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effect of environment on development of infectious plant diseases

Although all pathogens, all perennial, and, in warmer climates, many annual plants are present in the field throughout the year, almost all diseases occur only, or develop best, during the warmer part of the year. Also, it is common knowledge that most diseases appear and develop best during wet, warm days, or that plants heavily fertilized with nitrogen usually are much more severely attacked by some pathogens than are less fertilized plants. These general examples clearly indicate that the environmental conditions prevailing in both air and soil, after contact of a pathogen with its host, may greatly affect the development of the disease, and frequently they determine whether a disease will occur or not. The environmental factors that most seriously affect the initiation and development of infectious plant diseases are temperature, moisture, light, soil nutrients, and soil pH. Their effects on disease may be brought about through their influence on the growth and/or susceptibility of the host, on the multiplication and activity of the pathogen or on the interaction of host and pathogen and its effect on the severity of symptom development.

It is obvious then that, for a disease to occur and to develop optimally, a combination of three factors must be present: susceptible plant, infective pathogen, and favorable environment. However, although plant susceptibility and pathogen infectivity remain essentially unchanged in the same plant for at least several days, and sometimes for weeks or months, the environmental conditions may change more or less suddenly and in various degrees. Such changes influence the development of diseases in progress, or the initiation of new ones, more or less drastically. Of course, a change in any environmental factor may favor the host or the pathogen or both, or it may be more favorable to the one than it is to the other, and the expression of disease will be affected accordingly. Plant diseases generally occur over a fairly wide range of the various environmental conditions. Nevertheless, the extent and frequency of their occurrence, as well as the severity of the disease on individual plants, are influenced by the degree of deviation of each environmental condition from the point at which disease development is optimal.

effect of temperature

Plants as well as pathogens require certain minimum temperatures in order to grow and carry out their activities. The low temperatures of late fall, winter, and early spring are below the minimum required by most pathogens. Therefore, diseases are not, as a rule, initiated during that time and those in progress generally come to a halt. With the advent of higher temperatures, however, pathogens become active and, when other conditions are favorable, they can infect plants and cause disease. Pathogens differ in their preference for higher or lower temperatures, and many diseases develop best in areas, seasons, or years with cooler temperatures, while others develop best where and when relatively high temperatures prevail. Thus, some species of the fungi *Typhula* and *Fusarium*, which cause snow mold of cereals and turf grasses, thrive only in cool seasons or cold regions. Also, the late blight pathogen *Phytophthora infestans* is most serious in the northern latitudes, whereas in the subtropics it is serious only during the winter. On the other hand, most diseases are favored by high temperatures and are limited to within areas and during seasons in which such temperatures are prevalent. Such diseases include the fusarial wilts of plants, the *Phymatotrichum* root rots of plants, the brown rot of stone fruits caused by *Monilinia fructicola*, the southern bacterial wilt of solanaceous plants caused by *Pseudomonas solanacearum*, etc.

The effect of temperature on the development of a particular disease after infection depends on the particular host–pathogen combination. The most rapid disease development, i.e., the shortest time required for the completion of a disease cycle, usually occurs when the temperature is optimum for the development of the pathogen but is above or below the optimum for the development of the host. At temperatures much below or above the optimum for the pathogen, or at temperatures near the optimum for the host, disease development is slower. Thus, for stem rust of wheat, caused by *Puccinia graminis tritici*, the time required for a disease cycle (from inoculation with uredospores to new uredospore formation) is 22 days at 5°C, 15 days at 10°C, and 5 to 6 days at 23°C. Similar time periods for the completion of a disease cycle are required in many other diseases caused by fungi, bacteria, and nematodes. Since the duration of a disease cycle determines the number of disease cycles and, approximately, the number of new infections in one season, it is clear that the effect of temperature on the prevalence of a disease in a given season may be very great.

If the minimum, optimum, and maximum temperatures for the pathogen, the host, and the disease are about the same, the effect of temperature in disease development is apparently through its influence on the pathogen which becomes so activated at the optimum temperature that the host, even at its optimum growth, cannot contain it.

In many diseases, the optimum temperature for disease development seems to be different from those of both the pathogen and the host. Thus, in the black root rot of tobacco, caused by the fungus *Thielaviopsis basicola*, the optimum for disease is at 17 to 23°C, while that for tobacco is 28 to 29°C and for the pathogen is 22 to 28°C. Evidently, neither the pathogen nor the host grow well at 17 to 23°C, but the host grows so much more poorly, and is so much weaker, than the pathogen that even the weakened pathogen can cause maximum disease development. In the root rots of wheat and corn, caused by the fungus *Gibberella zeae*, the maximum disease development on wheat occurs at temperatures above the optimum for development of both the pathogen and wheat, but on corn, it occurs at temperatures below the optimum for the pathogen and for corn. Considering that wheat grows best at low temperatures while corn grows best at high temperatures, it would appear that the more severe damage to wheat at high temperatures and to corn at low temperatures is due to disproportionate weakening of the plants, in relation to the weakening of the pathogen, at the unfavorable temperatures.

The effect of temperature on virus diseases of plants is a great deal more unpredictable. Temperature determines not only the ease with which plants can become infected with a virus but also whether or not a virus multiplies in the plant and, if it does, whether the symptoms produced will be of one kind or another. The severity of the disease may vary greatly in various virus–host combinations depending on the temperature during certain stages of the disease. Temperature, probably in combination with sunlight, seems to determine the seasonal appearance of symptoms in the various virus diseases of plants. Viruses producing yellows or leaf-roll symptoms are most severe in the summer, while those causing mosaic or ringspot symptoms are most pronounced in the spring. New growth produced during the summer on mosaic- or ringspot-infected plants usually shows only mild symptoms or is completely free from symptoms.

effect of moisture

Moisture, like temperature, influences the initiation and development of infectious plant diseases in many interrelated ways. It may exist as rain or irrigation water on the plant surface or around the roots, as relative humidity in the air and as dew. The most important influence of moisture seems to be on the germination of fungal spores and on the penetration of the host by the germ tube. Moisture also activates the bacterial, fungal, and nematode pathogens, which may then infect the plant. Moisture, such as splashing rain and running water, also plays an important role on the distribution and spread of many of these pathogens on the same plant or from one plant to another. Finally, moisture affects disease by increasing the succulence of host plants, thus considerably increasing their susceptibility to certain pathogens.

The occurrence of many diseases in a particular region is closely correlated with the amount and distribution of rainfall within the year. Thus, late blight of potato, apple scab, downy mildew of grapes, and fire blight, are found or are severe only in areas with high rainfall or high relative humidity during the growing season. As a matter of fact, in all these, and other diseases, the rainfall determines not only the severity of the disease, but also whether the disease will occur at all in a given season. In the cases of the fungal diseases, the effect of moisture is on the germination of spores of fungi, which require a film of water on the tissues in order to germinate and, also, on the liberation of spores from the sporophores which, as in apple scab, can occur only in the presence of moisture. The number of disease cycles per season of many of these diseases is closely correlated with the number of rainfalls per season, particularly of rainfalls that are of sufficient duration to allow establishment of new infections. Thus in apple scab, for example, continuous wetting of the leaves, fruit, etc., for at least 9 hours is required for any infection to take place even at the optimum range (18 to 23°C) of temperature for the pathogen. At lower or higher temperatures the minimum wetting period required is higher, i.e., 14 hours at 10°C, 28 hours at 6°C, and so on. If the wetting period is less than the minimum for the particular temperature, the pathogen fails to establish itself in the host and to produce disease.

Most fungal pathogens are dependent on the presence of free moisture on the host or of high relative humidity in the atmosphere only during germination of their spores and become independent once they can obtain nutrients and water from the host. Some pathogens, however, such as those causing late blight of potato and the downy mildews, require at least high relative humidity in the environment throughout their development. In these diseases, the growth and sporulation of the pathogen, and also the production of symptoms, come to a halt as soon as dry, hot weather sets in and resume only after a rain or after the return of humid weather.

Though most fungal and bacterial pathogens of aboveground parts of plants require a film of water in order to produce successful infections, the spores of the powdery mildew fungi can germinate, penetrate, and cause infection even when there is only high relative humidity in the atmosphere surrounding the plant. In the powdery mildews, spore germination and infection are actually lower in the presence of free moisture on the plant surface than they are in its absence and, in some of them, the most severe infections take place when the relative humidity is rather low (50 to 70 percent). In these diseases, the amount of disease is limited rather than increased by wet weather. This is also indicated by the fact that the powdery mildews are more common and more severe in the drier areas of the world and their relative importance decreases as rainfall increases.

In many diseases affecting underground parts of plants, such as roots, tubers, and young seedlings—for example in the *Pythium* damping off of seedlings and seed decays—the severity of the disease is proportional to the soil moisture and is greatest near the saturation point. The increased moisture seems to affect primarily the pathogen, which multiplies, and moves (zoospores in the case of *Pythium*) best in wet soils, but it may also decrease the ability of the host to defend itself through reduced availability of oxygen in water-logged soil and by lowering the temperature of such soils. Many other soil fungi, e.g., *Phytophthora*, *Rhizoctonia*, *Sclerotinia*, and *Sclerotium*, some bacteria, e.g., *Erwinia* and *Pseudomonas*, and most nematodes usually cause their most severe symptoms on plants when the soil is wet but not flooded, while yet others such as *Streptomyces scabies*, causing the common scab of potato, are most severe in rather dry soils.

Most bacterial diseases, and also many fungal diseases of young tender tissues, are particularly favored by high moisture or high relative humidity. Bacterial pathogens and fungal spores are usually disseminated in water drops splashed by rain, in rain water moving from the surfaces of infected tissues to those of healthy ones, or in free water in the soil. Bacteria penetrate plants through wounds or natural openings and cause severe disease when present in large numbers. Once inside the plant tissues, the bacteria multiply faster and are more active during wet weather, probably because the plants, through increased water absorption and resulting succulence, can provide the high concentrations of water that favor bacteria. The increased bacterial activity produces greater damage to tissues, and this damage, in turn, helps release greater numbers of bacteria on the plant surface where they are available to start more infections if wet weather continues.

effect of wind

Wind affects infectious plant diseases primarily through its importance in the spread of plant pathogens and, to a smaller extent, through its speeding up of the drying of wet plant surfaces. Most plant diseases that spread rapidly and are likely to assume epidemic proportions are caused by pathogens, e.g., fungi, bacteria, viruses, that are either spread directly by the wind or are spread by insect vectors which themselves can be carried over long distances by the wind. Some spores, e.g., zoosporangia, basidiospores, and some conidia, are usually quite delicate and do not survive long-distance transport in the wind. Others, e.g., uredospores and many kinds of conidia, can be transported by the wind for many miles. Wind is even more important in disease development when it is accompanied by rain. Wind-blown rain helps release spores and bacteria from infected tissue and then carries them through the air and deposits them on wet surfaces which, if susceptible, can be infected immediately. Wind also injures plant surfaces while they are blown about and rubbing against each other; this facilitates infection by many fungi and bacteria and also by some mechanically transmitted viruses. Wind sometimes helps prevent infection by speeding up the drying of wet plant surfaces on which fungal spores or bacteria may have landed. If the plant surfaces dry before penetration has taken place, any germinating spores or bacteria present on the plant are likely to desiccate and die and no infection will occur.

effect of light

The effect of light on disease development, especially under natural conditions, is far less than that of temperature or moisture although several diseases are known in which the intensity and/or the duration of light may either increase or decrease the susceptibility of plants to infection and also the severity of the disease. In nature, however, the effect of light is limited to the production of more or less etiolated plants as a result of reduced light intensity. This usually increases the susceptibility of plants to nonobligate parasites, e.g., of lettuce and tomato plants to *Botrytis* or of tomato to *Fusarium*, but decreases their susceptibility to obligate parasites, e.g., of wheat to the stem rust fungus *Puccinia*.

Reduced light intensity generally increases the susceptibility of plants to virus infections. Holding plants in the dark for one to two days before inoculation increases the number of lesions (i.e., infections) appearing after inoculation and this has become a routine procedure in many laboratories. Generally, darkening affects the sensitivity of plants to virus infection if it precedes inoculation with the virus, but seems to have little or no effect on symptom development if it occurs after inoculation. On the other hand, low light intensities following inoculation tend to mask the symptoms of some diseases, which are much more severe when the plants grow in normal light than when they are shaded.

effect of soil pH

The pH of the soil is important in the occurrence and severity of plant diseases caused by certain soil-borne pathogens. For example, the clubroot of crucifers, caused by *Plasmodiophora brassicae*, is most prevalent and severe at about pH 5.7, while its development drops sharply between 5.7 and 6.2, and is completely checked at pH 7.8. On the other hand, the common scab of potato, caused by *Streptomyces scabies*, can be severe at a pH range from 5.2 to 8.0 or above, but its development drops sharply at pH below 5.2. It is obvious that such diseases are most serious in areas whose soil pH favors the particular pathogen. In these, and in many other diseases, the effect of soil acidity (pH) seems to be principally on the pathogen, although in some, a weakening of the host through altered nutrition induced by the soil acidity may affect the incidence and severity of the disease.

effect of host–plant nutrition

Nutrition affects the rate of growth and the state of readiness of plants to defend themselves against pathogenic attack. Abundance of certain nutrients, e.g., nitrogen, results in the production of young, succulent growth and may prolong the vegetative period and delay maturity of the plant, making it more susceptible to pathogens that prefer to attack such tissues—and for longer periods. Conversely, lack of nitrogen would make plants weaker, slower growing, and faster aging and would make them susceptible to pathogens that are best able to attack weak, slow growing plants. Thus, it is known that high nitrogen fertilization increases the susceptibility of pear to fire blight (*Erwinia amylovora*), of wheat to rust (*Puccinia*) and to powdery mildew (*Erysiphe*), etc. Reduced nitrogen may also increase the susceptibility of some plants to certain diseases, e.g., of tomato to *Fusarium* wilt, of many solanaceous plants to the *Pseudomonas solanacearum* wilt, of sugar beets to *Sclerotium rolfsii*, of most seedlings to *Pythium* damping off. It is possible, however, that it is the form of nitrogen (ammonium or nitrate) available to the host or pathogen that affects disease severity or resistance rather than the amount of nitrogen. Of numerous root rots, wilts, foliar diseases, etc., treated with either form of nitrogen, almost as many decreased or increased in severity when treated with ammonium nitrogen as did with nitrate nitrogen, but each form of nitrogen had exactly the opposite effect on a disease than did the other form of nitrogen.

Although nitrogen nutrition, because of its profound effects on growth, has been studied the most extensively in relation to disease development, studies with other elements such as phosphorus, potassium, and calcium, and also with micronutrients, have revealed similar relationships between levels of the particular nutrients and susceptibility or resistance to certain diseases. In general, plants receiving a balanced nutrition, in which all required elements are supplied in appropriate amounts, are more capable of protecting themselves from new infections and of limiting existing infections than when one or more nutrients are supplied in excessive or deficient amounts. Even a balanced nutrition, however, may affect the development of a disease when the concentration of all the nutrients is increased or decreased beyond a certain range.

the role of environmental factors in plant disease epidemics

For infection to occur at least once, the plant and the pathogen must be brought together and the range of temperature and moisture must be such that the pathogen will be able to grow and cause infection. Predisposition of the plant for disease by improper nutrition, lighting, soil pH, etc. may also be of some importance but these factors seldom determine whether disease will occur or not.

For a disease to become important in a field, however, and particularly if it is to spread over a large area and develop into an epidemic, the right combinations of environmental factors must occur and spread either constantly, or repeatedly and at frequent intervals, over a large area. Even in a single, small field, which contains the pathogen, plant diseases almost never become severe from just one set of favorable environmental conditions. It takes repeated disease cycles and considerable time before the pathogen produces large enough numbers of individuals that can cause an economically severe disease in the field. However, once large populations of the pathogens are available, they can then attack, spread to nearby fields, and cause a severe disease in a very short time—just a few days.

Plant disease epidemics are caused primarily by fungi, bacteria, viruses, and mycoplasmas which can either be carried directly by the wind (fungi, some bacteria) or by insect vectors (viruses, mycoplasmas, some fungi, and bacteria). In some cases minor epidemics occur when the pathogen is carried in or on the seed or any other propagative organ, but in this case the epidemic is limited to the plants propagated from such contaminated seed, etc., unless again the pathogen can become airborne and spreads to other plants.

A plant disease epidemic implies the development and rapid spread of a disease on a particular kind of crop plant cultivated over a large area—be that a large field, a valley, a section of a country, the entire country or even part of a continent. So, the first component of a plant disease epidemic is a large area planted to one, more or less genetically uniform crop plant, with the plants and the fields being close together. The second component of an epidemic is the presence or appearance of a virulent pathogen at some point among or near the cultivated host plants. Such cohabitations of host plants and pathogens occur, of course, daily in countless locations and cause local diseases of varying degrees of severity. But most of these destroy crop plants to a limited extent and do not develop into epidemics. Epidemics develop only when the combinations and progression of the right sets of environmental conditions, i.e., moisture, temperature, and wind or insect vector, coincide with the susceptible stage(s) of the plant and with the production, spread, inoculation, penetration, infection, and reproduction of the pathogen.

Thus, for an epidemic to develop the small original or primary inoculum of the pathogen must be carried by wind or vector to some of the crop plants as soon as they begin to become susceptible to that pathogen. The moisture and temperature must then be right for germination or infection to take place. Following infection the temperature must be favorable for rapid growth and reproduction of the pathogen (short incubation period, short disease cycle) so that numerous new spores, etc., will appear as quickly as possible. The moisture (rain, fog, dew) then must be sufficient and should last long enough for abundant release of spores, etc. Winds of proper humidity and velocity and blowing toward the susceptible crop plants must then pick up the spores and carry them to the plants while the latter are still susceptible. It so happens, of course, that most plant disease epidemics are effectively spread from south to north in the northern hemisphere (and in the opposite direction in the southern hemisphere). This occurs because the warmer spring and early summer weather, and the growth seasons also move in the same direction and so the pathogens constantly find plants in their susceptible stage as everything progresses northward.

In each new location, however, the same set of favorable moisture, temperature and wind or vectors must be repeated so that infection, reproduction and dispersal of the pathogen must occur as quickly as possible. Furthermore, these conditions must be repeated several times within each location so that the pathogen can multiply itself and the number of infections it causes on the host plants. It is these repeated infections that usually result in the more or less complete destruction of almost every plant within the area of an epidemic, although the uniformity and area of cultivation of the plant along with the prevailing weather (i.e., moisture, temperature, winds) determine the final spread of the epidemic.

Fortunately, the most favorable combinations of conditions for disease development do not occur very often over very large areas and, therefore, spectacular plant disease epidemics that destroy crops over large areas are relatively rare. However, small epidemics involving the plants in a field, a valley, etc. occur quite frequently. With many diseases, e.g., potato late blight, apple scab, and cereal rusts, the environmental conditions seem to be usually favorable and disease epidemics occur or would occur every year were it not for the control measures (chemical sprays, resistant varieties, etc.) employed annually to avoid such epidemics.

weather and forecasting of plant disease epidemics

The appearance and development of many plant diseases depend on the kinds of weather conditions that preceded, prevail during or are likely to follow certain stages in the cultivation of crop plants. Therefore, it is often possible to predict the likelihood and severity of a particular disease if the association of the weather conditions and of the development of the disease are known and if the changes in the weather are followed closely. Ability to forecast the appearance and occurrence of diseases, especially diseases that fluctuate widely from season to season, can help farmers reduce or avoid losses from them either by applying control measures or by planting crops not susceptible to these diseases.

The occurrence of some diseases during a growing season can be predicted quite acurately by analyzing the weather conditions, i.e., temperature, during the previous winter. For example, the incidence of bacterial wilt of corn depends on the amount of inoculum that survived the previous winter in the bodies of its vector, corn flea beetles. When the sum of the mean temperatures for the three winter months at a given location is less than −1°C, most of the beetle vectors are killed and so there is little or no bacterial wilt! Warmer winters allow greater survival of the beetle vectors and proportionately more severe wilt outbreaks. Similarly, when January temperatures are above normal, the downy mildew (blue mold) of tobacco appears early in seedbeds in the following season and causes severe losses, while when January temperatures are below normal, blue mold appears in seedbeds late and causes little damage. If the disease is expected and can be controlled in seedbeds, subsequent control in the field is made much easier.

With most diseases, however, the pathogen responds quickly to changes in temperature and moisture during the growing season and in these cases disease forecasting depends on much closer observation and correlation of the weather and the pathogen. For example, the occurrence of an infection period in apple scab is a function of temperature and duration of wetness in the area. Thus, if it is 6°C and the spores are wet for 28 hours, infection will occur, and similarly with 14 hours wetness at 10°C, 9 hours at 18 to 24°C, 12 hours at 26°C, etc. A grower need spray only when these combinations occur and he can get good control with less expense.

Because downy mildews of plants and late blight of potatoes are among the most destructive diseases where they occur, several systems of forecasting have been developed for these diseases. Weather forecasting for late blight of potato, caused by *Phytophthora infestans*, has been extensively studied in several countries in Europe and in the U. S. and effective systems for disease forecasting have been developed for various areas. The main conditions for late blight epidemics appear to be constant, cool temperatures between 10 and 24°C while the relative humidity is 75 percent or more for at least 48 consecutive hours. When this combination occurs, a late blight outbreak can be expected from 2 to 3 weeks later. Several hours of rainfall, dew, or relative humidity close to saturation point within that period and afterward serve to increase the severity of the disease and the likelihood of a major epidemic.

SELECTED REFERENCES

Chupp, C. 1928. Club root in relation to soil alkalinity. *Phytopathology* **18**:301–306.

Colhoun, J. 1973. Effects of environmental factors on plant disease. *Ann. Rev. Phytopathol.* **11**:343–364.

Dickson, J. G. 1923. Influence of soil temperature and moisture on the development of seedling blight of wheat and corn caused by *Gibberella saubinetii*. *J. Agr. Res.* **23**:837–870.

Gallegly, M. E., Jr., and J. C. Walker. 1949. Plant nutrition in relation to disease development. V. *Am. J. Bot.* **36**:613–623.

Hepting, G. H. 1963. Climate and forest diseases. *Ann. Rev. Phytopathol.* **1**:31–50.

Huber, D. M., and R. D. Watson. 1974. Nitrogen form and plant disease. *Ann. Rev. Phytopathol.* **12**:139–165.

Jones, L. R., J. Johnson, and J. G. Dickson. 1926. Wisconsin studies upon the relation of soil temperature to plant diseases. *Wisc. Agr. Expt. Sta. Res. Bull.* **71**.

Kassanis, B. 1957. Effect of changing temperature on plant virus diseases. *Advan. Virus Res.* **4**:169–186.

Keitt, G. W., and K. L. Jones. 1926. Studies of the epidemiology and control of apple scab. *Wisc. Agr. Expt. Sta. Res. Bull.* **73**.

Miller, P. R. 1953. The effect of weather on diseases. *Yearbook Agr.* (U. S. Dept. Agr.), pp. 83–93.

Miller, P. R., and M. J. O'Brien. 1957. Prediction of plant disease epidemics. *Ann. Rev. Microbiol.* **11**:77–110.

Schnathorst, W. C. 1965. Environmental relationships in the powdery mildews. *Ann. Rev. Phytopathol.* **3**:343–366.