Europe the weather during incubation is rarely limiting, and adequate primary inoculum is apparently common. Therefore, the multiplication of the pathogen is limited only by the conditions for dispersal, transfer, and infection. Satisfactory conditions for these three steps are defined by simple rules, and hence, late blight forecasting is straightforward in Europe.

In the central United States, drought or hot weather frequently persists long enough to destroy Phytophthora infestans in the host. Therefore, Wallin (1958) deletes from his forecasts of blight the effects of earlier favorable periods if unfavorable weather persists for 21 days or more.

The length of the incubation period can be the critical factor in epidemics. Shatsky's modification of Müller's incubation calendar for vine mildew illustrates this point (Miller and O'Brien, 1952). The incubation period is related quantitatively to the mean temperature, and fungicide spraying is indicated at the end of the periods thus estimated.

An integration with a strong family resemblance to the above devices has been employed in Connecticut for several years for the prediction of tobacco blue mold epidemics. The biology of the parasite has been reviewed by Stover and Koch (1951), and the spores are known to be air-borne in the morning (Waggoner and Taylor, 1958). Bearing this
information in mind, the forecaster examines the hygrothermograph, sky cover, and rainfall records, together with a census of primary inoculum from the tobacco region and decides whether the pathogen could or could not have completed dispersal, transfer, and infection. If an infection period is thought to have occurred a “2” is entered on the calendar. If two more periods occur before incubation of the first is complete, 2’s are added each time and the numbers entered on the calendar are “4” and “6.” If instead the second infection period occurs near the end of the incubation period of the first infection, the number is doubled and a “4” is entered on the calendar. When a drought or heat wave intervenes and sterile lesions appear, the number on the calendar is reduced to “1,” and the multiplication process must begin anew. Thus, the forecasting scheme is an estimate of the population of *Peronospora tabacina* derived from a knowledge of its biology, its primary population in seedbeds, and the weather. We have found in Connecticut that damage of consequence will appear in the field when the estimate on our calendar reaches “64.” The arrival of this level can be anticipated from the tempo of the disease and the weather outlook.

The preceding examples illustrate how the complexities of the pathogen’s biology can be digested into rational forecasting criteria. Therefore, the prospective forecaster need not become lost in a maze on the one hand or rely upon empirical criteria upon the other hand.

**IX. THE USEFULNESS OF FORECASTING**

When one speculates about the value of weather, yield, or disease forecasts, no difficulty is encountered in convincing oneself that forecasts are useful, even necessary. The desire to foretell the future is strong. Nevertheless an enumeration of the characteristics that determine the practical usefulness of predictions is healthy, especially if it is made before a forecasting system is initiated.

The first requirement of a forecast is that it be correct. Perfection is rarely possible in forecasting, and the natural tendency is to be conservative, to “overforecast.” In disease forecasting this leads to the warning “epidemic” whenever a chance of such exists. At the same time that the forecaster is being “conservative,” the growers’ other advisors are naturally enough behaving in the same manner: they urge the grower to exercise control measures at all times. Therefore, the usefulness of the forecaster’s warning of “epidemic” may be limited because his is but one more voice added to the chorus of voices urging him to repent and spray.

On the opposite side, the forecaster may be more helpful. He may lead the grower to omit costly control measures by forecasting “no epidemic.” Before he can persuade the grower to make such a savings
he must have established the accuracy of his predictions in the minds of the grower and his advisors and have overcome the natural tendency to be conservative. In France this happy state has apparently arrived: the warning service for vine mildew has led to the omission of two sprays in most years at an annual savings of two and one-half billion francs (Darpoux, 1949). Thus, if the forecaster can bring about the elimination of unnecessary and costly measures through accurate forecasting, he can be truly helpful.

The distance that the forecaster can see into the future, as well as his accuracy, affects the usefulness of his methods. If the prediction arrives in time for remedial action to be taken, it is helpful. If it arrives too late for action, it only lengthens the time over which the grower must bear his sorrow. The predictions of epidemics of seed-borne smuts and virus from the conditions during the flowering of the wheat or from an index of potato tubers has already been mentioned. Here the prognostication can be made for many months in advance, and the grower has ample time to remedy the matter.

The predictions of wheat leaf rust (Chester, 1946) and of bacterial wilt of sweet corn (Stevens, 1934) extend for several months into the future. Hence, the farmer has time in which to benefit from the forecast by planting an alternate crop or variety. The French warnings concerning vine mildew are of much shorter period; nevertheless, they arrive in sufficient time to be helpful because fungicidal control can be applied or omitted on short notice.

Long-range or climatological predictions of plant diseases have been made informally. Men have recognized that certain climates are conducive to a disease, others are not. Seed production has been located in regions where the climate makes important seed-borne diseases unlikely. In addition to this a formal study of long-range or climatological prediction would be interesting. The epidemics of certain diseases can be traced to critical weather events. The probability of these events can frequently be estimated from the series of weather observations that have now reached great lengths in many localities. The knowledge of biology and weather could be combined to produce estimates of the probabilities of disease at various localities and seasons. These "forecasts" should prove useful because of their long, almost infinite, extension into the future.

The discussion of the period of the forecast has brought out the importance of the control method. If the forecast is to provide more than intellectual satisfaction, there must be a control method that can be exercised and the impending epidemic forestalled. The usefulness of the above predictions of smut and virus epidemics depends upon the
existence of alternate, clean seed. The usefulness of the predictions of wheat leaf rust and bacterial wilt of corn depends upon the existence of profitable alternate crops or resistant varieties. The benefit from the warning systems for downy mildews is dependent upon the efficacy of fungicides.

Two diseases stand in contrast to the ones we have just examined. Apple scab infection can be eradicated by suitable chemicals. Hence, a census of infection can be used and the need for a forecast is consequently less. Wheat stem rust control at the present depends practically upon the choice of a resistant variety. Consequently, the forecast of a stem rust epidemic issued in the middle of the growing season is nearly useless to the individual farmer because there is as yet no remedy he can apply to forestall the impending calamity.

The use of a forecast necessitates changes in operations. Flexibility is a prerequisite to the employment of prediction. At least two things affect this flexibility. The first is the quantity of labor and equipment available for control measures relative to the acreage that must be treated. If the entire area can be treated in a day or two, treatment can be delayed safely until a forecast is issued. If the entire area requires many days for treatment, however, the machines must be kept in operation continuously; otherwise, a large proportion of the area might be damaged before treatment in response to a warning could reach it. The second thing that affects flexibility is the complexity of the farming organization. If the man who applies the treatment is also the man who decides when to treat and if supplies are readily available, a treatment can quickly follow warning. Alternatively, if a large organization is involved, planning must precede action. Here the confusion that would follow a change in plans following a warning might well cost more than the application of an occasional unnecessary treatment. Consequently, a short-range forecast is not highly useful; perhaps climatological "forecasts" would prove to be.

An important—perhaps the most critical—factor in the usefulness and in the adoption of forecasting is the ratio of benefit to cost. How great is the benefit from disease control relative to the cost of the control measure? If this ratio is large, the rational grower will apply controls whether the disease is forecast or not. If this ratio is small, no amount of urging will induce the rational grower to act.

In the northeastern United States apple and potato growers know that the yield, appearance, and keeping quality of their produce are profoundly affected by apple scab and potato late blight. They also know that including an effective fungicide among the pest sprays they are already applying is inexpensive. Thus, the ratio of benefit to cost is high,
and the growers tend to apply fungicides routinely with little regard for the likelihood of an epidemic.

At the opposite pole stands the owner of a large wood lot populated in part by elms. The death of the elms would not be disastrous to the production of the lot. The cost of an annual application of an insecticide to kill the vectors of the pathogen of Dutch elm disease would be large relative to the annual production of the lot. Therefore, the ratio of benefit to cost is small, and the owner is unlikely to apply a control measure, even when he is assured of the imminence of an epidemic of Dutch elm disease.

Between these two extremes lies a region where the benefit:cost ratio is favorable to the employment of forecasts. The example of the vine mildew warning system in France cited above lies in this region of a favorable ratio. The losses from mildew are disastrous. On the other hand, considerable savings can be made by eliminating unnecessary sprays. Hence, the warning system is employed by the growers (Dar­poux, 1949).

The benefit:cost ratio also depends upon the annual variation in the amount of disease. If the amount is nearly constant from year to year, experience has taught the farmer how to make his own forecast: next year will be just like this year and will have the same benefit:cost ratio and demand the same measures. This leaves little for the forecaster to do that is useful. When the amount of disease is variable from year to year, the forecaster can be useful, for he will predict when the benefit of treatment will be great or small relative to the cost of treatment.

X. Summary

The forecasting of disease is a contribution to the prediction of yields. It logically proceeds from a knowledge of the interaction of host, pathogen, and environment. In this review the etiology of disease has been examined for opportunities for prognostication of disease and subsequent loss.

The magnitude of the primary inoculum affects the subsequent epidemic. As a clue to the size of the epidemic it has the advantage of earliness, the disadvantage of being subject to many influences before harvest time.

The production of inoculum and its dispersal into the medium about the plant is one of the processes upon which weather can exert its influence and is, therefore, a rich source of forecast criteria.

The transfer of inoculum by air and soil, and as a contaminant is for the pathogen a risky business, because it is dependent upon fortune.
The forecaster profits from a knowledge of the proximity of the source of inoculum and of the number of vectors during this random process. Propagules are trapped and their numbers depleted more rapidly by some types of foliage and weather than by others. This is probably important in predicting the distribution of infection about a source of inoculum.

Infection is a late step in the pathogen's multiplication, but its requirements are sufficiently critical to provide a wealth of criteria for prediction. The general requirement for liquid water at this stage provides the basis for several classic forecasting schemes.

The incubation period is generally much longer than the preceding steps, and therefore is subject to changes of length. Thus, it can influence the rapidity of development of the disease and the level attained before unfavorable weather or harvest ends the annual race between host and pathogen.

The myriad influences can frequently be digested into simple forecasting rules because of the limitation placed upon epidemics by a few critical stages.

The usefulness of the prediction of epidemics depends upon the accuracy and range of the forecast, upon the existence of remedies and the ease with which they can be applied, and upon the benefits from disease control relative to the cost of remedies.

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8. FORECASTING EPIDEMICS


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