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THE PROPAGATION OF PLANT DISEASES THROUGH THE AIR

/Following is a translation of an article by Dr. Heinrich Carl Weltzien, Institute for Plant Protection, Hohenheim College of Agriculture (Director: Professor Dr. B. Rademacher), in the German-language periodical Fortschritte der biologischen Aerosol-Forschung, 1957-1961 (Progress in biological aerosol-research, 1957-1961), pages 154 to 159./

The Handbuch der Landwirtschaft (Manual of Agriculture) lists a total of 180 plants which are cultivated on a large scale in agriculture (Scheibe, 1953). In addition, there are another 60 cultivated species, approximately, in the subtropical and tropical climate zones (Esdorn, 1961), and, if we limit ourselves to the most important types, about 460 cultivated ornamental plants (Pirone et al., 1960), part of which also represent great economic assets. A nearly incalculable number of disease symptoms, parasitic as well as non-parasitic, has been described as occurring on these approximately 700 predominantly cultivated species of plants. If we exclude, for once, the animal pests, there remain, as in human medical science, the three groups of causative agents: viruses, bacteria, and fungi. The bacteria, of which Stapp (1956) lists about 260 types, are least significant numerically; they do, however, occur on a much greater number of host plants. The same is true for the nearly 320 viruses catalogued by Smith (1957), whose systematic classification is, to be sure, still very much in question. The fungi are most important, numerically as well as economically. It is not possible to present a complete survey here, but for example, Moore (1959) lists more than 3,000 kinds of mycosis on about 400 host plants in the case of England. If we inquire about the manner in which plant diseases are propagated, the most important role, in the case of the viruses, is played by intermediate carriers: mostly insects, but man with his equipment as well. Hitherto there have been no reports as to whether virus particles may be scattered directly via the air and cause reinfection. The same applies to plant-pathogenic bacteria, but here a certain degree of scattering holds true for bacteria-containing water splashes, comparable approximately to droplet infections. Among the plant-pathogenic bacteria there are absolutely no spore producers, which alone could be held responsible for a more extensive propagation through the air. The conditions are totally different with the pathogenic fungi, which we must chiefly bear in mind when we wish to concern ourselves with the air as carrier of pathogenic spores. Here, anemochory is the most important mode of propagation and, therefore, is of greatest significance in the epidemology of many diseases.

Aerobiology provides us with the fundamentals for the study of the live-organism content of the air. From among the species investigated within its scope, the reproductive cells of the fungi are of predominant interest here. We call them spores, regardless whether they are vegetative or generative cells. The first investigations of the spore content of the air date back to Pasteur (Large, 1940). He proved conclusively that the air acts as carrier for numerous and very different microorganisms. He made them visible indirectly by cultivating them in nutrient solutions. Today, we generally prefer methods which make the spores visible directly. In most cases, they are caught out of the air current by means of slides covered with an adhesive, f. ex. vaseline. Further development of these spore traps led to more precise catches from measured air volumes during defined units of time (Hirst, 1952). The spores in question are mostly spherical or oblong, with diameters varying from 2 to 20 microns. They are very well adapted to drifting in air currents, generally speaking, with their sedimentation velocities ranging from 0.5 to 20 millimeters per second. According to their order of magnitude they must, consequently, be classified as aerosols, and the physical laws determined for particles of this order of magnitude apply to them correspondingly. The spore density depends upon location, season, time of day, and weather. It can reach astonishingly high values. Thirty thousand spores per cubic meter of air have frequently been measured, and even one million spores per cubic meter do occur for short periods of time. Vertical air currents often carry the spores to high altitudes. Plant-pathogenic fungi were demonstrated by airplane catches at 4,000 meter levels, and during the "Explorer" program viable fungus spores were found in the zone between 11 and 22 kilometers altitude. On the other hand, it can be shown that the air above the water surface of the oceans may be practically sterile at a sufficient distance from the continent (Gregory, 1960).

Which are then the main types of fungi that occur in such significant numbers in the atmosphere? This question may be answered with sufficient accuracy by analyzing the captured spores. Far more than half of the spores usually derive from saprophytes which develop on dead organic matter, and for the most part, have plenty of opportunities there for sporulation. Gregory and Hirst (1957) determined, for instance, the spore content of the air above the experimental fields of an English research institute for six months. Nearly 50% of all spores belonged to the species cladosporium -- fungi, whose omnipresence is familiar to every plant pathologist, because they may be found frequently, especially on such plants which had been weakened by other diseases, f. ex. root rot. These spores appear in large numbers during the entire vegetative period, but they show a distinct maximum during August, that is, at a time when many plants ripen, especially the grain crops. Matters are different with the avowed parasites. They always occur only when the corresponding host is going through a phase of special susceptibility and, simultaneously, the weather conditions permit a mass increase of the spores. Thus we observe an increase in mildew spores during June, together with a high density of white rust spores. This may be explained from the biology of the causative agents. The genuine mildew affects preferably young, green parts of plants, which are plentiful during that time. White rust spores infect their host via the bloom: therefore, their sporulation must coincide with the flowering period of the host. Ordinary rust spores, which may be formed on all vegetative organs and originate even on ripening tissue, manifest themselves during a correspondingly longer period. The same applies to botrytis spores, which develop on many different hosts and at all times.

In order to be able to judge the practical significance of spore scattering, we must now turn to the question concerning the range of this mode of propagation. If we consider the above mentioned measured flight altitudes and the small size of the spores, it follows that the flight distance may be unlimited in theory. However, the cloud of spores ascending from a spore source undergoes rapid dilution, so that the probability of infection decreases quickly with increasing distance (Gaumann, 1951). This indicates at the same time how important the population density of the hosts is for the success of the infection. Furthermore, there is the limited life expectancy of part of the spores under varied meteorological conditions, which may be decisive especially during long distance transport. The various diseases differ greatly in their adaptation to these conditions.

As to the causative agent of our most important fruit disease, apple eschar (Endostigme inaequalis), there is always a high host density in the cultivation areas. The fungus hibernates on the leaves of the preceding year which are lying under the trees, and there it generates its spores for reinfection during spring. Thus, in this case the source of the spores is located directly next to the host, and only a relatively short distance remains to be bridged. During or after rain showers the spores are propelled into the air for several millimeters by means of a swelling mechanism, and then they are carried into the tree tops by air currents, at which location they find conditions favorable for infection during such weather conditions. The annually recurrent infection is caused by spore densities of up to 10,000 per cubic meter. Further propagation is then effected within the tree by newly formed spores and the rain water. Systematic control of the spore flight by means of spore traps has, therefore, become the basis for a successful combat against eschar in the case of this fungus, and it is being practiced throughout the world.

Rack demonstrated (1959) that even electrostatic forces can play a role during the introduction of spores into the atmosphere. He used the example of the fungus-parasitic needle loss of Scotch pine, caused by lophodermium pinastri. Similar to apple eschar, the spores ascend from infected needles on the ground and have to reach the healthy needles of young trees at the tree top. Rack tested the charge of ascending spores a few millimeters above the fruiting bodies by means of positively and negatively charged trapping plates, catching more than 80% of the spores on the positively charged plate. This means that the spores are negatively charged and are repelled by the negatively charged substratum, as well as by the mechanically effective propelling apparatus. Then, however, remarkably enough, a reversal of charges takes place, and at 1 to 1.5 meters altitude more than 90% of all spores are trapped on negatively charged plates; they are, thus, charged positively themselves. Therefore their descent upon the negatively charged host is effectively supported by electrostatic forces and is no longer dependent upon purely hazardous factors.

The propagation of the above mentioned rusts, for example, the grain rusts, also takes place over short distances only. But here we only have isolated diseased plants among the crops as a source of infection. Upon their transformed ears the fungus develops its spores. These must make their way into the open bloom of a healthy plant. New sporulation takes place only during the following year on a diseased plant grown from an infected seed. It follows that the number of sources of infection and the opening period of the blooms are decisive for the appearance of the disease. Propagation occurs along the main wind direction. The effective range of a source of infection depends upon the opening time of the blooms, and it was shown to extend for about 100 meters during experiments made by Oort (1940). Consequently, in this case several years are required for the accumulation of a strong attack, despite propagation by the wind. Therefore, the basis for counter measures is the reduction of the number of diseased plants among the crop. During seed certification, a maximum of three diseased plants per 100 square meters are permitted.

In the same manner, the causative agent -- phytophthora infestans -- of the most important potato disease, leaf- and tuber rot, produces infection emanating from isolated primary seats. Van der Zaag (1956) was able to show that the disease originates from isolated affected seed tubers which produce isolated diseased sprouts. In the Netherlands, he found approximately one seat of infection per 100 hectares. During favorable conditions for infection and growth the fungus has a fructification period of about five days. From the spore buds emerging from the leaves, the spores proceed directly into the air current and may be scattered widely. Leaf rot has occurred on islands at a distance of 11 kilometers from the continent, and observations in Florida make a scattering of up to 60 kilometers probable. The abundance of the host plant favors mass multiplication. During 1954 van der Zaag observed that only four weeks pass between the first appearance of phytophthora sources and the outbreak of an epidemic during which the parasite is literally omnipresent in the cultivation area. Similar reports come from England by Hirst and Stedman (1960).

Here, counter measures can consist only of direct safeguarding of the plants against infection through fungicidal sprays, and simultaneous use -- if possible -- of less susceptible varieties. To what extent a control of the spore flight can facilitate these counter measures, remains to be seen (Raeuber and Bochow, 1957).

A plant disease may be propagated through the air, not only within closed cultivation areas, but also between separate cultivation zones of a continent. Proof of such far scattering is, however, only possible under special conditions, such as prevail with the grain rust fungi. These fungi develop certain types of spores on a special host plant, the so-called winter host, and from there they transfer to the grain plants, as soon as his so-called summer host becomes available. There they produce large numbers of the so-called uredo spores, which in turn spread the disease throughout the grain. Initially, it appeared to be possible to interrupt the infectious chain and to eliminate the rust by destroying the winter host, in the case of the black wheat rust (puccinia graminis tritici), the barberry bush. If, however, susceptible grain is available throughout the year, as is the case on the North American continent with its various climatic zones, then the fungus can survive even without settling on the winter host. In North America, the uredo spores hibernate on the grain ripening during the winter in northern Mexico and southern Texas. If, now, an abundant supply of spores aggregates in this area, the predominant south winds can take up the spore cloud in spring and carry it to the north. The progression of the spores can be traced by means of spore traps (Stakman and Harrat, 1957). Approximately 3,500 kilometers separate them from the large wheat cultivation areas of the northern states and Canada. The mass of spores is not diluted to epidemological insignificance because there are smaller cultivation areas en route, where the fungus can reproduce and from which new, denser spore clouds ascend.

During years with favorable conditions for the rust, eight weeks can suffice for the bridging of the enormous distance, and there may be literally showers of spores over the main wheat cultivation areas of the north, leading to a sudden mass infection and crop failure. Since chemical counter measures have remained uneconomical up to now, all efforts concentrate upon the development of resistant types. Yet, the great successes of the American cultivators become repeatedly endangered by new varieties of the causative agent. It is mainly due to numerous natural barriers (oceans, mountain ranges) dissecting this area that the conditions do not favor rust in the Afro-Eurasian region to the same degree as they do in North America, because they prevent the build-up of uniform air currents. But it must not be overlooked that here, too, rust spores are scattered across all boundaries. This has been brought to attention only recently by Hassebrauk (1959).

The propagation of plant diseases through the air, which we were only able to observe through a few examples, therefore, proves to be extraordinarily effective during the bridging of short and long distances, and only a scattering across the oceans does not appear to be possible by this means. That gap was to be bridged only man with his means of transportation.

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