KONINKLIJK NEDERLANDS METEOROLOGISCH INSTITUUT

MEDEDELINGEN EN VERHANDELINGEN

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G. A. DE WEILLE

FORECASTING CROP INFECTION BY THE POTATO BLIGHT FUNGUS

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STAATSDRUKKERIJ- EN UITGEVERIJBEDRIJF / 'S-GRAVENHAGE

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A FUNDAMENTAL APPROACH TO THE ECOLOGY OF A PARASITE - HOST RELATIONSHIP

1964

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VOORWOORD

Epidemiologisch onderzoek, voorzover vallende binnen het bestek van de landbouwmeteorologie, wordt sinds vele jaren tot de activiteiten van het K.N.M.I. gerekend.

Het wordt uitgevoerd teneinde de onmisbare basis te verkrijgen waarop bepaalde waarschuwingsdiensten ten behoeve van land- en tuinbouw kunnen worden gevestigd. Een voorbeeld daarvan vormt o.a. de sinds 1927 door het K.N.M.I. verzorgde waarschuwingsdienst tegen het optreden van aardappelziekte. Van degenen die in het verleden in belangrijke mate aan de ontwikkeling in dit verband hebben bijgedragen behoren genoemd te worden Prof. dr. E. van Everdingen en Dr. ir. J. J. Post.

De onderhavige studie van Dr. ir. G. A. de Weille onderscheidt zich van die van zijn hiervoor genoemde voorgangers door een geheel nieuwe benadering. Uitgaande van het gedrag van de ziekteverwekker, *Phytophthora infestans*, onder invloed van straling, zowel in het zichtbare deel van het spectrum als in het ultraviolet, en verder van temperatuur en vochtigheid van de lucht in kunstmatige omstandigheden, werden laboratoriumuitkomsten in het vrije veld getoetst. Op grond van de verkregen resultaten kon het tot dusverre gevolgde waarschuwingssysteem, dat in feite was gebaseerd op de constatering van de kritieke aard van *waargenomen* weerssituaties, zodanig worden gewijzigd dat nu waarschuwingen kunnen worden gegeven op grond van de *verwachting* van zulk weer. Daarmede kon het waarschuwingstijdstip worden vervroegd, terwijl voor de landbouwer tevens de mogelijkheid wordt geschapen, het aantal bespuitingen te beperken.

Met erkentelijkheid zij gewag gemaakt van de medewerking welke in de aanvangsfase van het onderzoek is ondervonden van het Instituut voor Plantenziektenkundig Onderzoek te Wageningen bij enkele experimenten in een klimaatkamer van dit Instituut; voorts van de welwillende beschikbaarstelling van bijzondere ultraviolet-TL-buizen door Philips Gloeilampenfabrieken N.V. te Eindhoven.

De Bilt, 31 december 1963

De Hoofddirecteur van het
Koninklijk Nederlands Meteorologisch Instituut,
(ir. C. J. Warners)

PREFACE

Over the years epidemiological research, insofar as it lies within the scope of agrometeorology, has been considered to belong to the activities of the K.N.M.I.. It is conducted in order to provide the indispensable basis on which certain warning services operated for agricultural and horticultural purposes can be established. Inter alia the K.N.M.I.-operated warning service, in action since 1927, directed against the incidence of potato blight constitutes such an example. Among those who made considerable contributions to the earlier developments in this field mention should be made of prof. dr. E. van Everdingen and dr. J. J. Post.

The present study by dr. G. A. de Weille differs from those performed by his aforementioned predecessors by a completely new approach.

Starting from the behaviour of the causal agent of blight, *Phytophthora infestans*, as conditioned – in an artificial environment – by radiation, both in the visible and in the ultra-violet spectral region, and, in addition, by the temperature and the humidity of the air, laboratory results were tested in the field. On the basis of the results obtained the warning system hitherto applied – which, in fact, had been based on the establishment of the critical nature of *observed* weather situations – could be changed to the extent that warnings can now be issued on the ground that such weather is *expected*. The moment of issuance of a warning could thus be advanced. For the farmer this also implies that the number of spray applications is possibly reduced.

The assistance of the Instituut voor Plantenziektenkundig Onderzoek, Wageningen, experienced when carrying out, in the initial stage of research, experiments in one of this institute's climatic chambers, is acknowledged with appreciation; the help of Philips' Gloeilampenfabrieken N.V., Eindhoven, who kindly made available a number of special ultra-violet discharge tubes, is gratefully acknowledged.

De Bilt, December 31, 1963

The Director in Chief of the
Royal Neth. Meteor. Institute,
(Ir. C. J. Warners)

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CHAPTER I

GENERAL CONSIDERATIONS

1.1 Introduction

It is a deplorable but also well-known fact that, year after year, considerable losses of crop and capital are experienced as a result of the occurrence of plant diseases and pests, which constitute a continuous threat to the world's agricultural production and, by implication, to the nourishment of its population.

One of the best-known and most investigated plant diseases, which in the past gave rise to serious emergencies, is *potato blight* (in America also called late blight), a fungous disease of which the causal agent is *Phytophthora infestans* (Mont.) de By.. It is the most serious of the epidemic diseases attacking the potato crop.

Originating in America, it appeared in a serious form in Europe more than a hundred years ago. There it caused the failure of the Irish potato crop leading to the Great Famine of 1846.

In later years progress was made in the field of blight control, but nevertheless the damage the disease inflicts upon the annual potato yield is still considerable.

1.1.1 *The fungus*

Potato blight's causative fungus, *Phytophthora infestans*, belongs to the Phycomycetes, which have non-septate *hyphae* (fungal strands). The order of the Peronosporales, a smaller group within the Phycomycetes, embraces *inter alia* the downy mildews and the genus *Phytophthora* (HEALD, 48).

The disease is spread by means of small hyaline lemon-shaped vegetative spores called *conidia*, which are about 25 μ long. They are borne on branched stalks, growing out of the potato leaves, usually through the stomata, so that they appear on the lower surface of the leaves (for morphology: see MARSHALL WARD, 83). After being discharged from the stalks, which are named *conidiophores*, they constitute a more or less dense spore mass, which is wafted over the fields. One then speaks of a *spore flight* (HIRST, 57; RAEUBER & BOCHOW, 109). Most conidia fall within a few metres from their inoculum source (LIMASSET, 80; BONDE & SCHULTZ, 15; WAGGONER, 128), but in conditions favouring blight development some spores may cover greater distances, so that they may happen to alight on a potato leaf in a more distant field (HARRISON, 47; THOMAS, 117; VAN DER ZAAG, 149). If weather conditions are conducive to crop infection, that is if the foliage upon which the conidia fall remains or becomes wet during, say, more than 4 hours, the conidia can germinate, either by direct formation of a germ tube, – a thin hypha, whose pointed apex is rich in protoplasm –, or by dividing into a number of *swarm spores* or zoospores, small clumps of protoplasm which leave the conidial (now also called "sporangial") cell wall and swim about in the surrounding water droplet or water film by means of 2 *cilia*, hair-like colourless thin arms of plasm. After some time they become less motile and form germ tubes. In most cases there are 8, but sometimes even more, swarm spores per sporangium.

Consequently there are two ways of germination, *viz.* the direct and the indirect one. The indirect germination always predominates, but the proportion of direct germination increases with increasing temperature (MELHUS, 87; CROSIER, 29).

If the leaf wetness period required for germination persists, the germ tubes pierce the cuticle of the potato leaf on which they lie or enter through a stoma, thus effectuating *infection* of the crop. From this moment onward the fungus grows and ramifies in the leaf, forming a *mycelium*, an irregular network of hyphae.

After a period of 3 or more days, called the *incubation period*, the mycelium is able to send out aerial hyphae, which usually protrude through the stomata on the lower surface of the leaves. They develop into conidiophores bearing conidia. This only happens in a (nearly) saturated atmosphere.

One life cycle has now been completed and an increased number of conidia await their chance of infecting the crop. Meanwhile the diseased parts of the potato leaves become black, thus turning into typical blight leaf spots.

The above biological survey is too concise to be complete and was merely aimed at giving some information to the reader not particularly versed in botany, who is not familiar with the bionomics of fungi and the like. A more complete survey is given by ULLRICH (122).

Stated briefly, the conidia germinate and reinfect the potato crop under suitable meteorological conditions, spread the disease from blighted to healthy foliage, perpetuate its incidence during the growing season and intensify the degree of attack in diseased plantings. The latter phenomenon tends to reduce the potato yield.

Conidia falling on the ground may attack the tubers, especially those exposed to the air. At harvest time the infection danger threatening the tubers is a very real one (MURPHY & MCKAY, 94). The least we can expect after tuber infection is a depreciation of quality which, in turn, will affect the price.

The fungus hibernates in potato tubers in mycelial form (DE BARY, 4, 5, 6; BOCHOW & RÆUBER, 13). BONDE & SCHULTZ (15, 16, 17) showed that, in consequence, refuse piles perpetuate the disease, so that hygienic measures against such dangerous sources of crop infection are strongly advised (BONDE *et* *al.*, 16, 17, 18). Since diseased tubers *may* produce diseased shoots (MELHUS, 85), VAN DER ZAAG (149) was able to show that primary disease foci proceed from infected seed potatoes.

1.1.2 *Blight control*

Control of potato blight normally consists in fungicidal spray (or sometimes dust) application, either in regular rounds, so that the fungicide is applied at 7 to 10-day intervals, or more or less in accordance with spray warnings issued according to a warning system based on the occurrence of spells of weather favouring the spread of *Phytophthora.*

When spraying, the haulm is covered with the fungicidal agent, which is usually a copper and sometimes a zinc compound, which will kill any spores alighting on the plant, or their germ tubes should the arrival of the conidia have preceded spray application. Spray deposits applied after the fungus has penetrated the host tissue will be unable to prevent the incidence of disease; the fungus will then develop within the leaves as though no spray residue were present. Once within the host plant the parasite is beyond the reach of all fungicides, at least as long as there are no 'systemic' curative fungicides.

At any event fungicidal application can only be practised *preventively*, which implies that much of its success depends on correct timing.

Prior to harvesting the haulm of susceptible potato "varieties" (in fact potato *clones*) is often destroyed by mechanical or chemical means (herbicidal application), so that, when the tubers are lifted, the danger of direct tuber infection is minimized (cf. MURPHY & MCKAY, 94; WALLIN & HOYMAN, 131).

The following data will give some idea of the importance and urgency of blight control measures.

LARGE (78) found that the crop loss caused by potato blight depends on the moment at which the fungus stops the growth of the plants. Many spraying experiments carried out in England and Wales, as well as periodic liftings to determine the course of tuber development, show that in maincrops the relationship between loss of potential yield and date of stoppage of growth by blight is generally as follows (LARGE, 79):

End of July	Mid-Aug.	End of Aug.	Mid-Sept.	End of Sept.
50%	28%	13%	4%	0%

According to MORSTATT (88) average crop losses owing to *Phytophthora* amount to 5%; LARGE (79) mentions 3%. In bad blight years, such as 1916, MORSTATT (88) stated (in 1929), crop losses may even be as high as 33%. But in 1951 GÄUMANN (38) was able to state that ameliorated control measures mean that losses exceeding 20 to 30 per cent will very rarely occur. For the relative increase in crop yield that results from a successful extension of the life of the green foliage by means of chemical control measures can be considerable (LARGE, 73).

MASTENBROEK (84) assessed the average annual direct capital loss for the Netherlands (over ca. 13 000 ha) at *f* 15,000,000.–; adding *f* 5,000,000.– for the estimated control expenditures he arrived at a yearly loss of *f* 20,000,000.—, an amount which does not include the additional cost of assorting the harvested crop and the depreciation of quality. In 1956 VAN DER ZAAG (150) considered a yearly loss of *f* 40,000,000.— not improbable.

To revert to the fact that correct timing of spraying rounds is important because of the preventive character of chemical blight control, it will be clear that spraying should be carried out *prior to crop infection* and that spraying just after crop infection is too late to prevent the build-up ensuing from that infection. Although the reader will consider the above reasoning to be no more than plain logic and will agree with the author that the only way to time spray application is to base it on a system of forecasting the dates of infection, it is a striking fact that this logical train of thought is not adhered to when warning systems are being designed and warning services are established.

1.2 The significance of warning systems

The circumstance just noted gives rise to serious doubt as to the efficiency of the warning services hitherto founded. Will such services issue their warnings in time? In other words: are their warnings really *forecasts* of crop *infection* or are they issued too late? And even where a warning service is said to issue potato blight forecasts, are those forecasts really what their name would suggest them to be, or is it the visible *outbreak* of a blight epiphytotic that is presaged, the outbreak ensuing from infection? In the United Kingdom for instance, *outbreaks* of *Phytophthora* are forecast after "BEAUMONT conditions" (8) have been fulfilled, conditions whose prevalence is supposed to coincide with infection of the crop, so that at the moment a warning based upon the BEAUMONT rules is issued, weather conditions *have been* conducive to infection. Having observed the "critical period", it is not difficult to predict the coming outbreak of blight ensuing from the *noticed* infection because use is then made of the incubation period. Whether this use is justified is an item worthy of further consideration.

For the uninitiated reader some additional elucidation may be useful here.

Life cycles of *Phytophthora infestans* can only be completed if the external conditions comply with the requirements of the fungus. For sporulation a high air humidity is required, for germination and infection the presence of liquid water is necessary. This implies that infection of the crop only takes place under special weather conditions, "blight weather". Blight weather of a duration sufficiently long to allow infection is called a "critical period", which to all intents and purposes should be equal to "infection period".

One of the first workers to relate outbreaks of potato blight to preceding weather conditions was VAN EVERDINGEN (33, 34), who expressed the weather/disease relationship in the "Dutch rules", as they are called. Many workers after VAN EVERDINGEN and BEAUMONT established such criteria or modified existing ones. In this respect it may suffice to mention the "biological rules" drawn up by POST (195, 196). All these systems give criteria; as soon as these have been complied with it has to be assumed that circumstances conducive to crop infection have prevailed during so long a period that infection *has* indeed taken place. Hence the author's already mentioned scepticism with regard to warning systems "observing" critical periods, systems whose warnings may be compared with alerting the fire brigade after the house has burnt down.

If outbreaks indicated by warnings based on BEAUMONT periods (8) or related criteria occur x days after the issuance of those late warnings, we must bear in mind that the observational duration (= the lapse of time during which weather conditions have to come up to the criteria) is not negligible and amounts to y days, *i.e.* in the BEAUMONT case 2 days, in the POST case 33 hours or, say, $1\frac{1}{2}$ days. Crop infection is a matter of hours. If we assume that in an arbitrary infection period substantial crop infection takes place $\frac{1}{4}$ day after the onset of the critical conditions and if no time is lost when communicating the warning (immediately after compliance with the rules is noticed the warning is dispersed by telephone, recorded on tape and put into the automatic answering equipment giving disease warnings when the warning service's number is dialled), it will nevertheless have been issued $(y-\frac{1}{4})$ days too late.

In parts of England and France outbreak forecasts are dispersed by mail. This postcard method will involve an additional delay of 1 to $1\frac{1}{2}$ days, which will result in an increase of the arrears to $(y-\frac{1}{4}) +$ say $1\frac{1}{4}$ days $= (y+1)$ days. Since (for the purpose of predicting the first significant outbreak) the BEAUMONT rules are still applied in a part of the United Kingdom, so that $y = 2$, any warning will at least be 3 days late. The incubation period z consequently amounts to $(x+3)$ days and since in most cases $3 \leqslant z \leqslant 7$, so that $0 \leqslant x \leqslant 4$ [cf. NAUMOVA (96), in whose table of incubation periods $z = 5$ appears to have been most frequently observed], it will be understandable that the rapidity with which *Phytophthora* outbreaks follow the warnings – provided the BEAUMONT period concerned does represent a concurrent infection period – often strikes the growers. It will also be compreheded that this circumstance has resulted in a fairly well-established though not fully justified confidence in the BEAUMONT system.

In the Netherlands warnings are dispersed by radio and by telephone. Two regional telephonic disease warning services, one in the province of South-Holland and the other in Friesland, are already operative, thus eliminating possible arrears arising from the sometimes unfavourable uneven distribution of broadcasting times during the day.

Broadcasts in which blight warnings can be given take place at 5.45, 6.40 and 12.30 C.E.T.. The messages for the 12.30 broadcast are teletyped from de Bilt to Hilversum. The methodic loss of time amounts to about half an hour so that, as long as the complete POST rules were adhered to, the criteria had to be complied with by noon. A message received at, say, 12.15 will not be issued by radio the same day because of the gap between the 12.30 broadcast and the one at 5.45 next morning. As regards the 12.15 message the methodic loss of time will not be half an hour but $17\frac{1}{4}$ hours, so that the methodic loss of time m will lie between $\frac{1}{2}$ and $17\frac{1}{2}$ hours: $\frac{1}{2} \leqslant m \leqslant 17\frac{1}{2}$.

If we assume that in an arbitrary infection period substantial crop infection takes place 6 hours after the onset of the critical conditions, telephone warnings will be issued $(y - 6 + m_t)$ hours too late. If the observational duration $y = 33$ hours and if the methodic loss of time m amounts to, say, $\frac{1}{2}$ hour, then the arrears will amount to $33 - 6 + \frac{1}{2} = 27\frac{1}{2}$ hours.

In the case of radio warnings the arrears will amount to $(33 - 6 + m_r)$ hours $= (27 + m_r)$ hours, consequently varying from $27\frac{1}{2}$ to $44\frac{1}{2}$ hours.

If a warning is $1\frac{1}{2}$ days late, we get the following situation: incubation period $z = x + 1\frac{1}{2}$ days. If, again according to NAUMOVA (96), $3 \leqslant z \leqslant 7$ (at least in most cases), this implies that $1\frac{1}{2} \leqslant x \leqslant 5\frac{1}{2}$.

Although such warnings are essentially better than the corresponding British warnings, the speed with which *Phytophthora* outbreaks follow the warning, of which the POST period upon which it is based usually does represent a concurrent infection period, does not always seem to strike the layman as convincingly as do BEAUMONT type warnings which are issued very shortly before the outbreaks they announce. Though the rules of POST (105, 106) constitute a marked improvement as compared with the earlier criteria of POST & RICHEL (107), which were derived from those of BEAUMONT (7, 8), both by their shortening the observational period inherent to the warning system and by their enhanced indicatory merits, the POST system has not succeeded in winning the confidence of the farmers, who prefer to apply sprays at regular intervals or try to fix the most suitable dates for their spraying rounds by attempting to interpret the weather forecasts and by drawing conclusions after having listened to the television weather surveys.

Actually all warning systems noting critical periods with the help of rules will in principle issue late warnings. The *infection dates* should be predicted by a warning service so that the warnings, which in this case are indeed *forecasts*, are issued *previous to infection* (DE WEILLE, 143).

Meanwhile we must grant that systematically late warnings need not always be completely useless. There are some arguments in favour of them, though these are not strong.

In the first place conidia formed after the incubation period – *i.e.* the new conidial generation – may become the victims of a spray residue applied *during* that period.

Secondly, infection days do not often occur separately; they are usually grouped within spells of wet weather. Spraying in such a period – which is not always practicable since infection periods are characterized by rainfall – or between two of them, will help to reduce the intensity of attack. On the ground of these two arguments we may assume that, spraying in accordance with the classical late warnings, the onset of the epiphytotics will invariably be missed but the build-up may be partly prevented.

If this assumption is correct – and there are clear indications in that direction – we do much less than justice to the better systems by lumping them all together. For warnings based on a system with criteria involving a long observational period will be issued later and will, in consequence thereof, be less useful than warnings based on a system characterized by a shorter observational period. "Much too late" or "somewhat late": this difference may be very significant. As a matter of fact the time needed for communicating with the farmers also plays a very important part in this connexion.

Germination in particular is a slow process. Among the conidia there are early and late germinators. The maximum percentage of germination is reached after many hours (DE WEILLE, 141, 142). Late warnings may still result in the elimination of the slower germinators, the more so because it will take a germinated spore 2 or more hours to achieve successful penetration into host tissue, a phenomenon lengthening their vulnerable period.

In spite of the above arguments one is inclined to question the advantage of the better warning systems as compared with spraying rounds at regular intervals, irrespective of the weather.

The blight forecasting method developed by BOURKE (19, 21, 22, 23) already makes a better impression. The valuable work done by this meteorologist represents a purely meteorological approach to the blight problem, in which he is the undoubted pioneer. BOURKE (21) studied the conditions shown on synoptic weather maps that are suitable for blight and those hindering blight development. Since infection is the crux of blight development, the "conditions suitable for blight" which are to be forecast should in fact be the *conditions suitable for infection*. An analogous reasoning is applicable to inhibitory weather conditions. This restriction will delineate more exactly the concept of "blight weather". But in any case disease forecasts according to the BOURKE method stand a good chance of being real infection predictions. If the time needed for the dispersal of the messages is not a limiting factor those who spray in accordance with BOURKE'S forecasts stand an equally good chance of spraying effectively against potato blight.

This does not necessarily imply that the BOURKE system is beyond criticism; the author will revert to that point. But the system does not belong to the main category, which *in principle* is behindhand.

1.3 Existing warning systems

An account of potato blight "forecasting" systems which have been or are being operated in different countries and regions thereof was given by BOURKE (20), who classified them in accordance with the general weather criterion used to identify conditions favourable to the disease. He devoted an entire chapter to each of the following features:

1. abundant dew followed by dull rainy weather;
2. lengthy spells of moist conditions;
3. shorter periods of near-saturation;
4. cumulative rainfall;
5. flexible temperature-humidity-rainfall relations.

Since those interested in such surveys will find extensive information in the abovementioned paper and other publications there is not much point in describing *all* existing warning services in this article, and the author will restrict himself to a brief discussion of systems based upon fundamentally different starting points.

1.3.1 *The classical Dutch rules*

As early as 1926 VAN EVERDINGEN (33) published his findings regarding the blight warning problem. This first worker to tackle this problem found that outbreaks of potato blight occurred after the weather conditions had complied with the following rules, later usually called the Dutch rules. Four weather conditions were found to have been almost always present within the fortnight (!) preceding an outbreak, *viz.*:

1) $\geqslant$ 4 hours of dew in the course of a night;
2) minimum temperature $T_n \geqslant 10°$ C during that night;
3) mean cloudiness $\geqslant 0.8$ on the following day;
4) measurable rainfall (>0.1 mm) in the 24 hours following the dew night.

Since direct dew observations were rarely available, rule 1) was interpreted as requiring $\geqslant$ 4 hours of nocturnal temperatures below the dew point of the previous evening or the following morning.

As a substitute for rule 3) a sunshine duration (d) criterion could be applied: $d \leqslant 30\%$ (of d_x).

Screens in which dry and wet bulb temperature readings were made were mounted at a height of 40 cm in or close to potato fields.

From 1928 to 1948 the Dutch potato blight warning service made use of the above rules, which were tested in several countries: the Netherlands (VAN POETEREN, 104), Britain (WILTSHIRE, 146), France (DUFRENOY, 32), Russia (NAUMOVA, 95), Greece (ZACHOS, 151) and Germany (RÆUBER & BOCHOW, 109). The indicatory merits were considered satisfactory.

Meanwhile the disadvantages inherent in the system were found sufficient to warrant an attempt to dismiss it altogether. In the first place the rules, involving four different weather elements, were considered to be too complex. Owing to this complexity many cases occurred of "near-critical" weather, *i.e.* only 3 rules were fulfilled. This circumstance implied an uncertainty. Secondly, some people considered the operation of special observation posts (at 40 cm) as an undesirable burden. And, of course, the complex rules provided a bad basis for true forecasts. But in the years before 1948 that third drawback had not yet received so much attention.

1.3.2 *Air humidity rules*

Since conidiophores and conidia are formed in a (nearly) saturated atmosphere and since several biologists considered the humidity of the air to be the main factor responsible for the survival or death of these conidia, any decrease of the relative humidity (r.h.) invariably resulting in an accelerated loss of viability (see *i.a.* CROSIER, 29, and ORTH, 99), the air humidity gained such a predominant place in epidemiological thinking that it was bound to find expression in the majority of the rules, usually together with temperature (T).

The *units* in which the humidity factor is expressed are usually percentages of relative humidity of the air (% r.h.). POST (105) made use of the concept "dew point difference" (d.p.d.), which simply is the difference between the temperature T and the dew point T_d, measured simultaneously, so that d.p.d. $= T - T_d$. He did so because he used the synoptic humidity data, which are not given in % r.h. but are teletyped in the form of dew point measurements.

The *height* of r.h. observation varies. VAN EVERDINGEN introduced measurements at a height of 40 cm (in an otherwise normal screen). Following this example, BEAUMONT (8) measured the air humidity in a screen placed at ground level (among the potatoes) in order to correspond as closely as possible to the conditions among the potato plants.

Meanwhile a screen still constitutes an unnatural element. If one really wishes to measure the r.h. in the crop, hygrographs should be placed on the ground between two rows of potato plants. When comparing the r.h. in a standard louvred screen, 1½ m above ground, with measurements in the crops, level with the tops of the potato ridges, the humidity in the ecoclimate, *i.e.* the environment in which the processes of sporulation, germination and infection occur, appears to differ from that measured in the screen. Fig. 1, representing the results of measurements taken by HIRST (57) during the potato growing season of 1951, reveals how the growing crop gradually modifies its environment to one that favours the disease. The left-hand set of graphs shows T and r.h. in the week when, at Rothamsted, the emergence of plants was completed. The second set, from complete emergence to blight outbreak, covers the period during which a full canopy of foliage was established. The stratum of very humid air within the crop becomes pronounced (in the third set of graphs) owing to heavy rain that occurred early in August. By the 1st of September, 1951, half the foliage had been destroyed by blight. The last set of curves, for the period until the remaining foliage was destroyed, shows a tendency to revert to the relationship found at the beginning of the season, since the foliage no longer intercepts radiation or obstructs ventilation, thus enabling the soil to dry again more quickly.

The above findings of HIRST (57) demonstrate that there is certainly no justification for transforming screen data into crop data simply by means of a single term such as practised by VAN DOORN for onion crops (31), a much more "open" soil cover. For the purpose of warnings against downy mildew in onions (*Peronospora destructor*), a disease akin and similar to *Phytophthora*, VAN DOORN compared r.h. measurements at 10 cm and at 2.20 m and found that the difference amounted to *about* 5 %. In potato crops POST & RICHEL (107) found that *on an average* the 24-hours' mean of r.h. measured at a height of 40 cm exceeds that observed at 2.20 m by *about* 3 %. But "in" potato crops here means: in a screen placed in the way VAN EVERDINGEN (33, 34) did it. The differences between standard screen observations of r.h. and those taken between the rows (so in the way HIRST (57) did it) were generally found by the author to exceed 5 % except under conditions of prolonged drizzle, fog or more or less continuous rainfall. UHLIG (120) also investigated the relationship between

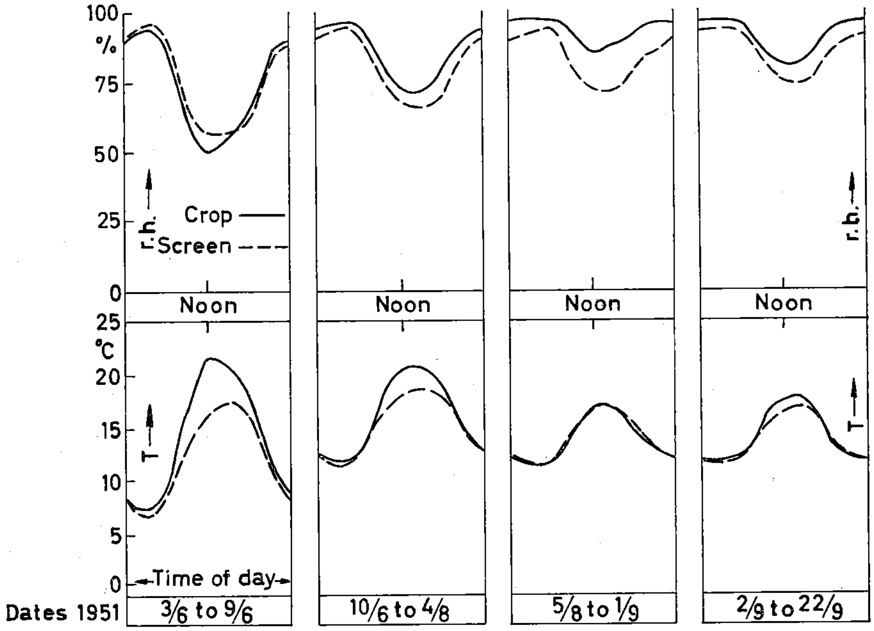

Fig. 1. Diurnal variation of T and r.h. during 4 development phases of the crop according to HIRST (57). See text.

screen measurements (at 2 m) and measurement in the crop. He states that if an r.h. of 95 % is to prevail in the crop, an r.h. of 88 % or a d.p.d. ⩽ 2° C has to be measured in the screen. He adds that during a blight period the minimum temperature T_n in the crop is 2° C lower than the T_n observed in the screen at 2 m. UHLIG (120), POST & RICHEL (107) and HIRST (57) all come to their conclusions by making use of data averaged in one way or another.

Again, there is the question of the value of averaged data, *e.g.* averaged humidity data, which are not valid for the situation from moment to moment. Momentanous situations will often contradict the relations existing between *means* of r.h.. The biological significance of these means is contested by the author (see p. 84); moreover the physical meaning of an averaged r.h. is doubtful.

It is biologically significant that the periods of high humidity (r.h. ⩾ 90 %) in the crop are longer than screen recordings indicate (see chapter III), at least from mid-June onward, when blight makes its appearance, this being the moment when the measurements are started in the K.N.M.I. experimental fields. This tallies with the experience of HIRST & STEDMAN (58), who state that in the drier summers measurements in crops forecast outbreaks more reliably than in screens, though they wrote: "The differences between crop and screen warnings are considerable, but smaller than might have been expected." (cf. HIRST & STEDMAN, 59). A corresponding experience induced POST & RICHEL (107) to return to routine screen observations in order to avoid special agrometeorological field practices and to profit by the usual synoptic messages that are received each day just the same.

The BEAUMONT rules (8) are as follows: the critical period preceding the *first* outbreak of blight is defined by the following criteria:

$$\left.\begin{array}{l}1)\ \text{r.h.} \geqslant 75\,\%\\ 2)\ T_n \geqslant 10^\circ\,\text{C}\end{array}\right\}\ \text{for a continuous period equal to or longer than 48 h. (w} \geqslant 48\ \text{h.).}$$

If the required conditions are interrupted for not more than 1 hour per day during period w a "near-critical period" is spoken of, a concept introduced for the sake of elasticity in applying the system.

Since BEAUMONT (6) says his critical periods precede the first outbreak of potato blight by 7 to 25 days, whereas the incubation time is much less than 25 days, one may wonder, with GRAINGER (45), how there can be any consistent relation between the subsequent occurrence of BEAUMONT periods and the rate of blight development. Yet LARGE (77), working with normal screen data, considers warnings from synoptic stations to provide valuable guidance in forecasting regional blight *outbreaks*.

From 1949–1958 a variate of the BEAUMONT system was operated in the Netherlands. The criteria, based upon standard screen observations expressed in terms of the average of only 3 observations per day, had been adapted to synoptic practices by POST & RICHEL (107). The modified criteria were:

1) 2 consecutive days on which the mean r.h. does not fall below 82 % on one day and below 79 % on the other, irrespective of the order in which these 2 days occur. The mean relative humidity ($\overline{\text{r.h.}}$) is the average of readings made at 8, 14 and 19 hours C.E.T..
2) $T_n \geqslant 10°$ C.

In short we can note:

either	1) $\overline{\text{r.h.}} \geqslant 82\,\%\,(w_1 = 24\text{ h})$	or	1) $\overline{\text{r.h.}} \geqslant 79\,\%\,(w_1 = 24)\text{ h}$
	2) $\overline{\text{r.h.}} \geqslant 79\,\%\,(w_2 = 24\text{ h})$		2) $\overline{\text{r.h.}} \geqslant 82\,\%\,(w_2 = 24\text{ h})$
	———— +		———— +
	3) $T_n \geqslant 10°\text{C}(w = 48\text{ h})$		3) $T_n \geqslant 10°\text{C}(w = 48\text{ h})$.

Not all BEAUMONT periods are followed by an epidemic (POST and RICHEL, 107; LARGE, 75, 76, 77); LARGE (77) then speaks of non-valid warnings. From a biological point of view we can hardly expect anything else. Under 90 % r.h. no sporulation can take place; nor can we expect germination or infection since those two phenomena require the presence of liquid water on the leafage during some hours, which is not consistent with an air humidity of less than 90 per cent. It therefore follows logically that as soon as the 75 % humidity criterion is replaced by a 90 % one the then modified rules will suddenly gain a much higher indicatory value.

Using an entirely empirical approach, the meteorologist SMITH (114) tried out a 90 % humidity rule. He felt that, instead of avoiding humidities under 75 per cent, there was more to be gained by taking the duration of really high humidities into account.

The rules of SMITH (114) are:

1) 2 days, each with at least an 11 h. duration of r.h. ≥ 90 %;
2) $T_n \geqslant 10°$ C (50° F).

SMITH (114) found that 29 out of 43 failures by the BEAUMONT system, forming part of a total of 220 forecasts from different stations quoted by LARGE (75, 77), would have been replaced by valid forecasts had the 90 % criteria been used. Thus the proportion of failures would have been reduced from 20 % to about 10 %. Meanwhile the observational period w still amounts to 48 hours, which, in fact, is too long. In Belgium JAIVENOIS (65) reduced w to 18 hours.

In Ireland BOURKE (19) developed his "Irish rules", according to which the minimum humid period favouring the spread of potato blight consists of

$$\left.\begin{array}{l}1)\ \text{r.h.} \geqslant 90\,\% \\ \\ 2)\ T_n \geqslant 10°\text{ C}\end{array}\right\}\left\{\begin{array}{l}w = 12\text{ h: if the foliage is likely to remain wet for a subsequent}\\ \qquad\qquad\ \text{spell of 4 h. (}\textit{e.g.}\text{ if there is any rain).}\\ w = 16\text{ h: otherwise.}\end{array}\right.$$

A "blight weather spell" is regarded as terminated as soon as a single hourly observation occurs in which the criteria are not met. There are blight weather spells with an effective duration of 1 hour (the minimum duration still entitling a period to bear that name), 2 hours *etc.*.

At the Irish Central Forecast Office the effective duration of a spell as recorded at the different stations is marked on a map. The responsible factor in the current weather situation is determined by examining the synoptic charts. As a result of this examination the probable geographical limits of a favourable spell are entered on the map (BOURKE, 20).

Warnings are issued when significant spells of blight weather have taken place and are liable to recur.

According to BOURKE (20) the Irish rules are not intended to define critical conditions whose occurrence in itself constitutes a warning of the disease. Unlike the rules dealt with earlier, they were intended to *detect* every progressive favourable spell however slight, the importance of the spells being assessed by their duration.

With the work of BOURKE (19, 20, 21, 22, 23) we have arrived, as it were, at the borderland of crop infection forecasts, or real forecasts. The use of current synoptic charts to determine the cause and the probable limits of favourable weather differs fundamentally from the adherence to rules on which the classical warning systems are based. Air mass analysis has proved to be a useful part of this procedure.

As suitable for blight BOURKE (21) mentions:

1) open warm sectors of maritime tropical air, particularly where a sequence of waves is involved;
2) stagnant or slow-moving depressions, giving lengthy periods of wet, overcast weather; and
3) active, quasi-stationary fronts giving similar weather.

All specifications are coupled with a minimum temperature of not less than 10° C, an obvious heirloom of VAN EVERDINGEN (33, 34), also represented in the BEAUMONT conditions (8).

As conditions hindering blight development BOURKE (21) mentions:

4) anticyclonic or ridge conditions accompanied by dry, sunny weather;
5) direct break-throughs of northerly currents of cold air following depressions.

BOURKE (20) states that "the regular determination and analysis of the synoptic causes of weather spells favourable to potato blight also facilitates the forecasting of such spells, and indeed warnings are not normally issued in Ireland unless further periods of favourable weather within 3–8 days can be forecast."

This would imply that in a series of blight inducing weather situations, which are no farther apart than 8 days, the first one would merely be noted while the following ones would actually be forecast.

BOURKE (19), as we saw, takes account of the occurrence of rain. The biological condition that connects infection with the temporary presence of liquid water – a leaf wetness period – indeed stresses the importance of precipitation.

A worker who wished to take advantage of biological knowledge, UHLIG (120, 121), made an attempt to take into account the duration of sporulation and germination in his criteria when composing his "Bestandsfeuchteregel". For standard screen observations the criteria are as follows.

If no rain has occurred:		Linked up with preceding rainfall:	
1) r.h. $> 88\,\%$ or d.p.d. $\leqslant 2°$ C	$\Big\}$ w $= 15$ h.	1)	$\Big\}$ id.; w $\geqslant 11$ h.
2) $12°\text{ C} \leqslant T_n \leqslant 16°\text{ C}$		2)	
3) $T_x \geqslant 20°$ C; $w' = w + 12\text{ h} = 37$ h.		3) id.; $w' = w + 12\text{ h} = 33$ h.	

So during a humid period the minimum temperature has to lie within the interval 12–16° C; in this period or in the following 12 hours T should reach or surpass the level of 20° C. The lower T secures a substantial degree of swarm spore formation; the higher T causes germ tubes already penetrated into leaf tissue to continue their growth inside the leaf (UHLIG, 120).

UHLIG (120) takes the line that, if the 15 hours' humidity rule is complied with, the last 5 hours of the humid period will be characterized by leaf wetness caused by dew deposition. These 6 hours can serve for infection by conidia formed in the 10 preceding hours. After rainfall the following period of high air humidity will prevent the foliage from drying.

Like BOURKE (20), UHLIG (129) makes use of codified synoptic data and geographical maps. The reader interested in the results of UHLIG's test warning service (in W. Germany) is referred to the latter's relevant publication (120), which, although of undoubted importance, cannot be discussed in detail here.

In Norway the results obtained with the BEAUMONT rules (8) were so unsatisfactory that a perhaps somewhat rashly set up warning service was abolished. New criteria which included *rainfall* data were therefore tried out (FÖRSUND & FLAATTEN, 36, 37). In fact a rainfall criterion derived from the COOK rule (27) was *added* to the classic BEAUMONT rules. FÖRSUND & FLAATTEN (36) found that in the years 1952–1954 the effectiveness of the warnings was 75 % as against 67 % had the BEAUMONT rules been applied and stated the 25 % omitted to apply to minor outbreaks, but they were aware of the disadvantage inherent in their system, *viz.* that the warnings reach the growers *too late.* When warnings were to be resumed, FÖRSUND & FLAATTEN felt that applying a T/r.h. rule "would have made the service unpopular for a second time" (36) and decided to start experimental *predictions* in as many cases as they could manage by making use of specially formulated 3-day weather forecasts. The situation is considered to be critical when the 3-days' weather forecast indicates that the conditions will be fulfilled within the pentade comprising the period covered by the forecast.

As important weather situations favouring blight incidence they mention (36, 37):

1) quasi-stationary depressions and fronts over the North Sea and the S. Norwegian area.
2) warm sectors with humid air over the country,
3) transport of maritime humid and unstable air from the west,
4) fog.

An example of a warning system in the U.S.A. is that of Wallin & Hoyman (131). The criteria are

$$\left.\begin{array}{l}1)\ \text{r.h.} \geqslant 90\%\\ 2)\ T_x \leqslant 21^\circ\text{ C } (75^\circ\text{ F})\end{array}\right\}\ w = 10\text{ h.}$$

The hygrothermographs used for the system's operation are exposed in wooden shelters staked 37 cm from the soil surface. Some weeks after they have been placed in the field the foliage canopy closes around the shelter.

The hygrometric charts are studied in conjunction with the U.S. Weather Bureau's 5-day forecasts for formulating a weekly blight prediction.

Post's biological rules (105, 106) also belong to the air humidity systems. They will be dealt with later on (see pp. 22–24).

1.3.3 *Rules comprising rainfall criteria*

The oldest system in the field of plant disease forecasting, the one designed by van Everdingen (33, 34), required "measurable rainfall" (see p. 8). But his "Dutch rules" were complicated; hence the development of the simpler T/r.h.-rules. Perhaps the existence of weekly recording thermohygrographs has advanced the omission of rainfall data for simplicity's sake. But simplicity is no merit if it is obtained to the detriment of accuracy. Beaumont conditions *can* be fulfilled without a leaf being wet, so without the slightest trace of infection. Clayson & Robertson (26) noticed that on the one hand blight development may be found under humidity conditions rather less than those required to satisfy the Beaumont criteria, but that on the other hand the importance of showery weather allowing the build-up of spore inoculum must be emphasized. Thurston *et al.* (119) and de Weille (143) likewise stress the significance of precipitation. It will therefore be understood that to workers like Bourke (19) and Uhlig (121) it makes some difference whether rain (or dew precipitation) occurs or not.

Since the occurrence of a leaf wetness period is an imperative requirement for crop infection to take place, rainfall criteria were bound to reappear in the rules. Hyre (61) could prove that, when comparing a rainfall/temperature criterion with temperature/humidity criteria applied irrespective of precipitation, the closest relationship with blight development occurred when applying the rainfall rule. A T/r.h. rule "was least accurate when rainfall was deficient". Glærum (40) also emphasized the significance of precipitation for blight development.

In France and Canada use is made of flexible temperature-humidity-rainfall (rf.) relations (see BOURKE, 20), whereas in East Germany RÆUBER & BOCHOW (67) advocate the VAN EVERDINGEN rules.

In the U.S.A. special attention has been paid to the *amount of rainfall.*

A method introduced by COOK (27) and applied by NUGENT (97), the *cumulative rainfall method,* is concerned with a region in which in more than 50 per cent of the years potato blight is not important enough to make chemical control measures necessary (Virginia, U.S.A.). Consequently the major object is to determine the probability of destructive blight development during the growing season in order to be able to advise the farmers whether to take control measures or not.

The conditions to be met simultaneously are

$$\left.\begin{array}{l}1)\ \overline{T} \leqslant 21^\circ\text{ C }(75^\circ\text{ F})\\ 2)\ \text{cumulative rainfall exceeding a critical amount}\end{array}\right\}\text{w} \geqslant 2\text{ weeks}$$

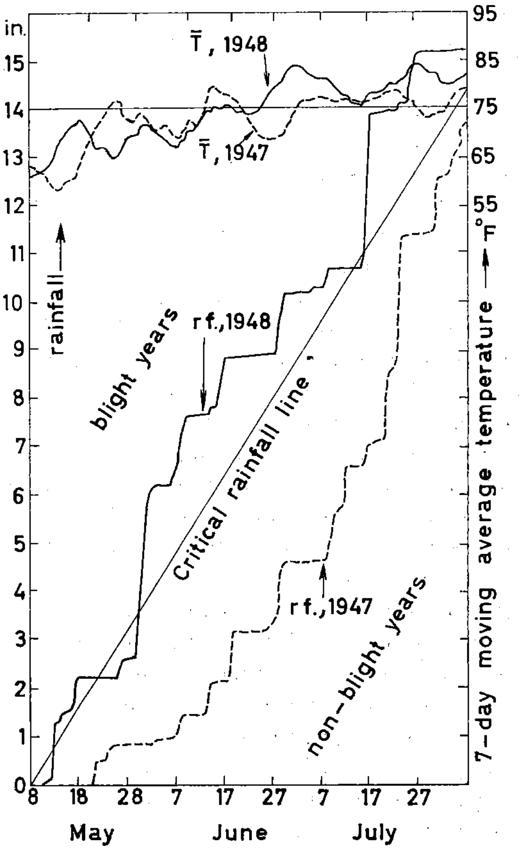

Fig. 2
After NUGENT (97). For explanation: see p. 16–17.

$\overline{T}$ = running 7-day mean of average daily temperatures. Cumulative rainfall is calculated from a date prior to the earliest recorded blight attacks in the area in question. At least 2 consecutive weeks of favourable weather are considered necessary for a serious outbreak to develop.

Fig. 2 shows the "critical rainfall line", the straight line dividing the chart into the sections of non-critical rainfall as recorded in earlier years in which the disease was not important and of critical rainfall, measured in years in which considerable damage was done.

Fig. 2 shows that weather conditions were consistently unfavourable for the spread of the disease in 1947, but that in 1948 cumulative rainfall was soon above the critical rf. line. The 7-day mean temperatures ($\overline{T}$) ranged between 64° and 73° F. Since on May 17 more rain was forecast for the next few days a warning was issued on that date. Chemical disease control was recommended until hot and/or dry weather, eliminating the threat of blight, should occur. A similar warning was issued on June 1, and NUGENT (97) stated that control measures were to be continued. A third message of this type was issued on June 9. It stated that with the prevailing moisture supply (!) only $\overline{T} > 75°$ F could check blight development. By June 11 this happened and NUGENT (97) wrote: "These temperatures checked the blight enough to prevent a serious general epiphytotic such as occurred in 1946."

The author is of the opinion that, in principle, the starting point of the COOK method is erroneous. Taking the line that the main environmental factors governing the spread of *Phytophthora* are high air humidity followed by a leaf wetness period, it should be clear that it is the *duration* rather than the amount of precipitation linked with leaf wetness that counts. When and where the cumulative rf. method is successful or effective (HYRE & HORSFALL, 64) such must be due to a regional close relationship between amount and duration of rainfall. Systems like COOK's are therefore of regional value and cannot be exported to regions with a slightly different climate. Tests by WALLIN & SAMSON (134) over a 37-year period indeed showed that (in Indiana) the effectiveness of warnings would not have been convincing had the COOK system been applied. They added that "these results suggest that other information in addition to rainfall and weekly mean temperature data is needed to predict effectively the development of the late blight pathogen."

In HYRE's opinion (62) some forecast failures are attributable to the use of *cumulative* rainfall; sometimes early-season rainfall is so deficient or excessive as to determine in itself the character of the c.rf. curves for the entire growing season. He therefore proposed a modified method which is stated to be highly accurate (92 per cent effectiveness) (HYRE & BONDE, 63).

This method's main feature is the *moving rainfall-total.* The rainfall plotted for any particular day represents the total for the k-day period ending that day.

Critical are according to HYRE & BONDE (63): temperature below 25° C (77° F) and as regards rainfall:

10 consecutive days with a 10-day mean of 1.05 inches or }
8 consecutive days with a 8-day mean of 1.21 inches or } Northern Maine

10 consecutive days with a 10-day mean of 1.21 inches: Connecticut.

1.4 The zero-date

At the beginning of the growing season the amount of blight inoculum present is not great. The fungus has perennated in diseased tubers in mycelial form (DE BARY, 4, 5, 6). The rare oospores have no significance for the overwintering of blight (PETERSON, 102). After planting part of the blighted seed potatoes will not emerge (MELHUS, 87); other tubers produce only healthy shoots (cf. PETHYBRIDGE, 103) – probably because of the fungus' killing the vegetation points – but in any case mycelium in infected tubers may not only spread into very young shoots but also to above-ground shoots (MELHUS, 85), so that a small minority of the blighted seed potatoes planted – and the blighted seed potatoes already make up a small minority in themselves in proportion to the total number of tubers planted – will produce sporing infected shoots. HIRST (55) obtained 2 diseased plants (0.8 %) from 246 blighted seed tubers; VAN DER ZAAG (149) got 5 such plants (4.4 %) from 297 infected tubers.

The small amount of infective sporal material available for the spread of blight early in the season is not usually important enough to justify large-scale control measures when the first critical period is recorded. After all the menace the grower has to cope with must be worth while. In this connexion the first warning (or forecast) of the year is justifiable if it is conditional on the incidence of a certain minimum amount of viable inoculum (BOCHOW, 12). That will be the case after a period of incipient build-up emanating from primary sources of infection (= the blighted shoots emerged from infected tubers), giving rise to initial inoculum foci of dangerous dimensions.

Starting from this point of view it is actually the development of the fungus that ought to determine the moment at which first critical period should be announced (VAN DER ZAAG, 149; HIEBEL, 51). The author is even of the opinion that, in principle, the development of the fungus ought to be determinant for any application of blight control measures throughout the whole of the blight season.

During the years 1960 and 1961 the author made daily biological observations in test fields situated at de Bilt and Bennekom. Sporing halved potatoes, the secant plane densely grown with conidiophores bearing conidia, were placed in the field on top of a small pole (Fig. 3) by means of a headless nail. The sporing plane, directed to the ground, was situated just above the foliage of the crop. Unless weather conditions clearly excluded the possibility of crop infection the halved tubers were replaced daily by fresh ones originating from the culture maintained at the agricultural laboratory of the K.N.M.I.. Though the artificial inoculum

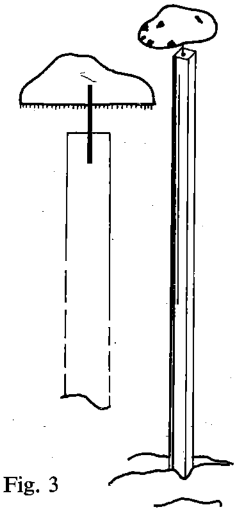

Fig. 3

source was gradually placed somewhat higher in accordance with the development of the crop the location of the stake remained the same. After the foliage canopy had closed, the haulm was allowed to outgrow the height of the sporing tuber.

When available, small bottles containing sporing potato leaves which had been artificially infected in the laboratory either took the place of the tubers or were inserted into the crop together with the latter but invariably at one and the same spot.

After some time, and of course under conditions favouring the spread of blight, one or two diseased leaflets were found next to the artificial inoculum source. The initial natural disease focus had come into being.

Before the stage at which spraying becomes economically justified could be reached, a considerable build-up of spore inoculum around the primary focus had to take place (cf. CLAYSON & ROBERTSON, 26, and ULLRICH, 124). The author found that after the successive development of 3 *consecutive generations of conidia*, belonging to 3 consecutive waves of infection, disease incidence *in the trial field* had become general. One more generation ensuing, these three would cause the blight outbreak LARGE (75) defined as "blight at the 0.1 per cent stage", a stage he considered significant for the purpose of the economic timing of spraying (74, 75) (cf. BJÖRLING, 9).

The author's findings are in fairly close agreement with those of CLAYSON & ROBERTSON (26), which are reflected in Fig. 4. As shown in Fig. 5, they noticed, in a completely naturally infected field, the first conidial generation one infection period after the 4th generation following on the appearance of the initial focus in the trial field in which infection had been effectuated as early as possible.

This substantiates the author's view that test fields inoculated in the most perfect way so that they *will* belong to the (few?) fields per region comprising primary foci may be used in order to determine the "0-date", after which spraying in meteorologically dangerous conditions is advisable. CLAYSON & ROBERTSON (26) showed that epidemic development which started in the few fields with foci was responsible for the blanket infection of a whole area. No blight warnings should be given before the 0-date. This realizes VAN DER ZAAG's (149) ideal that the development of the fungus ought to be the signal for starting the control practices. Extensive trials for the purpose of investigating the practicability of a biological determination of the 0-date were planned for 1962 and the following years. Three "focal" fields are planted with artificially blighted tubers and six spraying-experiments in which the new method is tested in comparison with other systems are now conducted each year.

MÜLLER & HAIGH (91) state that 5 generations of *Phytophthora* are needed to effectuate the build-up causing infection of larger areas; MÜLLER & MUNRO

(92) mention 4 to 6 generations. OORT (98) states that the frequency of primary foci in susceptible earlies in the Netherlands amounts to one per km^2 (= sq.km). After 5 to 6 spells of weather conducive to blight development a primary focus will have infected 1 km^2. After the incipient generations have built up (cf. ULLRICH, 124) the potentially dangerous inoculum mass, developments become *explosive.*

HIRST (57) calls the period between the appearance of the first diseased shoot and the recognition of the first epidemic the period of *cryptic spread,* this period ending with an abrupt change from local to distant infection (cf. WAGGONER, 128).

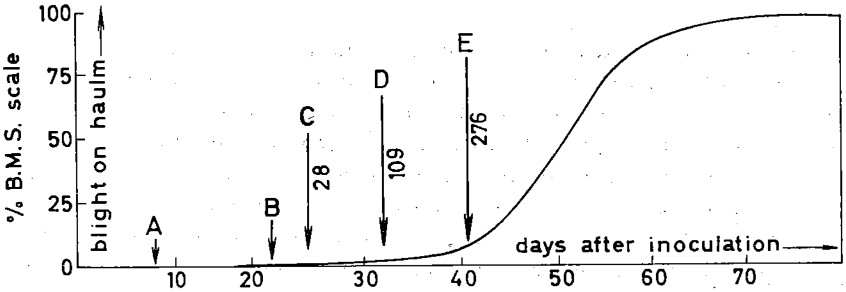

Fig. 4

Plot with artificial infector. At moment A: 1st lesions sporing. B: stem lesions sporing. C: 28 plants infected. D: 109 plants infected. E: 276 plants infected. After CLAYSON & ROBERTSON (26). "B.M.S. scale" applies to a grading system for estimating blight incidence (Anon., 2).

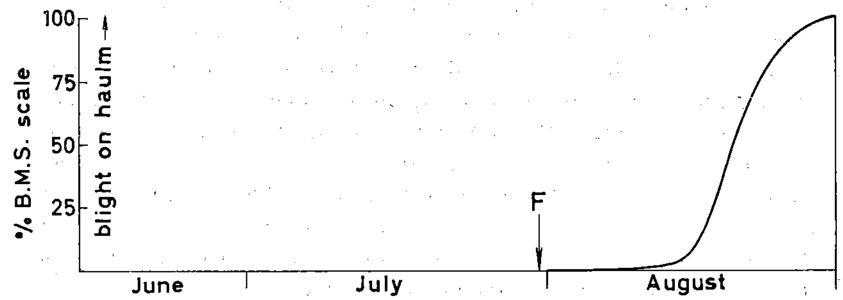

Fig. 5

Field without primary foci. At moment F: first 2 lesions found. After CLAYSON & ROBERTSON (26).

An epidemically significant amount of inoculum is not yet observed before June (GÄUMANN, 38), so that up to the end of that month the spread of blight is of local concern (HIRST, 55). It could be shown that the water in the soil may play a significant part in the local cryptic spread of blight inoculum (HIRST & STEDMAN, 60).

In fact, the 0-date hitherto dealt with is the one bearing upon the early susceptible "varieties". Maincrop and late varieties are infected by the earlies. In consequence thereof their 0-date can be chosen later than that of the earlies.

This induced the author to combine his focal field at de Bilt with strips planted with an early, a maincrop and a late fairly susceptible variety in order to study the spread of *Phytophthora* in the three plots.

In the method still applied in the Netherlands the difficulty of differentiating between earlier and later clones does not arise.

Shortly before the rows close together a message is broadcast in which a first spray application is advised in the early susceptible "varieties", irrespective of the amount of inoculum and irrespective of the weather conditions. This message is issued independently of the work done by the K.N.M.I. and is based upon the knowledge that the canopy's closing together usually prefaces the period in which appreciable blight development occurs and upon the argument that as long as the haulms have not yet closed together a fungicidal agent can still reach the lowest leaves; later on they can no longer be reached by the sprays applied.

But in most years this simple reasoning does not hold because in the first place more than 2 weeks will usually elapse before the onset of blight development. In those 2 weeks the spray deposit will have been washed off by rain water.

Secondly, climatic conditions in the lowest layer of the crop are extreme. This layer is a very humid stratum in which the lowest leaves get lost all the same, sprayed or unsprayed. Cryptic spread of potato blight in the lowest regions cannot be checked.

In the third place the lowest leaves do not contribute greatly to the plant's prosperity because their contribution to its total assimilation is not very substantial, a fact due to their age and to the circumstance that most radiation has been intercepted there (GEIGER, 39).

And finally, if it is so important that the lowest leaves be reached by copper, why not rely on the copper dripping off the higher leaves? In this connexion GOOSSEN & EUE (42) state that the loss of fungicidal substance owing to weathering is especially marked on the upper leaf surface. The rain water washes part of this substance onto the lowermost leaves (GOOSSEN, 41).

Assessing the 0-date according to the macrophenological criterion causes spray application to start too early in most years, so that sometimes the first warning issued on meteorological grounds – the second of the series of broadcast warnings – might also have been dispensed with. By ameliorating the procedures 1 or 2 spraying rounds could be saved by applying later 0-dates.

RÆUBER & BOCHOW (109) speak of an "elastic 0-date". They propose to adopt the emergence of the earlies as a phenological criterion for determining the 0-date, which would be reached 32 days after emergence. From this 0-date onwards compliance with the VAN EVERDINGEN rules were to be considered a valid basis for warnings.

GRAINGER (45) determines his 0-date on the ground of the "qualitative disease potential" which, in his opinion, is consistently related to the C_p/R_s-ratio of the potato plants. C_p = total weight of carbohydrate in the whole plant. R_s = residual dry weight of the shoots. The disease potential (*i.e.* the relative ability of a host plant to contract disease) (GRAINGER, 44) is high when the C_p/R_s is high and low when that ratio is also low. Before the onset of blight development in the course of July, when C_p/R_s begins to increase and, in consequence thereof, the "qualitative disease potential" also increases, there is a period of more than a month, characterized by an extremely low C_p/R_s-ratio, which forms a physiological barrier, so that in that period of approximately one month the host will not contract the disease; natural inoculation is more or less ineffective and no blight lesions develop on stems or leaves. The dates at which this period begins and ends differ from year to year, depending on the course of the C_p/R_s-ratio. The date at which the insusceptible period ends is regarded as "zero-time" by GRAINGER (45). From that moment onwards critical weather conditions will favour the occurrence of blight epidemics.

GRÜMMER (46) published other, but basically related 0-date criteria which find expression in the tuber weight per plant.

The views of GRAINGER and GRÜMMER are contested by some other workers, but it will nevertheless be clear that if *Phytophthora* is given the opportunity to determine the 0-time itself justice will be done to *all* external and internal factors involved in the epidemiology of blight.

1.5 Progress in handling an existing warning system

The author's criticism with regard to the usual blight warning systems, *viz.* that they provide late warnings, is not his personal monopoly. FÖRSUND & FLAATTEN (37) had already started the development of a technique for *forecasting* the fulfilment of their rules. In 1951 POST & RICHEL (108) stated that the possibilities of forecasting "some days before" the fulfilment of their criteria were still under investigation.

In connexion with the work of VAN DER ZAAG (149), who paid much attention to the spread of *Phytophthora* during the season, POST (105, 106) made *daily* observations of blight development. Making daily observations can be considered a merit in itself (DE WEILLE, 144), but the "biological rules" published as a result of these observations had, in spite of their name, been determined statistically like the rules of BEAUMONT (8) and other epidemiologists. The POST rules observed or *took note of* critical periods, so that the real merit of their designer should not be sought in his criteria but in his efforts to fix the classical disease warnings at earlier times. This means that they are issued when *part* of the rules have been complied with and it can be *expected* that the remainder of the conditions will also be fulfilled. In this way the issue of disease warnings takes place before the rules have been completely fulfilled.

Since this procedure has been practised in the Netherlands (from 1959 to 1961), the POST system (106) may serve as an example of the progress that can be achieved in the application of an already existing warning system. This method brings us into the borderland of real infection forecast work, which is the author's ultimate objective.

The criteria appertaining to the POST system are:

1) 6 out of 7 successive 3-hourly observations of T and T_d must show a d.p.d. $\leqslant 4^\circ$ C. In the field, POST (105) states, this roughly implies an r.h $> 75\%$ (in the standard screen); a d.p.d. $\leqslant 3^\circ$ C implies an r.h. $> 80\%$.
2) The 18-hour period mentioned should be followed by 5 additional consecutive 3-hourly observations showing a d.p.d. $\leqslant 3^\circ$ C. POST (106) communicated that the full period [1) + 2)] will include 2 nights.
3) During the second night T_n should be $\geqslant 8^\circ$ C.

Summarizing:

1) 6 out of 7 $\times$ d.p.d. $\leqslant 4^\circ$ C; $w_1 = 18$ h.

$$\begin{array}{ll} 2) & \left.\begin{array}{r} 5 \times \text{d.p.d.} \leqslant 3^\circ \text{ C} \\ T_n \geqslant 8^\circ \text{ C} \end{array}\right\} w_2 = 15 \text{ h.} \\ 3) & \end{array}$$

$$\overline{\qquad\qquad} + \\ w = 33 \text{ h.}$$

As mentioned in the foregoing, an observational period of 33 hours implies that the epidemical developments will precede the issue of a warning directed against them.

In practice the warning service soon began to issue warnings as soon as condition 1) had been met and the prospect of compliance with 2) and 3) pointed in the direction of an epiphytotic. Thus w was reduced to 18 hours. Thus modified, the POST system became the basis of the two regional telephonic warning services.

On page 6 we saw that complete adherence to the rules with their observational period of 33 hours would result in arrears of 27½ hours in the telephone warnings. Reducing w to 18 hours has meant a corresponding reduction of the arrears to 12½ hours.

In the radio service the arrears (with respect to the fact of infection assumed to have taken place 6 hours after the commencement of the critical period), which formerly varied from 27½ to 44½ hours (p. 6), were reduced to 12½–19½ h.

Of course the last word in disease forecasting had not been spoken by POST, whose warnings were not yet the really timely ones strained after and whose observational period (w) still exceeded the one appertaining to the Irish rules and the rules of WALLIN & HOYMAN (131). But the improved way of manipulating the criteria has to be considered an important step in the direction of true infection forecasts; until 1959 w had been 48 h., in 1959 it became 33 h., and in 1960 18 h.; in 1961 further improvement was made, this time as a result of the fundamental research described in this treatise.

On re-reading the defence of late warning systems on pp. 6 & 7 it becomes clear that the arguments brought forward there are especially applicable to the 18-hour POST method. Comparative disease control tests, conducted by the Plant Protection Service substantiate the arguments in favour of POST (105, 106). It was shown that spraying immediately after (telephonic) warnings issued in accordance with the *modified* POST system provides a degree of protection equalling that given by spray application in 10-day rounds. Application of the warning system involves some economization by reducing the number of rounds.

Yet the ideal of eliminating w and *preventing* infection even on the very first day of critical spells of weather had not yet been attained.

In addition the system – not unlike other similar systems – takes no account of the potential infection danger inherent in the *germinative power* of the inoculum. Moreover, the additional condition $T_n \geqslant 8°$ C is a remarkable feature which is more or less alien to the biology of *Phytophthora infestans*; it is attributable to the statistical way of determining the criteria.

1.6 The approach to the problem

If some pest or disease regularly threatens some crop – to put it in the most general way – and one wishes to arrive at an alarm system in the interests of crop protection in order to time control measures as perfectly as possible, how can that problem best be tackled? What kind of approach should be made? There are conflicting opinions as regards the answer to this question.

The easiest approach to the problem of designing a warning system is secured by establishing a relationship between weather conditions and attacks by pests and diseases according to the *empirical procedure*: an association is sought between data derived from plant disease or pest surveys in a particular area and some weather factor(s) thought to correspond in some way or other with the epidemics reported in the agricultural surveys.

This was the line along which ORTON (101) and VAN EVERDINGEN (33, 34) came to grips with the potato blight problem. In 1924 LÖHNIS (82) published data on initial blight attacks in the Netherlands in the five years from 1919 to 1923, confessing that she was still unable to discover a definite link with weather elements. VAN EVERDINGEN re-examined the data with the deftness of a skilled meteorologist, published his rules and, in 1928, put the spray warning service into operation. Thus, without the potatoes having been as much as glanced at, an alarm system was devised from behind the desk. Armed with a certain amount of knowledge concerning the environmental factors favouring blight, criteria were determined more or less *statistically*.

Honour is due to VAN EVERDINGEN for his initiative, for his pioneer work in blight forecasting and for his sound meteorological thinking underlying his rules. But the fact that his and all similar systems that ring the bell after complying with certain rules issue late warnings is directly imputable to the way in which the subject was approached (DE WEILLE, 144).

In itself the meteorological working method of BOURKE (20, 21, 22, 23) is also empirical, though fundamental knowledge has been assimilated in the Irish rules connected with his forecast system (19).

The opposite of the empirical approach is the *fundamental procedure*. It makes use of results obtained under accurately controlled laboratory conditions, so that the influence of each single weather factor upon the parasite in each of its development phases, within and outside the host, is known. Armed with this knowledge, the effect of the complex of weather elements upon disease incidence we are confronted with in field trials leading to the establishment of a warning system, may be interpreted and better understood. Exact biological and meteorological observations are made at short intervals; the results of recordings obtained on the spot are related to the climate and the successive weather conditions prevalent in the area concerned.

The author's research outlined in this treatise is to a great extent an example of the consistent appliance of fundamental procedures. A second example of a fundamental approach is the research conducted by UHLIG (120).

The fundamental approach makes high demands on the reliability and frequency of biological observations. They must match the usually reasonably precise meteorological observations in conjunction with which they will be elaborated for the purpose of correlating the two sequences of events to which they belong. It is a basic error to think that biological observations can be rendered simpler and less frequent as soon as one shifts from the laboratory to the field. Field observations can*not* be neglected with impunity (DE WEILLE, 144).

SUTCLIFFE (116) gave it as his opinion that it would be a fallacy to suppose that, in meteorology, fundamental methods are necessarily better than empirical ones. BOURKE (20), who related the view taken by SUTCLIFFE (116) to the blight problem, stated that neither of the two procedures has a marked advantage over the other. Yet he later advocated a close and continuing co-operation between the plant pathologist and the meteorologist (22), thus exactly voicing the author's feelings on this subject.

The latter meanwhile disagrees with the general view taken by BOURKE (20), who may be right as long as the pests or diseases in question can be combated by *curative* means (*e.g.* apple scab, leaf damage inflicted by caterpillars), but whose attitude can no longer be shared when the disease involved can be combated only by *preventive* spray or dust application. Then the warning system bearing on that disease must by implication be a system *forecasting* crop infection. Such a system can only be arrived at by applying the fundamental method of approach (DE WEILLE, 144). Statistical analysis of surveys or damage reports cannot possibly constitute a solution to the problem, *viz.* determination of the *dates* of crop infection. Even statistical analysis of field tests cannot achieve this aim.

Of the mixed environmental factors which together make up the complex of weather elements one factor may be important for one development phase, a second factor for another phase. In the results of field tests the various effects will have been mixed up. After disentangling this mixture with the help of laboratory knowledge concerning the key weather elements – if there are any – for each individual phase, it may be possible to judge whether or not there are real possibilities for warnings, preferably forecasts.

Only after such a comprehensive preliminary knowledge has been gathered has the time come to attempt to devise a warning or forecasting technique. The disregarding of this logical train of thought has led to several failures (DE WEILLE, 144). The theory put forward by this treatise is that the first approach should be a fundamental biological one. This should be followed by an empirical meteorological approach when it is precisely known what exactly should be forecast (cf. ULLRICH, 125).

CHAPTER II

LABORATORY INVESTIGATIONS

2.1 Prefatory remarks

Because of the interrelation of the weather elements it is of importance that for each development phase in *Phytophthora infestans'* life cycle the element with the closest relation to the existence of that phase be discovered. Ideally this can be done by studying the abundant literature on potato blight. But a survey of biological literature will still leave some questions unanswered. There are many data concerning the air humidity responses of *Phytophthora* and its relatives, in general the Peronosporales, but strikingly few about their reactions to irradiation in various regions of the solar spectrum.

As a result of earlier experiences with another fungus, *Exobasidium vexans* Massee, the organism causing blister blight in tea – when laboratory data (DE WEILLE, 136) led to the development of a warning system based upon sunshine observations (137, 140) and to a change in cultural practices (139) – the author, who had previously advocated research into the possibility of using sunshine observations for epidemiological purposes (139), also wanted to study these possibilities in the case of *Phytophthora infestans*. Since the existing literature was insufficient in this respect the author started atmospheric humidity and irradiation experiments of his own.

2.2 A survey of existing biological knowledge

With respect to *Phytophthora*'s life cycle "from spore to spore" a study of the existing literature reveals many facts as regards the influence which environmental factors exercise on the fungus' existence, its survival or death in each of its microphenological stages and on the transition from each separate stage to the phase succeeding it. Surveying the complete sequence of stages we obtain the following picture.

2.2.1 *The longevity of conidia*

It is generally assumed that the viability of potato blight conidia is chiefly determined by the *humidity* of the ambient atmosphere. In this connexion *viability* means the ability to germinate. For the sake of simplicity we shall assume that the *longevity* lasts as long as the conidia are viable and terminates when the viability is lost. From an epidemiological point of view this definition is certainly usable.

Fig. 6 illustrates laboratory results obtained by CROSIER (29). On the base of these data CROSIER concluded that conidia cannot stand an appreciable saturation deficit in the field. He found that at temperatures exceeding 20° C spore viability is lost in 1 to 3 hours in dry air and, still fairly rapidly, in 5 to 15 hours in moist air.

CROSIER's view (29) is confirmed by ORTH (99) and contested by MURPHY (93) and WALLIN (130).

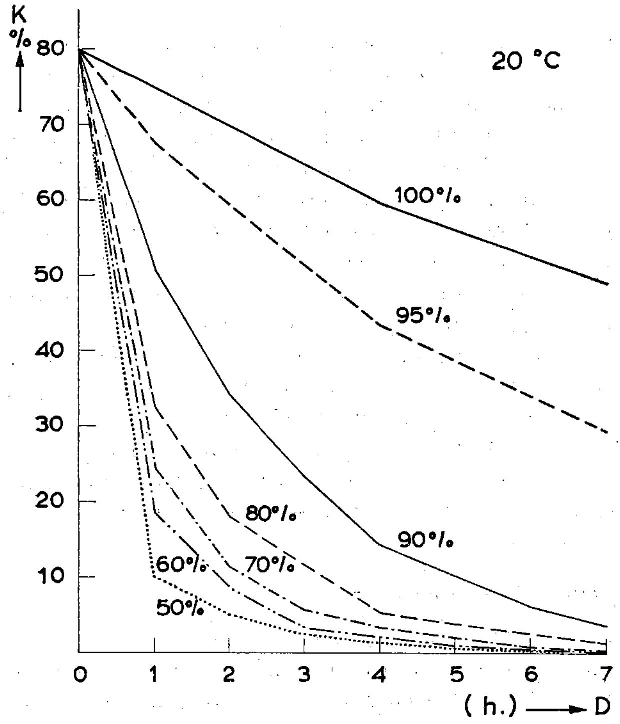

Fig. 6
Relation of r.h. to the longevity of conidia after CROSIER (29). K = germinative power in percentages; D = duration of exposure to the various humidities (in hrs.).

As regards the significance of *temperature* (T), CROSIER (29) and WALLIN (130) agree that T > 20° C is unfavourable for the viability of the conidia.

JONES *et al.* (69) consider 25° C to be more or less the fatal point for spores. JENSEN (66) also mentioned this T, stating that in his tests no conidia survived T > 25° C longer than 84 hours. But 84 hours is certainly not a convincingly short period. In fact the results obtained by JENSEN (66) rather indicate that, should an epidemiological temperature barrier have to be adopted in a given climate, this ought to be fixed at a level considerably higher than 25° C.

According to CROSIER (29) exposure of conidia to temperatures of 30° C or even higher result in a gradual loss of viability, which will have become complete within 6 hours. Research conducted by WALLIN (130) shows that temperatures exceeding 30° C are of epidemiological importance in the field.

Meanwhile in many countries such relatively high temperatures will practically never coincide with saturation of the air. In countries like the Netherlands, where, in addition, the prolonged occurrence of temperatures exceeding 30° C is very infrequent, *high T* is certainly not one of the key weather elements governing the spread of blight.

Low temperatures above freezing point constitute an inhibitive factor in the life of *Phytophthora* (BOCHOW, 12), though they are not exactly fungicidal in their effect. In fact $T=0°$ C marks the lower border of the temperature range within which the conidia can live (comp. MELHUS, 86). Prolonged exposure to $T=0°$ C is unfavourable.

As $T \leqslant 0°$ C would make potato growing impossible such temperatures are not of substantial epidemiological significance. THOMAS (117) found conidia of *Phytophthora infestans* unable to survive $T=-5°$ C for more than some hours.

MURPHY (93) stated that some conidia survive up to 9 days in saturated air. On the other hand data published by CROSIER (29) give the impression that the longevity of conidia is a matter of hours rather than of days.

2.2.2 *Germination*

Liquid **water** is an essential prerequisite for germination. Germination occurs chiefly by the production of about 8 minute swarm spores formed by the conidial (sporangial) protoplast's previous splitting up. The swarm spores swim actively for a time in water droplets. Then they settle and form cell walls. Finally each produces a germ tube. *Some* zoospores may complete these complex processes within *2 hours* of deposition if the temperature is optimal (HIRST, 57). The process described is called *indirect* (or sporangial) *germination*; it can take place at *temperatures* ranging from 2 to 28° C. The optimal T is 12–13° C (MELHUS, 87).

A second way of germination is observed at higher T, *viz. direct* (or conidial) *germination*: the conidium produces a germ tube itself; sometimes 2 tubes are observed. The optimum T for direct germination is 24° C (MELHUS, 86, 87). REDDICK (110) states that at 21° C there is no failure to germinate but a failure of swarm spore production. Old conidia are more inclined to germinate directly than newly formed ones (MURPHY, 93), so that some workers relate direct (conidial) germination to senescence of the sporal material involved. MURPHY (93) stated that conidia which have remained ungerminated in the air for some time are only capable of giving rise to germ tubes. Where oxygen is lacking the tubes soon terminate in a new conidium, a secondary one, which is capable of forming swarm spores, a process not requiring oxygen (GOTTLIEB, 43). By forming a secondary conidium a spore lengthens its original longevity (MURPHY, 93).

CROSIER (28) stated that germ tubes die quickly at T ⩾ 26° C. Yet MELHUS (87) mentioned 30° C as the upper T-limit for direct germination; MURPHY (93) mentioned 32° C as the marginal temperature.

Fig. 7 shows a combination of one graph by MELHUS (86) and one given by CROSIER (29); their data were averaged by the author. Moreover, the data produced by the two cited workers were in agreement.

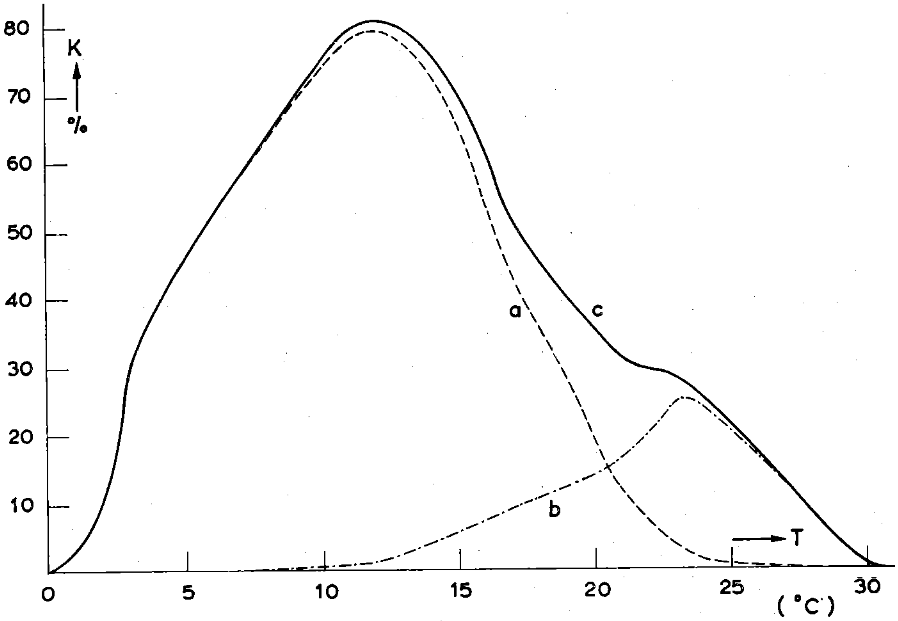

Fig. 7

Relation of germination temperature to the rate of germination obtained according to MELHUS (86) and CROSIER (29); averaged data. a = indirect germination; b = direct germination; c = (a + b) = total percentage germinated.

Speaking in general we can say that temperature greatly influences the longevity of spores. Long viability is associated with low temperatures; high T shortens this period. The loss of viability is especially rapid above the maximum temperature for germ tube formation (GOTTLIEB, 43).

Light is not favourable for the germination of conidia of Peronosporales (DE BARY, 5; FARLOW, 35). MELHUS (86) stated that light does not interfere with the germination of conidia of *Phytophthora infestans* if the optimum temperature for germination is not exceeded.

2.2.3 *Infection*

Infection of the host plant is effectuated by germ tubes piercing the leaf cuticle and penetrating into host tissue. Several factors are of importance once incipient germination has taken place, *viz.*

1) the motility of the zoospores,
2) the longevity of the germ tubes,
3) the rate of germ tube elongation,
4) the occurrence of a weather situation making infection possible.

Re 1): At lower temperatures spore *motility* is observed much longer then at higher T. MELHUS (87) reported that at 5–6° C swarm spores may keep moving during a period of 22 hours, whereas at 24–25° C they stop swimming after 19 minutes. Similar results were reported by CROSIER (29). From the moment the swarm spores leave the sporangial envelope the percentage motility starts decreasing. The higher the temperature the more quickly the percentage motility will have fallen to the zero level. At + 1° C a small percentage of the swarm spores is still able to move after 24 hours.

Re 2): Although it is generally assumed that after having produced a *germ tube* a spore is particularly vulnerable, MURPHY (93) reported that after a germ tube has been produced the resistance of the conidium is increased. This applies in particular to conidial germ tubes. Zoospore germ tubes may remain alive for several days. Conidial germ tubes can lengthen the original conidium's life by more than 7 days. It is further lengthened when a new conidium results (by transformation of the germ tube's apical cell). Whereas a conidial germ tube was seen to be able to infect in water 15–16 days after the conidium had been put into it when freshly harvested, germination of secondary conidia was observed 24 days after the original conidium was placed in water. Again, the resultant germ tubes were able to live for 10 days or longer (MURPHY, 93).

These laboratory results, obtained under optimal conditions, may be interesting but they do not reflect field conditions. They indicate however that infective fungal material can be preserved very well *in water*. This points once more to the extreme epidemiological importance of *precipitation*.

Re 3): The rapidity with which *swarm-spore germ tubes* develop is a relatively thermo-indifferent process, at least in the temperature interval between 3° and 21° C (CROSIER, 29). The growth of *conidial germ tubes* is optimal at *ca.* 20° C, which is in accordance with the optimum temperature for mycelial growth stated by VOWINCKEL (127). For optimal germ tube elongation in general MELHUS (86) mentioned a temperature of 22° C.

Re 4): The necessity of the presence of water has already been emphasized. According to ULLRICH (122) the shortest time needed for infection amounts to about 2½ h.. A 50% infection result was obtained in 4½ h.

> of leaf wetness. In the temperature interval between 10° and 21° C CROSIER (29) obtained about equal degrees of infection. At higher T the maximum was reached earlier than at lower T. At 25° C the total infection rate was somewhat lower. At 10 to 25° C penetration continues to increase for as long as 8 h. (CROSIER, 28).

If the germ tube meets resistance when trying to pierce the leaf cuticle it may form an *appressorium*, *i.e.* it swells and presses itself, as it were, against the leaf. From the appressorium, the swollen part of the infecting hypha, a new pointed apex protrudes and penetrates the epidermal cell. If a germ tube happens to find a stoma it enters without an appressorium having been formed.

Mycelial growth within host tissue is merely intercellular along the pectin lamellae. Host cells are invaded by branched haustoria that extract nutritional material from their environment.

2.2.4 *Mycelial growth*

The vegetative growth of the fungus in the potato plant is influenced by the degree of blight resistance of its host and by the *temperature* in the host tissue. According to CROSIER (29) the optimal temperature for mycelial growth is 20–23° C. $T < 3°$ C and $T > 31°$ C inhibit the growth of the mycelium (VOWINCKEL, 127, JOHANNES, 67). Prolonged exposure of potato leaves containing blight mycelium to $T > 40°$ C may kill the fungus (WALLIN & HOYMAN, 132). Temperatures below freezing point are also detrimental to *Phytophthora* (BOCHOW & RÆUBER, 13).

2.2.5 *The incubation period*

The incubation period is the time elapsing from the moment of infection until the results of that infection become visible in the form of incipient necrosis of leaf tissue. It should not be confused with the "fructification period" between infection and new spore formation, which thus embraces almost one complete generation, including the incubation time.

The length of the incubation period is not independent of the growth rate of the mycelium. Hence the incubation period is likewise linked with *temperature* (MÜLLER & GRIESINGER, 90) (cf. THRAN, 118).

A temperature of 23° or 24° C (CROSIER, 29; WALLIN, 130) is optimal. At 24° C WALLIN noticed incubation periods of 66–77 h., these being the shortest he observed (130). VOWINCKEL (127), MÜLLER (89), NAUMOVA (96), VAN DER ZAAG (149) and HIRST (57) also consider 3 days to be the minimum duration of the incubation period. At a comparatively low temperature level NAUMOVA (96) once noted an incubation period of 13 days.

The relationship between the incubation period (z) and T is not a singular one. T_n and T_x, the daily minimum and maximum temperatures are of importance as well as $\overline{T}$. From a table by NAUMOVA (96) it appears that under Dutch summer conditions z will mostly lie in the range 4–6 days, at least in susceptible potato clones. Blight resistance tends to lengthen z (MÜLLER & HAIGH, 91).

2.2.6 *Fructification*

The process of fructification consists of the formation of conidiophores – also called sporophores, sporangiophores, aerial mycelium or aerial hyphae – and subsequent sporulation, the formation of conidia.

Fructification is highly dependent on the *humidity* of the air, which should exceed 90% r.h.. Formation of aerial hyphae and conidia is abundant in saturated air and becomes slight if the r.h. is $<95\%$. Conidia are never formed in an atmosphere of less than 91% r.h.; no aerial mycelium appears below 85%. Really abundant fructification only occurs at 100% r.h. (CROSIER, 29).

Aerial mycelium is formed at temperatures ranging from 3 to 26° C. At 23°–26° C aerial hyphae may develop abundantly, but they are most often either sterile or their spore production is very slight (CROSIER, 29). At 27° they are always sterile. A temperature of 18° to 22° C is optimal for *sporulation*, both in its rapidity and in its intensity (VOWINCKEL, 127; CROSIER, 28, 29; BUTLER & JONES, 25).

In a saturated atmosphere conidia appear within 8 hours at optimum temperatures; they are abundant in 14 hours (CROSIER, 29). At $T \leqslant 22°$ C and r.h. $> 90\%$ WALLIN (129) was able to harvest fresh conidia 13 hours after he had brushed the potato leaflet lesions producing them free of spores.

At 9–15° C conidia are fairly numerous in 24 hours and plentiful in 48 hours. At 3° C only a few will have been formed in 6 days (CROSIER, 29). In practice, GRAINGER (45) states, there is little sporulation below 50° F (10° C). Hence this T is generally taken as the minimum when assessing weather conditions suitable for the disease.

According to CROSIER (29) *daylight* has no effect on spore formation, but HIRST (57) states that conidia are known to be formed chiefly *at night*.

The fact that spores are only formed under special weather conditions explains why the fructification period is extremely inconstant. Within the plant *Phytophthora* may grow for months without forming spores. As soon as the environment becomes favourable sporophores appear on leaves and stems (KEAY, 71). This accords with the idea of overwintering mycelium (cf. *i.a.* VAN DER ZAAG, 149).

2.2.7 *Spore flights*

After their formation the conidia may remain attached to their sporophores for some time. This time varies considerably. The spores formed at night are not air-dispersed until the following morning, when rising temperature and falling humidity produce *drying conditions* (HIRST, 57). It is consequently not surprising that the discharge of conidia is closely related with *radiation* (HIRST, 54, 57).

Conidia are also detached very readily in water. HIRST (57) reported that about half the lesions that appeared on healthy plants placed between rows of infected ones seemed to be caused by sporangia carried in water dripping from leaf to leaf. They may travel further if they are splashed about in raindrop fragments.

According to HIRST (57) spore liberation is an active process and not merely passive dislodgement. The operative mechanism is not yet completely known, but experiments showed that the factors governing it are *wetting* (giving rise to water transport of inoculum), very rapid changes in *r.h.* and strong *light* (giving rise to aerial dispersal of inoculum; spore flights).

The remark made by HIRST that "strong light" effectuated conidial discharge in almost still air and not when the air was moving quickly (in his wind tunnel) suggests that humidity changes constitute the real operation mechanism. In still air radiation may have caused the r.h. in the microclimate to decrease via increasing T.

Meanwhile these wind tunnel experiments also indicate that conidia are not simply blown off their conidiophores by wind (which HIRST would have called passive dislodgement).

On being disengaged from their conidiophores the conidia together make up a *spore flight*, at least in as far as they are actually wafted above the fields, in which connexion *wind* is important.

HIRST (54, 57) showed that, when catching airborne potato blight conidia with the help of the Hirst spore trap (53), ½ m above ground level, it will be found that the typical course of events is for liberation to start at 7.00, to reach a peak at about 11.00 and then to decline, so that few conidia are found after 19.00 G.M.T..

The flight of conidia may be discontinued abruptly by a rain shower, which brings down airborne spores to the plants again, thus contributing to local intensification of blight incidence (HIRST, 54; BOURKE, 22) while checking wider spread of the disease.

In that wider spread the most important part is played by the *wind*. A *strong wind* after critical days can hinder blight development (VAN EVERDINGEN, 34). Apparently its bringing about a desiccating effect by increased evaporation then plays a role. But as regards spore flights it is *wind in general* we must think of. The aerial dissemination of *Phytophthora* mainly takes place downwind (WAGGONER, 128; VAN DER ZAAG, 149).

Phytophthora conidia are relatively heavy as compared with bacteria and some other kinds of spores. In consequence it is a small minority that covers greater distances. Though conidia have been found to be borne by the wind to places more than 30 miles away from their focus (HARRISON, 47), the deposition of conidia in relation to the distance covered is such that their number limits the distance covered by the ones that alight on the most remote spots (WAGGONER, 128), so that in the beginning of the season the number of blighted plants decreases to nought within a few metres from the inoculum source (LIMASSET, 80) and distant spread does not usually occur (WAGGONER, 128; HIRST, 55).

As the inoculum material becomes more numerous the chance of infection after long-distance air transport of conidia increases. The probability of disease being caused by conidia deposited at a considerable distance from the source will be sharply reduced by adverse atmospheric conditions.

Here we have returned to the item "longevity".

2.3 Reactions of detached conidia to the environment

2.3.1 *Appliances and procedures*

The author wished to obtain an impression of the potential infection danger (in the field) at any hour of the day, so that, in practice, forecasts need only be considered when the inoculum is indeed able to infect. His previous work on blister blight in tea having taught him that solar *radiation*, in particular ultraviolet (u.v.) radiation, can exert a not inconsiderable influence on the germinative power of fungus spores (136, 137, 140), he decided to investigate the significance of radiant energy for *Phytophthora infestans*. If, in the case of potato blight, r.h. is as important for spore viability as the literature would have us believe, it is clear that the conidia's response to radiation should be studied at different levels of r.h., whereas comparative tests at these levels without irradiation would serve to show which part of the effect found is due to the level of r.h. and which to u.v. or other radiation. Finally the complete test series would have to be repeated at various levels of *temperature* (T). From the start T was treated as the possibly modifying (secondary) factor presumably influencing the extent of primary humidity and radiation effects.

In order to check the findings of CROSIER (29) and other scientists the author used the period during which he had not yet obtained suitable sources of (artificial) radiation for conducting *humidity* experiments.

For these experiments he had at his disposal an *environmental control unit* consisting of 4 cylindrical glass climatic cells with "Perspex" lids mounted in a water-filled rectangular reservoir. The temperature of the water surrounding the climatic chambers is controlled by a thermostat regulating the operation of an electric water heater. An air pump conducts a constant air current to the bottom of the cells. A hole in their lid permits surplus air to leave the climatic cells. Before entering the cells the air supplied by the pump passes through a bottle filled with a mixture of water and glycerine. Those bottles are also surrounded by the temperature-controlled water filling the whole environmental control cabinet, so that the water-glycerine mixture has the same temperature a that desired in the climatic chambers.

The ratio water/glycerine is a determinant for the r.h. of the air leaving the mixture. If glycerine is predominant water is withdrawn from the washed air, so that its r.h. is decreased. If water is predominant in the mixture the r.h. of the washed air may have been raised before it enters the cells.

If an extremely low r.h. is required the water-glycerine mixture will withdraw so much water vapour from the incoming air that the ratio water/glycerine will quickly increase; this phenomenon will have an impact on the r.h. in the climatic chamber concerned. In this case, in order to avoid undesirable changes in air humidity, the pumped air is led through an additional bottle filled with dry silica gel before being washed in the hygroscopic mixture. The lowest r.h. that could be maintained in this way amounted to 31 %.

Acting as described in the foregoing paragraphs the change in r.h. attributable to water ingestion in or withdrawal from the mixture contained in the washing bottles could be kept as low as 2 % per week.

Measurement of T was performed by regularly reading mercury thermometers mounted 8 cm above the bottom of the glass climatic chambers. Maximal departures from the water temperature indicated by the mercury column thermostat amounted to ± 1° C.

Measurement of r.h. was performed by reading indications in Ω showing the resistance met by a battery-induced direct low-voltage current conducted through Negretti & Zambra resistance hygrometers. After an establishment period of ½ hour measurements showed no departures from the required r.h. level exceeding 2 per cent. The indications were verified regularly with the help of an aspirated Assmann psychrometer.

The resistence hygrometers were hanging in the centre of the climatic chambers of which one is pictured in fig. 8.

A glass box in which the air was kept saturated by means of wet filter paper, cohering to the bottom and the vertical cylindrical wall, floated in the water filling the cabinet, thus making it possible to control 5 different air humidities simultaneously. For the level of 100 % r.h. maintained in the glass box does not require aeration. Meanwhile 4 other r.h. levels were maintained in the cells, *viz.* 35, 58, 72 and 90 %.

The above contrivance, to which an irradiation unit was later added, was called "mycotron" by the author, *i.e.* a phytotron for fungi.

Prior to the experiments conducted in the mycotron at the agricultural laboratory of the K.N.M.I. a number of test series were performed at the I.P.O. (Inst. for Phytopathological Research) at Wageningen, the Netherlands. That institute then possessed a large single climatic chamber in which the temperature could be regulated and kept constant by a mercury thermostat. Finely nebulizing spray nozzles produced "mist" clouds from which the exposed plants or spores could be protected by means of plastic curtains. Meanwhile the air remained constantly saturated. By not making use of the curtains it was possible to expose spores to drizzle or rain according to their distance from the atomizers by means of manipulating the supply cock.

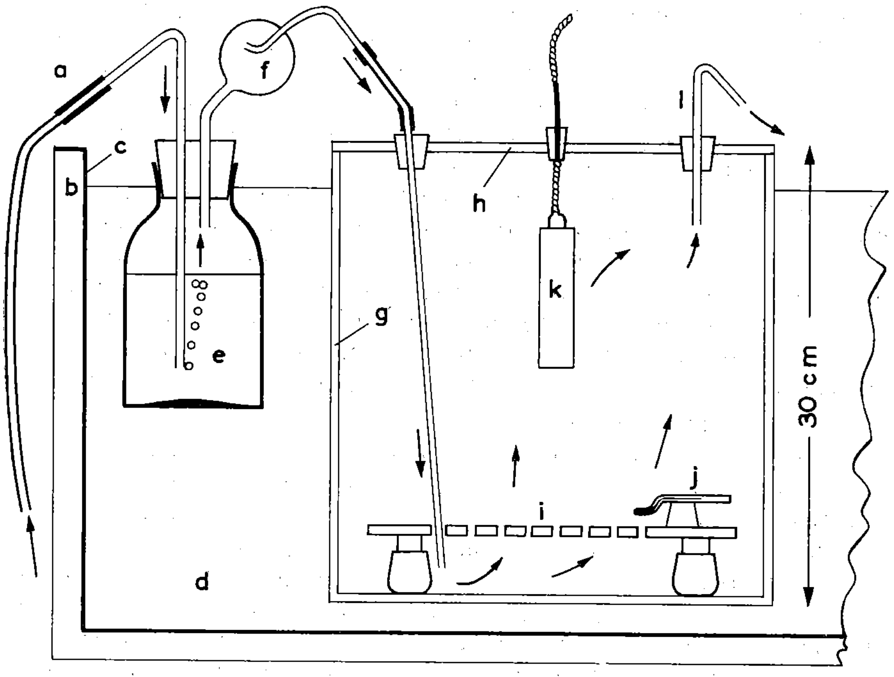

Fig. 8
Sectional view of one single climatic cell in the "mycotron". The arrows indicate the direction of the air current.

a = air intake,
b = wooden wall of climatic control cabinet,
c = zinc lining,
d = water,
e = water-glycerine mixture in washing bottle,
f = splash receiver,
g = glass climatic chamber,
h = perspex lid,
i = perforated circular table leaf,
j = mercury thermometer mounted on a cork,
k = Negretti & Zambra resistance hygrometer,
l = air outlet.

A battery of Philips TL 29 discharge tubes was used to illuminate the interior of the cabinet, which would otherwise have been dark.

The only environmental element able to be fixed adequately at a range of levels was the temperature. The highest T attained in the author's experiments was 31° C. Thus the possible influence of T as such upon the germinative capacity of *Phytophthora* conidia could be studied.

The *plant material* examined consisted of conidia of *Phytophthora infestans*, cultured on complete potato plants or on cut-off leaved stalks, on decised leaves or, in most cases, on tubers. From time to time culturing on tubers has to be interchanged with culturing on foliage in order to ameliorate the viability, which tends to decrease gradually in the tubers (ORTH & LEHMANN, 100).

Culturing *Phytophthora* on *green plant parts* is practised by placing these parts (or complete plants) in exsiccators or other closed spaces in which the presence of liquid water secures continuous saturation or near-saturation of the enclosed air. If the plant material put into such a closed space is already blighted, conidiophores bearing conidia will readily be formed after a sojourn of one night in the humid medium. If not yet blighted, the green plant material has to be wetted with the help of a finely nebulizing plant sprinkler, fresh sporal material has to be brushed on to the moist foliage, whereupon the inoculated plants, leaved stalks or leaves are incubated under optimal conditions. After the plant material has been placed for one day in a saturated atmosphere so that infection can take place, the space in which it is stored is opened in order to prevent putrefaction. After a suitable incubation time – *i.e.* at least 2 days – the material is again placed in the closed space with saturated atmosphere in which sporulation is then achieved.

Tubers can be inoculated by putting conidia taken from sporing tubers or leaves into holes cut into them with the help of a simple apparatus especially designed for removing small conical plugs from tubers. The inoculum used is harvested from diseased leaves or tubers with the help of a sharply tapered glass rod of which the extreme point has been broken off, the resulting rough end facilitating the removal of aerial hyphae from their substratum. They come off readily in water. Before the conidial material is inserted into the holes the latter are filled with *aqua bidestillata* and kept filled for at least 3 or 4 hours. The inoculated tubers are stored in closed glass boxes placed at a suitable temperature, preferably 15–16° C. Wet filter paper cohering to the bottom and lids of the boxes again secures (near-)saturation of the enclosed air.

As soon as aerial mycelium protrudes from the inoculated holes the tubers are halved by cutting them longitudinally in such a way that the original inoculation holes are cut too. In order to avoid the dissemination of bacterial rot as far as possible, each cut is started at the end opposite to that in which the holes are located. In addition, the knife is disinfected with the help of alcohol and a gas flame prior to each separate cut. All glass boxes, Petri dishes, instruments and filter paper sheets used in this work are treated as hygienically as possible. The exterior of the tubers used, and the boxes they are stored in, are also disinfected with alcohol.

With the cut plane uppermost, the halved potatoes are put into high-rimmed Petri dishes, with wet filter paper again cohering to bottom and lid. After some days conidia can be harvested from the secant plane.

Harvesting the conidial material is performed by means of a soft paint brush. After the brush has been moistened somewhat by breath the conidia are cautiously brushed off their substratum and are then applied to a clean object slide also dimmed by breath. The conidia will easily cohere to the dimmed surface, which soon clears after the spores have been applied. In most cases the harvested sporal material originates from quite a number of tubers or leaves. It is therefore advisable to return to each of the object slides two or three times, each time applying conidia originating from other substrata.

In addition, test numbers which determine the part each sample will play in the storage experiment are given at random so as to avoid selective bias.

Then the actual experiment is carried out. The samples are exposed to the environmental factors under investigation during a period of varied duration (D) which is referred to as the *storage* period D. The storage medium may be, for instance, the earlier described mycotron.

The samples taken from the storage medium are conveyed to the germination medium. To that end the conidia are surrounded by artificial dew, which is obtained either by breathing on the slides in a cold room, so that they dim, or by means of a plastic atomizer filled with *aqua bidestillata.* In order to prevent the dew from evaporating the slides are placed in cool Petri dishes in which a saturated atmosphere is maintained in the manner already described.

The dishes are placed in a cool shed at a temperature of 12 to 16° C (for particulars: DE WEILLE, 142). The samples are germinated for a period of 16 hours or longer, but in any case during a fixed time which is the same for all samples.

On being removed from the dishes the sporal samples are killed by flambation and stained with methylene blue. Now they are prepared for microscopical observation in a glycerine film under a cover slide.

The results of the experiments depend (to an incredibly great extent) on the examined material's previous history, whereas conidia attached to leaves by their conidiophores react entirely differently to low r.h., for instance, than do detached ones. For this reason detached and attached conidia are dealt with separately.

DE WEILLE (142), who studied the variability of the germinative power of conidia in *Phytophthora infestans* and some *Peronospora* species, summed up the various conditions the examined sporal material has to meet if the results obtained from the tests are to be of real scientific value. This enabled him to draw up a *procedure*. Adherence to this procedure is imperative for the avoidance of any bias in the results.

This procedure, which may not be the only possible one, is discussed and described in the paper listed as No. 142 in the list of references. Readers interested in this matter are referred to that paper and to items broached further on in this publication. Several of the principles underlying the author's method still remain to be dealt with. But the results themselves are indispensable at this juncture, so the special procedure will now be discussed point by point.

1. Only sporal material formed in the night preceding the experiment is used.
2. In order to obtain such material formation of aerial mycelium upon the living substratum is only allowed to take place under a continuous illumination of at least 400 lux.
3. After (sterile) aerial hyphae have been formed the culture is exposed to natural nocturnal darkness or to an artificial dark period of an 8 to 15 hours' duration.
4. The interval, in light again, between the end of the dark period and the harvest of the conidia should not be less than 3 hours.
5. The substratum on which the sporal material is cultured has to be as uniform as possible. Sporal samples obtained from halved tubers should not be mixed with samples harvested from leaves, nor is it justifiable to mix samples of diverging previous history.
6. Samples from putrefied or apparently decaying plant material should not be included in the test series.
7. No *Phytophthora* conidia should be harvested from tubers affected by *Penicillium*, which adversely influences the viability of potato blight conidia.
8. The sporal material to be examined should be harvested *en bloc* at the start of the experiment.

   Only strict adherence to the above 8 principles will yield a (more or less) statistically homogeneous sporal population fit for the purpose of comparing conidial responses to environmental elements.

   As will be shown later, the method of gradual harvest will exclude the achievement of the desired result by superimposing the specific behaviour of attached conidia on that of detached conidia, while it is only the latter category which is being investigated.
9. The circumstances and duration of germination after the (variable) storage period should be identical for all samples concerned. This implies that the investigator has to accept the fact that the microscopic preparations for determining the germinative capacity can*not* be made en bloc in one action so that making them will take quite a lot of time.
10. When counting germinated and ungerminated conidia with the help of a

microscope in order to calculate the germinative capacity (K), *at least 500 conidia* should be counted, and preferably more. The research worker should not stop at n = 100.

11. Neither should he count precisely all 500 spores in one corner or along one side of the preparation's cover slide. Owing to the marked (mathematical) persistence usually occurring in the samples the chance of recording "outliers", *i.e.* exceptions disturbing the general picture, would be greatly enhanced. The microscopic visual fields in which spore counts are performed should be chosen so that they are more or less evenly distributed over the surface under the cover slide.
12. Test series in which all (or all but one *etc.*) determinations of K show values under 5% should be considered statistically worthless and be left out of account. In such series most values of K and their standard deviations s are of the same order of magnitude. One outlier may then determine the result of the whole experiment.

The 12 above items do not of course make up the whole method of handling plant material. They are superimposed on the more general procedures described on previous pages.

Before discussing the experimental results some elucidation with regard to item 8 may further the understanding of the implications of the basic difference between two methods of harvesting conidia. We distinguished harvesting *en bloc* from *gradual* harvesting, the former being advocated and the latter rejected.

The matter is illustrated by fig. 9. Conidia are subjected to the influence of an environmental variable during a period of 0, 1, 2, 3, 4, 5, 6 or 7 hours, so D = 0 to 7. The experiment is due to start at 10 o'clock local time, so that storage ends at 17 p.m.. Consequently t = 10.00 to 17.00 or, in the figure, 10 to 17. When harvesting *en bloc* at 10 h. and putting all slides in the mycotron at about 10 o'clock the duration of exposure D_a means that samples from the 8 treatments

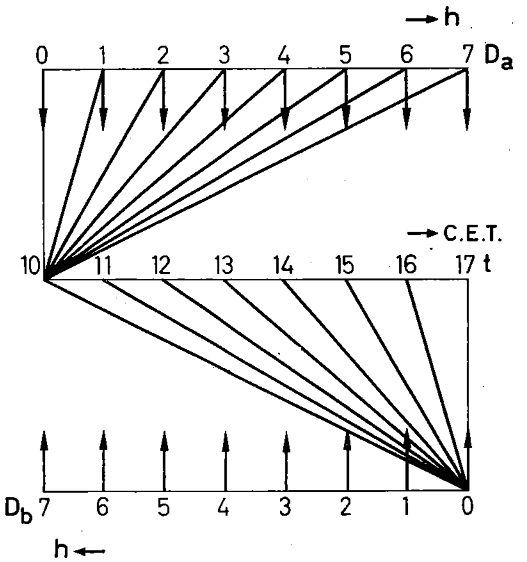

Fig. 9
Comparison of harvesting at once and gradual harvesting. For explanation: see text.

are taken out – follow the arrows – at t = 10, 11, 12 *etc.*. If the duration of germination is fixed at, say, d = 24 hours, the method of harvesting at once ultimately implies gradual preparation next day, a tedious occupation indeed if practised on a routine basis.

Gradual harvest of sporal material, *i.e.* harvesting them the same number of hours before the experiment's termination as the desired duration of exposure D_b amounts to – follow the arrows – implies in this case that samples are put into the mycotron at t = 10, 11, 12 *etc.* and that all samples are taken out at one and the same moment, *viz.* t = 17. If, again, d (duration of the germination period) is fixed at 24 hours, gradual harvesting ultimately involves the preparation of all samples in one action at 17 p.m. next day; at first glance a substantial labour-saving improvement. No wonder the author soon passed to this improved way of working. The mere accident that the average age of the harvested conidia progresses at a rate corresponding to that of the D_b decrease was willingly accepted as a factor of minor importance. We shall look at the results.

2.3.2 *Temperature and humidity responses*

It is generally believed that potato blight conidia are readily killed by desiccation brought about by the prevalence of a saturation deficit. The less saturated the ambient atmosphere the more easily spore viability is lost.

In experiments conducted at Wageningen and de Bilt serious doubt arose as to whether the above view is indeed correct.

As regards the effect of *temperature* as such, some trials were performed in the temperature control cabinet at the I.P.O., Wageningen. Object slides with conidia were exposed to humid air, fog, drizzle or rain at specified levels of T ranging from 17° C to 26° C. No indication was found that T = 26° C, usually considered as the upper limit of existence of *Phytophthora*, did any harm to the conidia in otherwise favourable circumstances during a storage period of up to 16 hours. On the contrary the material even started to germinate (in the rain) during exposure to T = 26° C.

After storage the conidia were germinated at 16° C during 18 hours, either in complete darkness or under continuous illumination provided by Philips TL 33 discharge tubes. No appreciable difference in germination resulting from the difference in illumination could be shown.

In later experiments performed at the K.N.M.I., de Bilt, it appeared that in otherwise favourable circumstances a 7 hours' exposure to temperatures of up to 31° C did not appreciably affect spore viability.

As regards the effect of *low air humidity* the results obtained with the help of the mycotron diverge from those published by CROSIER (29).

When still applying the erroneous procedure of gradual harvesting the germinative power K usually attained a peak rate in the afternoon, thus giving rise to formerly inexplicable data. This is due to the periodicity dealt with on pp. 55–63.

When working according to the lines stipulated on pp. 40–41 the results were as follows:

1. immediately after the conidia are dislodged from their sporophores K may start to decrease. The sporal material often shows, as it were, a fright reaction; the condia's detachment frequently involves a limited knock-down effect with regard to K;
2. *during at least 10 hours* following the initial decrease of K, *the germinative power is not affected by low air humidity*, even if the r.h. is as low as 31 %.

R.h. = 100%						R.h. = 82%					
D	G	n	K	$\overline{K}$	$\sigma_{\overline{K}}$	D	G	n	K	$\overline{K}$	$\sigma_{\overline{K}}$
0	288	503	57.6	64.7	4.2	0	288	503	57.6	64.7	4.2
0	484	789	61.3			0	484	789	61.3		
0	680	951	71.5			0	680	951	71.5		
2	385	520	74.0	69.7	3.0	2	170	522	32.6	49.0	5.5
2	465	655	71.0			2	263	480	54.8		
2	330	517	63.8			2	229	655	35.0		
						2	226	388	58.2		
						2	129	219	58.9		
						2	380	585	65.0		
3¼	398	670	59.4	63.7	5.5	3¼	114	486	23.4	49.7	9.9
3¼	307	436	70.4			3¼	346	672	51.5		
						3¼	280	407	68.8		
						3¼	217	360	60.3		
4½	294	381	77.2	75.8	1.2	4½	220	460	47.8	63.6	11.4
4½	406	543	74.8			4½	143	344	41.6		
						4½	367	406	90.4		
						4½	298	404	73.8		
9¾	479	530	90.4	73.9	15.9	9¾	143	431	33.2	48.5	11.9
9¾	332	567	58.6			9¾	286	887	32.2		
						9¾	248	482	51.5		
						9¾	469	564	83.2		

Table 1

Results of exposure (during D hrs.) of detached conidia to 2 different air humidities. After exposure G spores from a sample of n elements were able to germinate. Resulting germinative power in percentages of n is K.

A few examples may illustrate these two items. Table 1 gives results of an experiment carried out on the 28th of September, 1961. T = 20° C. Compared levels of r.h.: 100% and 82%. D = duration of exposure in hours. K = germinative power in percentages, computed from the number G of conidia germinated under optimal conditions in a sample of n elements, d = duration of sojourn in germination medium = 65 hours; δ = temperature during germination = 16° C. $\overline{K} = 100 \times \sum G/\sum n$. Values of K in this experiment were the highest ones ever found in the author's work on *Phytophthora*.

Table 2 shows results of an experiment carried out on the 24th of August, 1961, T = 19° C. Levels of r.h.: 92% and 41%. d = 82 h.; δ = 16° C. Low values of K, frequently occurring in the experiments – also in the field – render the series very representative.

R.h. = 92%						R.h. = 41%					
D	G	n	K	$\overline{K}$	$\sigma_{\overline{K}}$	D	G	n	K	$\overline{K}$	σ_K
0	38	566	6.7	7.0	1.3	0	38	566	6.7	7.0	1.3
0	31	633	4.9			0	31	633	4.9		
0	55	591	9.3			0	55	591	9.3		
½	10	556	1.8	2.0	0.3	½	26	429	6.0	4.9	1.0
½	15	546	2.7			½	19	492	3.9		
½	11	638	1.7								
1¼	12	606	2.0	4.9	2.0	1¼	24	539	4.4	4.9	0.4
1¼	25	640	3.9			1¼	29	549	5.3		
1¼	58	675	8.6								
2½	31	581	5.3	5.0	0.25	2½	75	674	11.1	9.7	1.4
2½	30	631	4.8			2½	54	661	8.2		
4	16	565	2.7	3.1	0.5	4	40	597	6.9	4.8	2.0
4	22	569	3.9			4	18	619	2.9		
4	19	493	3.9								
4	11	566	1.9								
6	16	519	3.1	3.6	0.4	6	25	563	4.4	4.2	0.25
6	27	671	4.0			6	24	615	3.9		

Table 2.
Results of exposure of detached conidia to 2 different air humidities. For meaning of symbols see Table 1.

In both tables the computed standard deviations from the mean values of K demonstrate the variability of the living material. Although the denounced variability is substantially restricted by means of special standardized procedures, the values of σ indicate that studying one single series of experimental results could easily lead to erroneous conclusions, even though the theoretical values of s, the standard deviation (of the internal frequency) of each individual sample, might suggest a fair degree of reliability. In an earlier publication (142) the author pointed out that the empirical exceedance probability of the boundary values $K \pm 2s$ is about twice the theoretical 5 per cent, so that untypical or discordant observations, so-called "outliers", occur more often than expected. The outliers show significant departures from similar surrounding K-values and their recognition therefore requires frequent repetition of the same experiments.

In very recent statistical examinations, the results of which will be published separately, it was shown that germinated spores are not normally or binomially dispersed over the preparations. Mathematically speaking, this cluster formation fully accounts for the variability of the germinative capacity encountered in the experiments.

Though more or less arbitrary, the examples given on these pages were yet carefully chosen, *viz.* so that they neither contain "outliers" nor comprise too many samples of too small a size. For in undersized samples the mathematical persistence, the cluster formation brought about by interaction of germinating conidia, results in extreme variability. This phenomenon becomes the more marked as the average general level of K falls (cf. DE WEILLE, 142).

On comparing the data contained in Tables 1 and 2 with those depicted in Fig. 6 on p. 28 it cannot be denied that CROSIER's data conflict with those of the author. Yet neither of the two workers is at fault. The difference between their results is occasioned by a corresponding difference in their working methods. This difference is so fundamental that it is worth while to quote CROSIER's technique as he described it (29). His procedure made it "possible to follow the hourly loss of viability of the sporangia. Plants were held at 15° to 18° C in a saturated atmosphere where sporangia formed in abundance. The plants were then removed to the controlled chamber so that the sporangia could be exposed to the desired temperature and relative humidity. Sporangia were collected while the plants were confined in the chamber and were placed to germinate at 13° C. At intervals of $\frac{1}{2}$ hour several samples were removed from the leaves and allowed to germinate ...". This consequently means that Fig. 6 applies to *attached* conidia in contrast with Tables 1 and 2 which apply to *detached* conidia.

Not only with regard to potato blight does this contrast exist. It seems to be common among the Peronosporales. As regards *Peronospora destructor* – downy mildew in onions – JONES (68), WHETZEL (145) and VAN DOORN (31), who examined conidia attached to the plant, reported that the germinative power cannot be retained under less humid conditions, whereas SHIPLEY (113) and KATTERFELD (70), who examined loose conidia, mentioned longer life periods than those stated by the former two scientists. Diverging opinions with regard to conidia of *Bremia lactucae* and *Peronospora hyoscyami* and related species also appear to be due to the application of different experimental procedures.

2.3.3 *Appliances and procedures in irradiation experiments*

For the study of the radiation responses of loose conidia the contrivances that had been so useful in investigations into humidity and temperature responses were used again. Artificial sources of radiant energy were added to the standard equipment.

The influence of *visible*, *ultra-violet* and *infra-red* radiation was examined separately. Since neither visible nor infrared radiation proved to exert any influence on *detached* conidia, a description of the lamp types used for studying the possible biological effects of those kinds of radiation will be omitted. As expected, u.v. irradiation did influence the germinative power of the conidia. A concise description of the appliances and procedures used in the irradiation research conducted is most certainly indispensable.

The u.v. *radiation sources* used in the experiments are special discharge tubes made for experimental purposes by Philips Ltd., Eindhoven, the Netherlands. They are not supplied to the trade but were kindly put at our disposal by the manufacturer.

Several kinds of germicidal ultra-violet discharge tubes are on the market. They are used for the purpose of air disinfection (see *i.a.* DE WEILLE, 136, 137). All radiation sources officially rated as germicidal or put on the market as altitude sun lamps, "alpine sun" or the like have one feature in common that renders them useless for the author's work. Their spectrum contains much short-wave u.v. radiation, the maximum emitted radiation usually being found at a relatively small wave length. On the other hand the solar spectrum as received after having passed the atmosphere contains no radiation of a wave length (λ) less than, say, 2950 Å. The longer the λ, the higher the intensity of the u.v. radiation received. When considering the wave-length interval between 2900 and 3900 Å, the maximum thus lies at 3900 Å.

Biological effects brought about by u.v. radiation are the more marked when λ is smaller (DE WEILLE, 141). The difference in the biological effect of two kinds of monochromatic u.v. radiation whose difference in wave length is *e.g.* 500 Å is extremely great. And since the author wished to imitate as far as possible the sun's u.v. spectral range in order to obtain an impression of possible influences exerted by *natural* radiant energy upon *Phytophthora* the normally available u.v. lamps could not be used.

Therefore the tubes lent by Philips constituted a solution to the problem of finding a suitable imitation of the solar u.v. radiation as normally observed on the earth's surface. Fig. 10 represents the emission spectrum of one of the borrowed types. It contains no waves of a wave-length not found in the solar

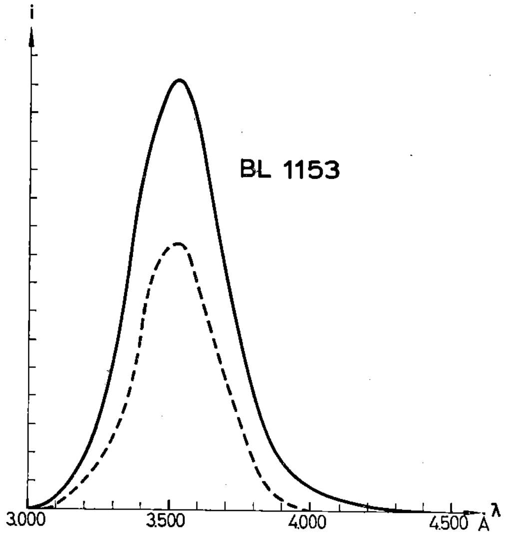

Fig. 10
Emission spectrum of the BL 1153 discharge tube as procured by the manufacturer. Dash line represents the energy measured after transmission.

spectrum. The maximum intensity emitted lies at $\lambda = 3500$ Å and not at a greater wave-length as in the solar spectrum. This implies that in the artificial radiation the predominant part of the total radiant energy emitted consists of a physiologically probably slightly more active kind of radiation than in natural sunshine. But on the other hand the intensity of u.v. irradiation attained by using the described discharge tubes is, at best, of the same or an equivalent order when compared with natural u.v. intensity (DE WEILLE, 141). Meanwhile it is not *equal* to solar u.v. intensity. Irradiation intensity (i) in most laboratory experiments did not exceed 200,000 ergmm^{-2}h^{-1}, the highest value of i – measured at a 9 cm distance from the middle of a BL 1153 discharge tube – amounting to 364,500 ergmm^{-2}h^{-1}. If we bear in mind that the intensities of solar ultra-violet radiation computed for de Bilt by DE BOER (14) may easily surpass 1,000,000 ergmm^{-2}h^{-1}, we can conclude that the discharge tubes are suitable for the purpose, but that the intensity of irradiation obtained with them is modest as compared with that of the u.v. part of sunlight. This may make up for a somewhat more favourable spectral composition of the former (cf. DE WEILLE, 141).

Ten tubes were placed in parallel position in an iron frame, which could be placed higher or more directly above the mycotron in order to vary the intensity of irradiation and to fix it at any desired level.

Measurement of u.v. intensity was carried out according to an indirect method, making use of a Pressler photo-electric cell equipped with a more than semi-spherical quartz bullet for measuring direct and diffuse radiation at the same time and with an U G 11 u.v. filter cutting off all radiation of a wave length > 3900 Å. This antimony cell of the type used by DOGNIAUX (30) for his investigations into the radiation conditions in Belgium has been described by VASSY (126). The principal features are shown in Fig. 11.

Having connected the cell with a mV-meter we obtain relative data concerning the u.v. radiation transmitted by the filter and absorbed and converted into a voltage by the cell. If the spectral composition of the irradiation in question is known we are now able to express the total u.v. intensity in *relative units* after having multiplied the data in mV with the value of the ratio total solar u.v. radiation divided by u.v. radiation converted into an electric voltage by the Pressler cell. In articles on irradiation experiments several authors have accepted such relative values. Since the experiments described in this treatise deal with naturally prevailing environmental elements *and* imitation thereof we cannot be satisfied with relative figures concerning the imitations which ignore their proportion to absolute figures regarding natural u.v..

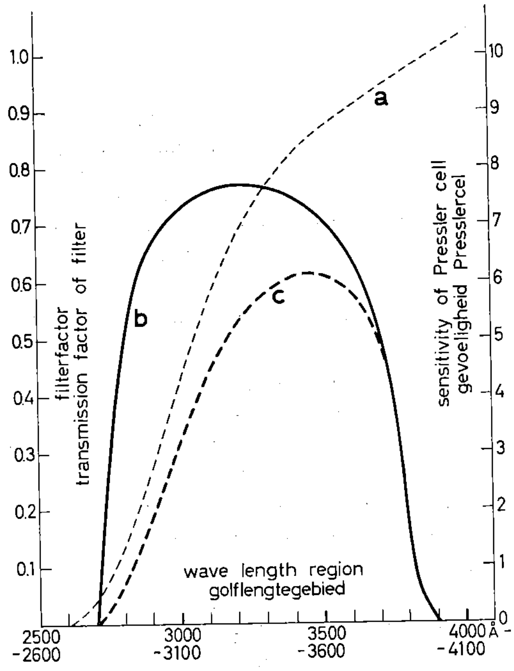

Fig. 11
Characteristic features of the Pressler cell (a) and its UG 11 filter (b). Curve c (= a × b) includes the part of the total u.v. radiant energy that is ultimately recorded (in mV).

We therefore made observations in the open when the sky was clear. The voltages measured were compared with the data given by DE BOER (14), which had been slightly modified so that they only covered u.v. radiation with λ not exceeding 3900 Å. Of course the ratio of converted u.v. to total u.v. was, again, taken into account for the spectral composition of the measured natural u.v. at each separate moment of measurement. DE BOER's mcals were converted into ergs. A graph was composed showing the (very regular) relation between converted u.v. radiation and measured mV. This graph enabled the author to interpret the measurements of artificial u.v. in the laboratory, so that in this paper radiant energy is expressed in the unit ergmm^{-2}h^{-1}.

Irradiation experiments were carried out with conidia-covered object slides located at several depths in the climatic chambers, which were used open, covered with a thick plastic lid or with a plastic film. For irradiation tests at higher intensities object slides were also placed on the lids of the climatic cells. Irradiation could thus be carried out either at room humidity and temperature (slides in open Petri dishes or not in dishes at all) or at a r.h. of 100% and room temperature (slides in Petri dishes covered with a thin plastic film; wet filter paper present).

2.3.4 *Radiation responses*

1. It appeared from the experiments that small doses of u.v. energy stimulate virulence by raising the germinative capacity;
2. larger doses of u.v. energy reverse this effect and are even fungicidal.

R.h. = 100%						R.h. = 70%						R.h. = 70%					
U.V. 130,000 ergmm^{-2}h^{-1}						U.V. 175,000 ergmm^{-2}h^{-1}						not irradiated					
D	G	n	K	g	s	D	G	n	K	g	s	D	G	n	K	g	s
0	6	444	1.4	8	0.6	0	6	444	1.4	8	0.6	0	6	444	1.4	8	0.6
0	6	415	1.4	6	0.6	0	6	415	1.4	6	0.6	0	6	415	1.4	6	0.6
¼	23	426	5.4	7	1.1	¼	7	563	1.2	11	0.45	¼	24	581	4.1	11	0.8
¾	35	395	8.9	6	1.4	¾	23	585	3.9	11	0.8	¾	25	600	4.2	12	0.8
1½	7	290	2.4	3	0.9	1½	6	573	1.0	11	0.4	1½	21	584	3.6	11	0.8
2½	49	338	14.5	4	1.9	2½	28	265	10.6	2	1.9	2½	26	533	4.9	11	0.9
3¾	59	471	12.6	9	1.5	3¾	68	448	15.2	8	1.7	3¾	34	542	6.3	11	1.0
4¾	87	494	17.1	10	1.7	4¾	57	320	18.0	3	2.1	4¾	34	528	6.4	11	1.1
5¾	30	232	12.9	2	2.2	5¾	29	157	18.5	1	3.1	5¾	23	517	4.4	11	0.9
6¾	37	299	12.3	3	1.9	6¾	18	553	3.3	11	0.8	6¾	37	544	6.8	11	1.1

Table 3

Results of an irradiation experiment with loose conidia. D = duration of irradiation. G = number of conidia germinated; n = number of conidia in the sample. K = percentage germinated; g = weight allotted according to Fig. 12; s = theoretical standard deviation (of the internal frequency) of the samples in case of binomial distribution of germinated elements.

Table 3 illustrates the aforementioned results. The left hand set of data applies to conidia irradiated through a thin plastic film. Although a high air humidity could thus be maintained in the Petri dishes, the film intercepted a moderate part of the radiation. The other 2 sets of data were obtained at room humidity varying from 69 to 70%. The fact that the various samples are not equally reliable is expressed by the weights, g, assessed according to a method developed for the purpose of averaging corresponding data in parallel series (DE WEILLE, 141, 142). For completeness' sake the graph representing the values of g allotted according to various values of n is reproduced here as Fig. 12. Though no data are averaged in the case of Table 3 the values of g nevertheless reflect the relative weight we can attach to the various values of K.

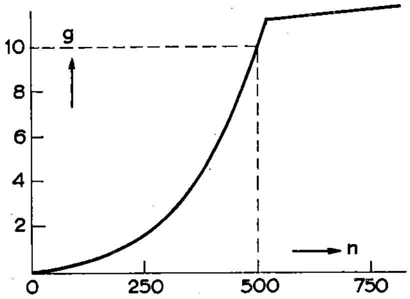

Fig. 12
Allotment of g according to n. After DE WEILLE (142).

When considering the data in Table 3 the impression is obtained that K is maximal after irradiation with a dose in the neighbourhood of, say, 600,000 ergmm^{-2}h^{-1}, for r.h. as such does not play an important part (cf. DE WEILLE, 141). But undersized samples occurring in the table cloud the correctness of the picture. For that reason all K-data having a weight of less than 8 were omitted when composing a table in which K was compared with the doses Q of radiant energy applied to the samples. Q = duration × intensity = D × i. The result is shown in Table 4.

In complete accordance with the irradiation results published elsewhere with regard to related fungi (141, 142, *Peronospora* spec.) stimulation of germination increases with increasing doses of u.v. energy until a maximum is reached, whereupon the values of K decrease more strongly when the dose of u.v. energy applied is further increased.

The theoretical values of 2 × standard deviation of internal frequency (= 2s), a quantity already stated in Table 3, are included in Table 4 in order to give an impression of the reliability of the data.

It should borne in mind that the exceedance probability (P_k) of the boundary values $K_k \pm 2\,s_k$ is, theoretically, 5% (assuming a binomial distribution) but, as stated earlier, it actually appears to be 9% to 10% owing to persistence (skew distribution; P found empirically; DE WEILLE, 142). This circumstance is shown

dose (Q)	K	g	2s
0	1.4	8	1.1
43,750	1.2	11	0.9
131,250	3.9	11	1.6
262,500	1.0	11	0.8
487,500	12.6	9	3.1
617,500	17.1	10	3.4
656,250	15.2	8	3.4
1,181,250	3.3	11	1.5

Table 4
Results of irradiation with different doses Q in ergmm^{-2}h^{-1}. For other symbols see Table 3.

in Fig. 13, which presents in graphical form the data already given in Table 4. In drawing the trend curve one observation had to be discarded as untypical; in the sample concerned the persistance had not (yet) been overcome by the irradiation applied.

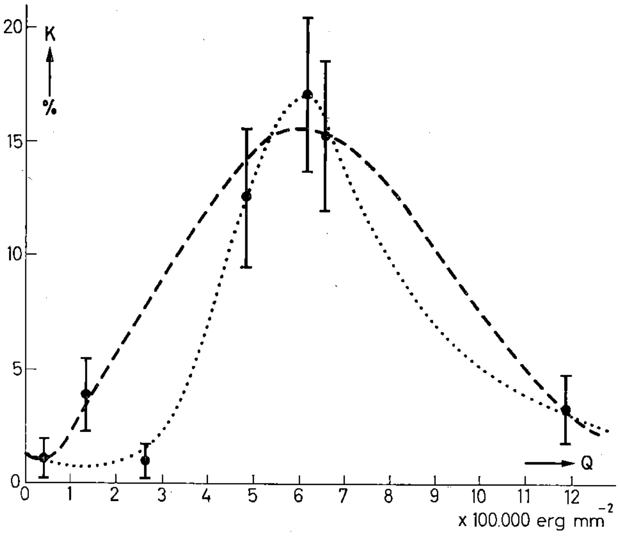

Fig. 13
Graphical representation of values of Q and K ± 2s contained in Table 4.

In earlier publications the curve of the type shown in Fig. 13 had been named the "inactivation curve" (141, 142), for in the open field activating daily quantities of u.v. radiation are readily attained even on sunshine deficient days so that the inactivating power of bright sunshine is more conspicuous.

Table 5 gives data obtained in an experiment comparing low intensity irradiation with a non-irradiated parallel treatment at the same r.h. of 82 per cent. The latter treatment shows the knock-down effect. Stimulation brought about by u.v. was sufficiently strong to counterbalance that effect. The activating influence exercised by the irradiation is demonstrated in the separate right hand

	Diffuse daylight			U.V. 45,000 $\mathrm{ergmm^{-2}h^{-1}}$				ratio
D	G	n	$K_{diff.}$	G	n	$K_{irr.}$	Q	$K_{irr.}/K_{diff.}$
0	1,452	2,243	64.7	1,452	2,243	64.7	0	1.00
2	662	1,657	40.0	735	1,192	61.7	90,000	1.54
$3\frac{1}{4}$	460	1,158	39.7	497	767	64.8	146,250	1.63
$4\frac{1}{2}$	362	804	45.0	665	810	82.1	202,500	1.82
$9\frac{3}{4}$	541	1,672	32.4	717	1,046	68.5	438,750	2.12

Table 5

Effect of weak u.v. irradiation on loose conidia as compared with exposure to medium otherwise the same, but in diffuse daylight.

column of Table 5, showing it in a relative measure. Since doses exceeding 600,000 $\mathrm{ergmm^{-2}}$ were not attained inactivation did not occur in this experiment. Meanwhile the results substantiate the findings of RENTSCHLER *et al.* (111, bacteria) who showed that the dose is the sole determinant of biological effects. The intensity, one of the components of the dose ($Q = d \times i$), is not in itself a determinant. According to the adduced article the mean lethal dose of u.v. radiation remained the same even when delivered in a time of the order of 10^{-6} sec.. In our considerations d is only measured in hours within each individual day.

2.4 Sporulation and environment

The conditions permitting fructification to take place were summarized on page 33. According to the available literature the main condition to be met is the prevalence of *r.h.* > *90* % within fairly wide temperature limits.

It was shown at the K.N.M.I. that *light*, i.e. *visible radiation*, also plays a role of extreme importance with regard to fructification.

1. *Conidiophores* are indeed formed in a saturated or nearly saturated atmosphere, independent of the light intensity in that atmosphere. Aerial mycelium is formed equally well in complete darkness, under continuous illumination or in the natural alternation of night and day. Consequently the formation of aerial hyphae is a photo-insensitive process.
2. Conidia are also formed in saturated or near-saturated air. But with regard to *sporulation* light also plays a part.

2.1 Very few conidia are formed under continuous illumination of 400 lux or more. An illumination of 250 lux already constitutes an impediment to normal sporulation.

2.2 In continuous darkness (or at a very low level of illumination) continuous sporulation can be expected to occur. This implies that a sporal population obtained by culturing *Phytophthora* in darkness will comprise a broad range of age classes.

2.3 In the natural alternation of night and day sporulation only takes place during the night, so that as long as the humidity condition remains fulfilled and the substratum remains fit for spore production, a new generation of conidia is added every night to the sporal population present on the substratum. After a light period inhibiting sporulation the spore production is more abundant than in continuous darkness. In fact light inhibits spore formation, while at the same time advancing subsequent sporulation in the following dark period (cf. YARWOOD, 147, 148; DE WEILLE, 142).

It follows that samples of conidia harvested on the third morning after the night in which sporulation commenced (*i.e.* after 3 subsequent waves of spore formation) contain various proportions of 3 age groups of conidia, each showing its own responses to environmental factors. Such a collection of conidia will undoudtedly constitute a heterogeneous population not suited to experiments as conducted at the K.N.M.I.. Hence the rigid rules listed in the items 1 to 4, forming part of the general method of working (see p. 40).

Meanwhile the basis of this procedure will have become clear. By suppressing sporulation with the help of illumination the subsequent period during which the then abundant formation of sporal material can take place furnishes *all* conidia to be harvested at the beginning of an experiment. That implies that all conidia harvested will belong to one age group. Since the lowest conidia on a conidiophore are formed earlier than the more apical specimens the research worker is obliged to put up with at least a limited variety in age.

In a laboratory experiment with controlled light conditions in a constantly saturated atmosphere the first, still very thin-walled conidia appeared on previously formed undifferentiated aerial hyphae 4 hours after the sudden onset of (artificial) darkness. So if a suitable summer night lasts 8 hours, 4 hours will be devoted to the *induction* of sporulation. The maximum age difference thus amounts to only 4 hours.

Item 4 on page 40 prescribes a period of light between the preceding dark period and harvest. This interval stops further sporulation and permits the youngest conidia to grow out. Thanks to this procedure no half-developed conidia need ever be harvested; this will considerably improve the homogeneity of the material used in experiments.

An important advantage of the aforementioned prescription lies in its securing a more or less uniform degree of maturity at a not too low level of germinative capacity.

2.5. Reactions of attached conidia to the environment

In order to judge the influence of age upon the properties of the conidia at the moment they are harvested or anyhow dislodged from their sporophores it is of the utmost importance to study the responses of the conidia to their environment when still attached to their substratum.

2.5.1 *Appliances and procedures*

Potato plants, tubers and leaves were kept in a saturated atmosphere by the methods already described. They were kept in either continuous darkness or under continuous illumination followed by one dark period or in a natural or artificial alternation of light and dark periods.

For larger lots of decised sporing leaves a small glasshouse was contrived. It consisted of two Dutch windows, one upon the other, so that the wooden frames together enclosed a flat glass space, in which near-saturation was secured by two layers of wet filter paper, one lying upon the bottom and one cohering to the upper window. Additional daytime or nocturnal illumination was provided by TL tubes suspended above the glass-house.

Samples were taken at specified times of the day by brushing conidia off the conidiophores. Great care was taken to ensure that conidia from at least three different tubers or three different leaves were applied to every object slide in order to check any bias attributable to disparity in substratum.

The samples were germinated and prepared in the usual way.

2.5.2 *Humidity responses*

Fig. 6 on page 28 showed the influence of exposure to various air humidities upon the viability of attached conidia as determined by CROSIER (29). Speaking in general, these results were confirmed by duplicate tests which indeed showed that attached and detached conidia cannot be compared or lumped together in any study of their reactions upon environmental conditions. The usual train of thought, in which the results obtained by CROSIER (29) with attached conidia are applied to the loose sporal material constituting the spore flights wafting over the fields and onto the foliage, must therefore be repudiated.

Meanwhile there are two items that are not in accordance with Fig. 6.

In the first place the very high values of K given in literature were not corroborated in the laboratory, nor were they obtained in field samples taken under ideal conditions.

In the second place the progression (in Fig. 6) of the full line r.h. = 100% with time is not consistent with the results obtained at the K.N.M.I.. Starting from K = 80% the course of K with t as given by CROSIER (29) is to be expected, but starting from a lower initial value it is not. An upward trend is equally probable in such cases.

It was found that in a saturated atmosphere the level of germinative power is connected with *age* and since we have already noted the relationship between age and light (see p. 53), the latter environmental element should also be taken into account.

2.5.3 *Radiation responses*

In respect to solar radiation we can distinguish between its ultraviolet, its visible and its infrared components.

Indications were obtained that ultraviolet radiation is detrimental to attached conidia and that infrared rays do not exert any appreciable influence on them. Results obtained with u.v. irradiation of blighted plants are not yet available in such quantities as to allow the author to present statistically reliable results.

An indirect response to *visible radiation* exists; this response is very marked and may be considered the principal topic of this treatise because of its far-reaching implications.

As stated on p. 53 sporulation is directly related to the occurrence of darkness or dark periods, so that the *age* of the conidia is also connected with it. We shall see what happens to the conidia (after each dark period) with increasing age.

A saturated or nearly saturated atmosphere allows newly-formed conidia to *mature*. When harvested in the early morning hours their germinative power is still negligible. As a result of maturation it will increase gradually until a maximum value of K is reached. In an earlier reference to the subject (142) the following definition was given: **maturation is the phenomenon of the germinative power increasing with time.** In this connexion the rate of change of K, dK/dt, may be called the maturation speed.

Maturation does not take place in an atmosphere which is not completely or almost saturated.

If the conidia are formed at night and are not yet viable in the early morning this implies that subsequent maturation will take place at daytime. This is

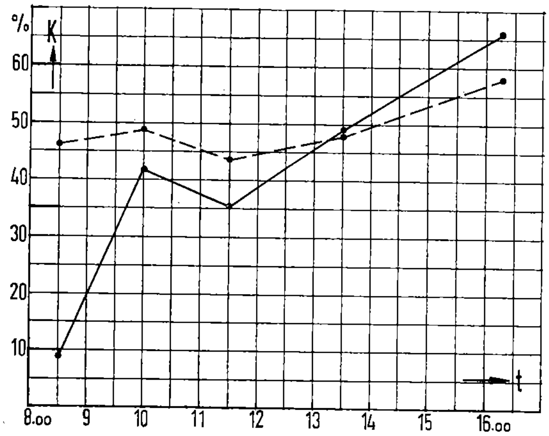

Fig. 14

Germinative power K of sporal samples taken from a uniform substratum at different times t (C.E.T.). Duration of germination d = 45 h. at $\delta = 13°$ C. R.h. = 100%.

- - - - -: continual darkness after a normal 24 h. day.

———: natural alternation of night and day.

confirmed by Fig. 14, which shows the results of an experiment conducted on 14th November, 1960.

30 hours prior to the test a uniform substratum grown with mycelium of one origin and inoculation date was split into two parts. One part was incubated further in complete darkness, while the other half was exposed to natural conditions of light and darkness, both at 100% r.h..

In the "natural light" treatment sporulation occurred abundantly after having been checked temporarily during the day. At 8.30 on the day following sporulation the germinative capacity of the young sporal population was still low. Gradual sampling showed gradual maturation. At 16.15 (C.E.T.) this test was terminated.

In the "complete darkness' treatment gradual sporulation and ripening had already begun before sampling started; it continued during the experiment. The values of K showed no significant differences.

Table 6 shows the various data together with the corresponding values of n (sample size) and s (theoretical standard deviation of the internal frequency of K), so that this table also serves as a *reliability test.*

C.E.T.	natural light and darkness				complete darkness			
t	K	n	s	index	K	n	s	index
8.30	8.7	285	1.7	a	46.5	456	2.3	α
10.00	42.0	686	1.9	b	48.8	719	1.9	β
11.30	35.6	881	1.6	c	43.7	524	2.2	γ
13.30	49.3	1066	1.5	d	48.1	389	2.5	δ
16.15	65.7	825	1.7	e	58.0	638	2.0	ε

Table 6

Progression of K with time t ($\equiv$ K(t)) in darkness as compared with that under natural light conditions. The data correspond with Fig. 14.

A "continuous light" treatment is not represented since no sporulation of any significance occurs under continuous illumination.

A *significance test* was also carried out in order to judge the differences x_k between each value of K_k and the germinative capacity of the first sample taken, *viz.* K_a, so $x_b = K_b — K_a$. Accordingly, $x_\gamma = K_\gamma — K_\alpha$, *etc.*. It should be noted that the differences observed are not attributable to pure chance. A difference is considered significant and not ruled by chance if the exceedance probability P of a deviation $|x|/\sigma \geqslant 2$ does not exceed 5 per cent, in which $\sigma_k = \sqrt{s_a^2 + s_k^2}$, where k may have the values b, c, d, *etc.* (cf. DE WEILLE, 141). It is assumed that if the probability of $|x|_k/\sigma_k > 2$, or the probability that a deviation of 2σ is exceeded is less than 5%, it is improbable that the samples compared originate from one and the same unchanged universe, in which case the observed differences were fortuitous.

In the same way the differences $x_{k\varkappa}$ between corresponding values of K in both treatments were examined.

Table 7 gives the results of the significance tests within each separate treatment. See Table 6 for the values of K and the meaning of the indices.

natural light and darkness				continuous darkness			
index of x_k	σ_k	x/σ	P	index of $x_\varkappa$	$\sigma_\varkappa$	x/σ	P
differences with K_a				*differences with K_α*			
$k =$ b	2.55	12.8	0.0	$\varkappa = \beta$	2.9	0.8	0.22
c	2.3	11.6	0.0	γ	3.2	0.9	0.19
d	2.3	17.9	0.0	δ	3.4	0.5	0.32
e	2.4	23.7	0.0	ε	3.05	3.8	0.00
$x_e = K_e - K_a$ etc.				$x_\varepsilon = K_\varepsilon - K_\alpha$ etc.			
other differences				*other differences*			
$k' =$ c − b	2.5	2.6	0.0	$\varkappa' = \gamma - \beta$	2.9	1.8	0.04
d − c	2.2	6.3	0.0	$\delta - \gamma$	3.3	1.3	0.09
e − d	2.3	7.2	0.0	$\varepsilon - \delta$	3.2	3.1	0.00
$x_{e-d} = K_e - K_d$ etc.				$x_{\varepsilon-\delta} = K_\varepsilon - K_\delta$ etc.			
Conclusion: the phenomenon of maturation observed is certainly no fortuitous course of events.				Conclusion: the occurrence of a majority of insignificant differences in this treatment substantiates the assumption of a special influence on the data in the other one.			

Table 7

Significance test in each treatment separately. Values of P refer to unilateral testing (2½%).

Although table 7 makes the prevalence of an active external factor in the 'light and darkness' treatment lacking in the 'continuous darkness' treatment extremely probable, an additional test was carried out in order to examine the significance of deviations between corresponding values of K (given in table 6) in both of the two objects. In this connexion the difference $|x|_{a\alpha} = K_\alpha - K_a$ *etc.*; $\sigma_{a\alpha} = \sqrt{s_a^2 + s_\alpha^2}$ *etc.*.

Table 8 shows clearly that after the split-up of the original culture of *Phytophthora* into two parties constituting two treatment groups, the conidia formed in the parties concerned no longer belong to one population but constitute two universa with different properties. Hence all differences found between corresponding fixed points of the lines drawn in Fig. 14 are mathematically significant, except of course the difference next to the intersection of those lines.

index of $x_{k\varkappa}$	$\sigma_{k\varkappa}$	x/σ	P
$k\varkappa = a\alpha$	2.9	13.2	0.00
$b\beta$	2.7	2.5	0.01
$c\gamma$	2.7	3.0	0.00
$d\delta$	2.9	0.4	0.34*
$e\varepsilon$	2.6	2.95	0.00
$x_{e\varepsilon} = K_e - K_\varepsilon$			
etc.			

*) near point of intersection of the curves in Fig. 14, p. 55.

Table 8
Significance of departures between corresponding values in both treatments reciprocally.

Fig. 15 represents K(t), the progression of K with time in an experiment carried out on 29th December, 1959, when gradual harvesting was continually applied. No wonder that the results obtained in that way (in air humidity or irradiation experiments) without knowledge of the process of maturation were surprising in those days. The progression of the germinative capacity with the time of the day represented by Fig. 15 was determined more or less by accident

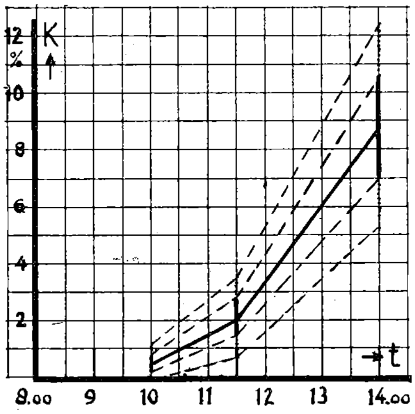

Fig. 15
Maturation in a conidial generation of *P. infestans*. Dash lines indicate boundaries K ± s and K ± 2s.

and was detected later when scrutinizing the various observational data. Table 9 gives the data pertinent to Fig. 15.

C.E.T. t	K	n	σ
10.00	0.5	623	0.3
11.30	2.1	373	0.7
14.00	8.8	238	1.8

Table 9
K(t) in a maturing conidial population. Data correspond to fig. 15.

Of course the increase of K cannot go on *ad infinitum*. After a maximum has been reached the process of maturation is followed by its counterpart, the *decline* of K, because of the senescence of the conidia. It should be remembered in this connexion that we still discuss *attached conidia in a (nearly) saturated atmosphere.* In this context **decline** (of viability) **is the phenomenon that the germinative power decreases with time.** We can say that a sporal population matures if $\frac{dK}{dt} > 0$, whereas it declines if $\frac{dK}{dt} < 0$.

In continuous darkness maturation and senescence may occur simultaneously. In the natural alternation of night and day maturation will start afresh every morning after nocturnal sporulation has given rise to a new sporal generation. If the ambient air remains in a state of (near-)saturation the maximum value of K may be reached in the afternoon or evening following sporulation. It appeared that the rate of decline of K becomes increasingly faster in the early hours of the second morning of the sporal generation's existence, so that during that morning K will soon become a negligible quantity. Meanwhile a new generation begins to mature, thus completing a picture of *periodicity.*

The periodicity of the germinative power K of conidia of Phytophthora infestans implies that in a constantly saturated or nearly saturated atmosphere K is very low in the early morning hours, increases until a maximum is attained in the afternoon or later, *whereafter it decreases again to a low value* in the early hours of *the following morning, when this daily variation* of K *recurs.*

Experimental results underlie the above theorem. In graphical form fig. 16 depicts data obtained in an experiment conducted on 25th and 26th November, 1960.

After splitting up the cultures into two parties, sporulation in the "continuous darkness" treatment started earlier than in the "night and day" treatment. This was expressed in an initially marked difference in phase. In the first morning of sampling the treatments were clearly out of phase. Thereafter the object "darkness" did not follow the maturation line. After a period of reaction K again increased. The behaviour of K in the treatment "night and day" shows the specific periodicity already described.

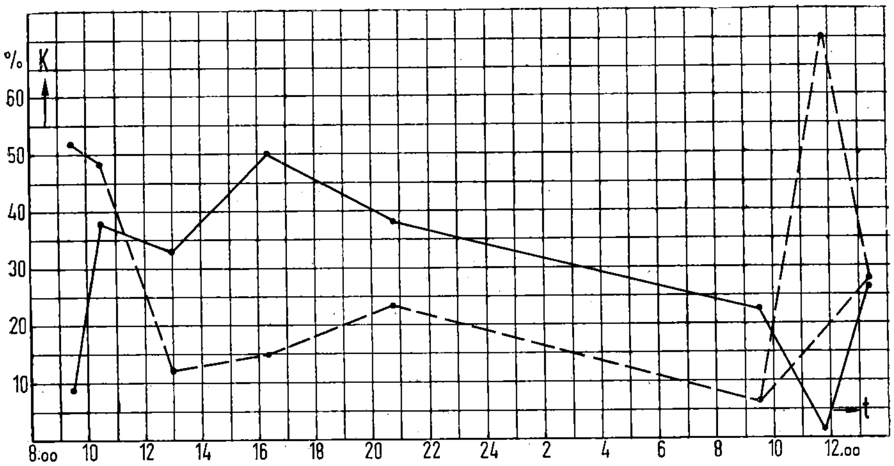

Fig. 16

K(t) in saturated air in what originally was one universe; t in C.E.T. . R.h. = 100%; d = 50 h.; δ = 11.8° C.

———: development in natural alternation of night and day.

- - - - -: development in continuous darkness.

Note typical "outlier" on right hand side of graph; data in Table 11.

Table 10, in which the meaning of all symbols remains unchanged, shows that the data on which Fig. 16 is based are reliable.

As a last example out of the extensive laboratory work on *Phytophthora infestans* and some of its relatives the results are given of a periodicity test carried out in two replications derived from one universe. One full line was drawn through the points representing the higher values of the ordinate K for various values of t and a second one was drawn through the points representing the lower K-values, while the weighted means of the corresponding data in the two sets of figures gave rise to the dash line. Weights (g) were allotted in accordance with Fig. 12 on p. 50. The variability shown in Fig. 17 is partly to be ascribed to the circumstance that in December, 1960, when the experiment was

C.E.T.	natural light and darkness			continuous darkness		
t	K	n	s	K	n	s
9.30	8.9	441	1.4	51.7	586	2.1
10.30	37.8	423	2.4	48.3	547	2.1
13.00	32.7	599	1.9	12.3	569	1.4
16.15	49.8	544	2.1	14.8	609	1.4
20.45	38.1	587	2.0	23.4	292	2.5
9.30	22.4	663	1.6	6.3	543	1.1
11.45	1.7	668	0.5	69.9	672	1.8
13.45	26.1	278	2.6	27.5	589	1.8

Table 10
K(t) under different light regimes. Data correspond to Fig. 16.

carried out, the substrata were not yet as homogeneous as in more recent experimental work. In part the encountered variability illustrates the usual difficulties met when evaluating experimental results of this type.

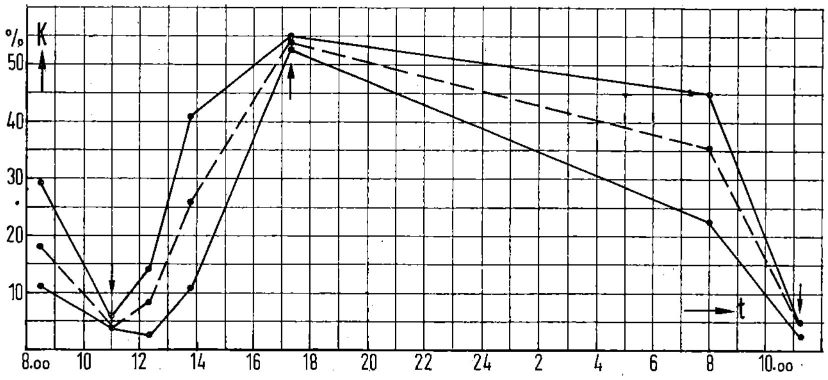

Fig. 17
K(t) in one universe in saturated air under natural daylight conditions. Test was carried out *in duplo*; dash line represents weighted mean values; data in Table 11.

The data of Fig. 17 are reliable as is shown by table 11. This table also shows that averaging only 2 sets of data does not enhance the accuracy of the results. After averaging the sets of data only 3 points remain in fig. 17 to prove the reality of the phenomenon of periodicity. In those points the mean error σ, the standard deviation of the weighted mean, is smaller than each of the two values of s, the theoretical standard deviation (of the internal frequency) of either of the two values of K.

K	g	s	K	g	s	$\overline{K}$	σ
29.3	7	2.2	11.2	11	1.3	18.2	8.8
6.3	1	1.7	4.0	11	0.8	4.2	*0.6*
14.1	11	1.4	2.7	11	0.7	8.4	5.7
41.0	11	2.1	10.8	11	1.3	25.9	15.1
54.8	11	1.9	53.2	11	1.8	54.0	*0.8*
22.7	8	2.0	44.7	11	1.9	35.4	10.9
2.8	1	1.2	5.0	4	1.2	4.6	*0.9*

Table 11
Two conformable sets of data and their weighted means $\overline{K}$. Data refer to Fig. 17.

2.6 Survey and conclusions

The findings resulting from the laboratory work have an impact on the classical picture of the life cycle of *Phytophthora infestans*. The new picture regarding the bionomics of the potato blight fungus' inoculum, which we now have in mind, is briefly outlined in the following survey:

1. Conidia still *attached* to their substratum by conidiophores are extremely susceptible *to low air humidities*, which decrease the viability of the sporal material. The lower the r.h. the faster the rate of viability decrease.

   This process should probably be associated with the host plant's evapotranspiration because loose conidia do not share the above-mentioned susceptibility.
2. Conidia newly formed during the night still have to attain an appreciable level of germinative power (K). In saturated or nearly saturated air the conidia mature: K increases. In the afternoon or later K reaches a maximum unless decreasing r.h. involves a corresponding premature fall of K.

   In a non-saturated atmosphere no maturation takes place.
3. In the course of the morning conidia are detached from their sporophores; according to HIRST (57) this process is probably associated with solar radiation. The spore content of the air is highest by noon. *Phytophthora* conidia are rare after 5 *p.m.* (HIRST, 54).
4. *Detached* conidia survive low air humidity; they are susceptible to ultraviolet radiation. Low daily doses may add to the virulence of the inoculum; doses exceeding, say, 1,000,000 ergmm^{-2} are fungicidal.
5. Meanwhile the remainder of the still *attached* conidia may have passed the peak value of K. During the following nocturnal hours K decreases. The *decline* in viability will be completed by the early morning, the germinative capacity of the senescent sporal generation having become negligible.
6. Nocturnal air humidity permitting, a new generation of conidial material is

formed during the night. Conidia are not formed when receiving an illumination exceeding or equalling 400 lux, so that large scale daytime sporulation is checked by visible radiation. Light, however, has no impact on the previous formation of aerial hyphae.

7. Germination of (viable) conidia necessitates the presence of (liquid) water.

From 5. and 6. we may conclude that under conditions of constant atmospheric near-saturation the germination capacity of the inoculum displays a definite periodicity: viability is lowest in the early morning and highest after mid-day.

The periodicity characterizing *attached* conidia and the u.v.-sensitivity of *detached* infectans shed new light upon the epidemiology of blight. In this connexion account should be taken of the imperative requirement of the presence of *water*.

In the next chapter it will be shown what could be done in the open field with the above laboratory results.

CHAPTER III

FIELD TESTS

3.1 The probable course of events in the field

From the results obtained *in vitro* we can derive some assumptions regarding the organism's behaviour in the field. Newly obtained information with regard to the properties of the inoculum and its formation provides new insight into the developments leading to epiphytotics and those preventing the occurrence of such outbreaks. Within the framework of this renewed epidemiologic picture the presumed sequence of events is as follows.

1. Since sporulation is a nocturnal process fresh, newly formed conidia are to be found in the early morning hours. Conidia are not formed later in the day.
   The majority of the *newly-formed conidia are still unable to germinate.*
2. They will not mature if the air in the ecoclimate is not completely or almost completely saturated with water vapour. At *high atmospheric humidity* maturation does occur. The required saturation implies in most cases drizzle, fog and prolonged leaf wetness.
3. The conditions mentioned under 2. are not consistent with the occurrence of a prolonged period of bright sunshine. Sunshine will cause air temperature to rise and in such circumstances a fall in r.h. is to be expected. Indirectly, *sunshine is thus antagonistic towards maturation.*
4. In the course of the day many conidia are detached from the conidiophores. Intense afternoon sunshine kills the loose conidia in the air and the exposed foliage, thus minimizing the danger of subsequent nocturnal crop infection. Directly, *sunshine reduces the potential danger of infection.*
5. If maturation has occurred, and the germinative power of the inoculum present is not reduced by the action of sun radiation, infection will take place *after mid-day provided the foliage remains wet long enough* after noon *or is wetted* after mid-day by precipitation.
6. The occurrence of a leaf wetness period of a duration sufficiently long for infection to be achieved can be counteracted by spells of more or less intense solar radiation and by wind, the occurrence of both or of either of the two elements enhancing the rate of evaporation of the water.

Pursuing this train of thought, an infection day will involve a considerable increase in blight incidence if it is deficient in sunshine and includes precipitation by noon or after mid-day.

3.2 The test fields

In both 1960 and 1961 the above picture of the presumed natural development of epiphytotics was tested in two experimental fields, one situated at Bennekom, the other at de Bilt. The aerial distance between the two fields amounted to 36 km. This distance is so small that *climatic* differences are negligible. But on the other hand *weather* differences may occur, so that after a period of nearly identical weather conditions infection may be brought about at Bennekom at a day in which such is impossible at de Bilt. Similarly, crop infection may occur at de Bilt whereas at the same date and after identical previous weather conditions the crop at Bennekom is not attacked. Provided accurate daily observations are made, the special cases of unequal simultaneous epidemiological developments will supply conclusive data concerning the causal organism's natural environmental responses.

3.2.1 *Bennekom 1960*

The first Bennekom test field, already described as an example of how to collect epidemiological data (DE WEILLE, 144), measured 100 m × 25 m. The distance between the plant rows amounted to 50 cm and the mutual planting distance within each row was *ca.* 40 cm. The rows were laid out in longitudinal direction, at right angles to a secondary road along which the narrow frontage of the plot was situated. The potato clone grown was the highly susceptible early "variety" *Sirtema*. Fig. 22 on p. 73 shows the location of the artificial source of infection maintained in the lot until the first matural focus had been established. It was placed 10 m from the roadside and circa 7 m from the left hand border as seen from the road. This implied that the artificial inoculum source, of which a description is given on p. 18 (see Fig. 3), was located in the S.-W. corner of the field.

A standard meteorological screen was mounted in the N.-W. corner. In addition, several meteorological instruments were placed above and in the crop.

3.2.2 *Bennekom 1961*

In the second experimental year the epidemiological research was resumed on a field of 90 m × 16 m. The direction of the (longitudinal) rows was NNW to SSE. The eastern longitudinal half of the lot was planted with the fairly susceptible maincrop clone *Burmannia*, the other half with the still later and yet less susceptible clone *Libertas*. Unlike Sirtema, both clones have blight-resistant tubers.

Planting distances conformed to those of the preceding year. The artificial inoculum source was placed in Burmannia in the NE part of the field.

In the second experimental year advantage was thus taken of previous experiences, *viz.*

1. Once the amount of inoculum has become considerable, the dispersal of sporal material in the main wind direction may suddenly happen so rapidly that the successive outbreaks can hardly be distinguished any more owing to a lack of perceptible zoning. Dissemination of spores in the opposite direction progresses more slowly; differences in intensity of attack are observable in the form of zones around the foci.
2. If a too susceptible clone is used as a test crop the rapidity of epidemic developments tends to shorten the period during which biological observations can be made.
3. The latter period can be extended by combining strips planted with early, maincrop and late clones.
4. A test field planted with only one clone does not allow adequate observations to be made with regard to the transition of blight from earlier to later potato clones.

No fungicidal protection was applied in the test field. Contrary to the method followed in the 1960 experimental field the Stevenson screen had been mounted outside the potato crop, *viz.* along the plot's wire fence, in an adjacent meadow. An extra screen housed an automatic recorder and its electronic equipment. The recorder was connected with a photo-electric instrument measuring duration of sunshine.

3.2.3 *De Bilt 1960*

The experiment in the relatively large trial fields (resp. 25 are (= *ca.* 0.6 acre) and 14½ are (= *ca.* 0.35 acre)) situated at Bennekom was duplicated in both test years in a plot located on the premises of the K.N.M.I..

In 1960 the nearly square lot at de Bilt measured 5½ are (= *ca.* 0.14 acre). Row direction was about N.–S. The planting system was 50 × 50 cm. A standard screen with the usual instruments had been mounted on a grass lawn next to the potato fields. Extra instruments were located in the field, both in and above the crop.

The potato clone planted was *Sirtema.* The artificial inoculum source was maintained in the S.W. of the plot.

3.2.4 *De Bilt 1961*

In the second experimental year there was a 14½ are (= *ca.* 0.35 acre) potato field, characterized by the same row direction and planting density as in 1960. But now the southern half had been planted with Burmannia and the northern half with Libertas. This change had been made for the same reasons as at Bennekom (see p. 65). The instrumental arrangements were the same as those made in the preceding year.

The artificial inoculum source was located in Burmannia in the southern part of the plot.

3.3 Meteorological observations

3.3.1 *Standard routine observations*

The meteorological screen placed at standardized level 1.50 m above ground contained in all cases the following instruments:
dry- and wet-bulb thermometers,
a "Six" maximum/minimum thermometer,
a thermograph (weekly rotation),
a hydrograph (weekly rotation).

The following instruments were placed in the field:
a Campbell-Stokes sunshine autograph,
a weather vane.

At de Bilt the daily readings were performed at ca. 8.15 C.E.T., and at Bennekom between 9.00 and 9.15 C.E.T.. The weather vane merely served as a rough indication of the main wind direction which was necessary for the biological sampling work.

The thermograph and the hygrograph were checked every day.

3.3.2 *Non-standard observations*

Whereas sunshine observations were made in order to test the influences of direct and indirect solar radiation on spore flights and the attached infectans, the ecoclimate in itself was not considered to be sufficiently represented by a combination of screen and sunshine data. For that reason in each parcel a *hygrograph* and a *thermograph* with weekly rotation were installed between the rows (see Fig. 18). Care was taken to ensure that the plants were damaged as little as possible. For that reason the instruments involved were not checked every day but only once or twice a week. In order to check the accuracy of the crop instruments, they and the screen instruments were regularly interchanged when the charts were changed. As a matter of fact the drawback of this system was that an instrumental error could remain unobserved for some days. It must be admitted that sometimes this did happen indeed during the experiments, though in general no difficulties were experienced.

Originally the special aim of using hygrographs was the composition of a kind of inventory of the periods with an r.h. $\geqslant 90\%$ so that insight could be obtained into the natural possibilities and natural limitations of sporulation.

Another item of great epidemiologic significance, the duration of leaf wetness periods, was studied at de Bilt only, *viz.* by placing in the crop a *leaf wetness recorder* (see Fig. 19). This is an apparatus developed by *Post* from the original hemp-thread wetness recorder by Woelfle (see HEIGEL, 50). It is manufactured by messrs. *de Wit*, Hengelo, Netherlands.

The measuring element is a piece of four-thread sail yarn which contracts when moistened and expands on becoming dry again. A change of length of the yarn is transmitted to a stylus by a mechanism similar to that used in hygrographs. A marked deflection of the recorded circular curve shows the transition from dry to wet and vice versa. If the yarn is moistened by rain an almost

Fig. 18
Bennekom, September 12, 1961. Thermograph and hygrograph located between the rows.

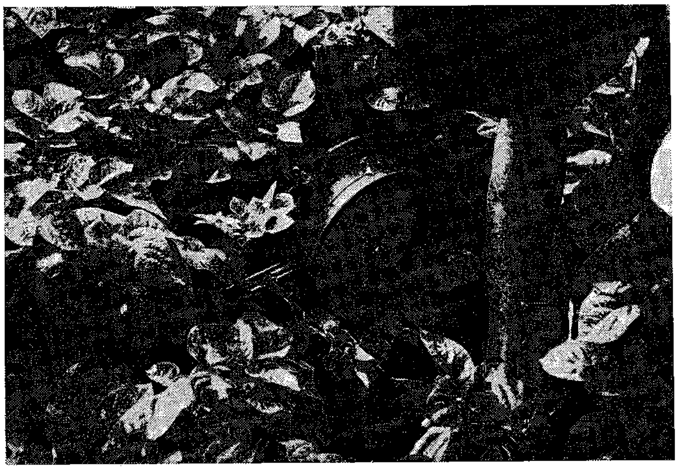

Fig. 19
De Bilt, July 31, 1961. A de Wit leaf wetness recorder in the potato crop. The "sail yarn" is located under the foliage canopy: lower left portion of the photo.

perpendicular deflection is recorded. If dew is the moistening agent a more sloping deviation is drawn.

Though the instrument had been designed for the apple scab warning service its indications of leaf wetness in a potato crop seem to be definitely more reliable

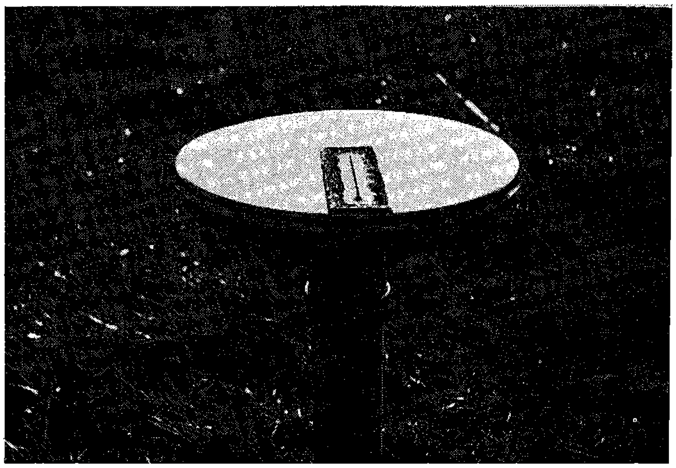

Fig. 20

A pluvioscope.

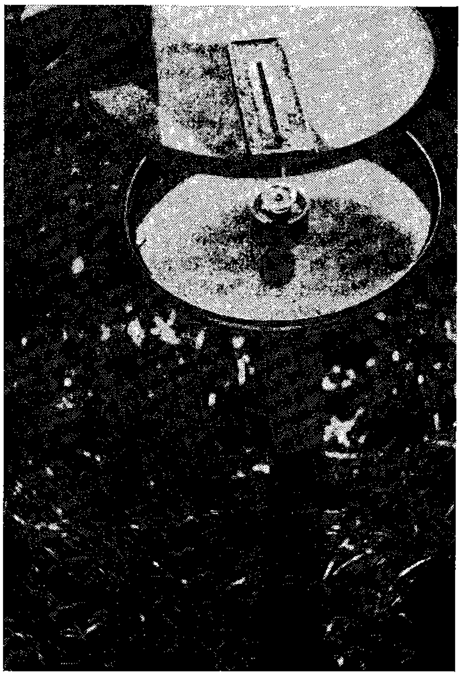

Fig. 21

than those in orchards, where sometimes the recordings lag considerably behind visual observations.

For epidemiological reasons rainfall is important as the cause of both high air humidity and leaf wetness. Since in this respect the amount of rain is not as important as the duration of rainy periods, only the latter were determined with the help of *pluvioscopes*, instruments recording duration of rainfall (see Fig. 20 and 21).

Under a metal lid with a radial slit diaphragm a disc with a circular sheet of pink paper is rotated (in daily rotation). When rain falls through the slit, the paper under it will redden where it is wet. The red sectors thus indicate the approximate rainfall duration. Like the leaf wetness recorder, the pluvioscope is also an instrument designed for the scab warning service.

In addition to the aforementioned non-routine measurements special attention was paid to the possibilities that might exist for simple measurements of the total daily amount of ultraviolet radiation. For that purpose tentative measurements were made, based on a method described by WEBSTER *et al.* (135), KIMBALL & HAND (72) and by HILL (52). In short, the method is based on the decomposition of aqueous acetone by u.v. radiation. This decomposition is measured by the reduction of methylene blue, a hydrogen receptor. If a (standardized) mixture of distilled water, acetone and a 0.1% methylene blue solution is exposed to the light in *quartz tubes*, the bleaching of the blue mixture is proportional to the time of exposure and/or the quantity of u.v. energy received. After exposure the tubes are compared with a series of 10 color-match tubes containing the unexposed blue mixture diluted with resp. 0, 10, 20, 30 etc.... % of *aqua destillata.* The comparison tubes are marked with the numbers 10, 9, 8, 7 ..... etc. In this way indications concerning u.v. irradiation are obtained in a scale ranging from 0 to 10.

Since, partly owing to technical difficulties, no conclusive results were obtained in the two experimental years, this part of the observations will not be discussed any further. Renewed tests were set up for 1962, including measurements at different levels above and in the crop with both *Webster* tubes and *Pressler* photo-electric cells.

At Bennekom an electronic recorder of sunshine duration was tried out in 1961. Because of a deficiency in the paper transportation of the recorder used, only a limited number of data were obtained. This instrumental test work, which is carried out more or less independently of the epidemiological blight research, was continued in 1962.

3.3.3 *Data processing*

In order to carry out a joint examination of two sequences of events as different in nature as the coincident meteorological and the biological developments and in order to bridge, in a way, the gap between continuously recorded physical phenomena and usually daily registered biological ones, the measurements of meteorological elements were partly converted into averages and totals covering periods of 3 hours or more. Readings taken at specified moments at 3-hourly intervals were made use of in other cases.

The following quantities were computed (Table 12).

Computed quantities	Period for which computed			
	B'kom 1960	De Bilt 1960	B'kom 1961	De Bilt 1961
d.p.d. at 0, 3, 6, 9, 12, 15, 18 & 21 h. C.E.T.	1/7– 5/9	9/6– 5/9	7/6–12/9	16/6–21/9
duration of compliance with 1st (18 hours) POST period	1/7– 5/9	9/6– 5/9	7/6–12/9	16/6–21/9
duration of compliance with all POST criteria	1/7– 5/9	9/6– 5/9	7/6–12/9	16/6–21/9
duration of hygrograph recordings $\geqslant 90\%$ *in screen*	1/7– 8/9	1/7–15/9	7/6–12/9	16/6–21/9
idem *in crop*	1/7– 8/9	1/7–15/9	7/6–12/9	16/6–21/9
leaf wetness period *in crop*	—	1/7– 8/9	—	16/6–21/9
3-hourly values of s.d. *in screen*	1/7–15/9	1/7–15/9	7/6–12/9	16/6–25/9
idem *in crop* (in mm Hg)	1/7–10/8	1/7– 5/9	7/6–12/9	16/6–25/9
rf. duration in min. p. 3-hourly period	1/7–15/9	1/7–15/9	19/6–29/9	16/6–21/9
duration of bright sunshine *a.m.*	1/7–15/9	1/7–15/9	19/6–27/9	16/6–21/9
idem *p.m.* (in hours)	1/7–15/9	1/7–15/9	19/6–27/9	16/6–21/9
Period covered by inventory graph	1/7– 5/9	1/7– 5/9	7/6–12/9	16/6–21/9

Table 12

Meteorological quantities computed for insertion in inventory graph; 3-hourly readings refer to times specified in 1st line (d.p.d.);

d.p.d. = dew point difference $(T - T_d)$;
s.d. = saturation deficit (mm);
rf. = rainfall.

The quantities summarized in Table 12 were inserted in 4 comprehensive descriptive graphs. These inventorial graphs brought together clearly arranged surveys of the progression of the computed quantities through long sequences of days and some directly read meteorological quantities, namely maximum day and minimum night temperature in screen and crop and 3-hourly readings of T and r.h. in screen and crop.

By studying all these data jointly it was hoped to find predictable criteria characteristic of crop infection leading to major blight epiphytotics. In earlier work (137) the inventorial procedure, that of *descriptive* statistics, had proved to be the only feasible one because of the impracticability of handling many kinds of biological data in any truly mathematical way. Some use will be made here of previous experience.

3.4 Biological observation

The biological observation was carried out in complete accordance with the directives published elsewhere (DE WEILLE, 144). In the present treatise the leading train of thought and the principles underlying the applied methods of working will therefore be discussed in a more concise way.

Before dealing with a number of different types of observation, some marked features of all procedures are sufficiently noteworthy to justify a description. Common characteristics are *frequency* of observation and the fact that *counts* replace every kind of evaluation. The generally applied method of evaluating the damage inflicted by disease by means of numbers (or percentages) belonging to a scale like the "key for potato blight on the haulm for use in the U.K." (Anon., 2) has not been used by the author (144) because of the impossibility of noticing *daily* changes in the epidemiological pattern with the help of categorisations of that kind. No real observation of *damage* was therefore made.

The rapid response of the blight inoculum to environmental changes, as demonstrated in Chapter II, implies that important epidemiological changes occur within time periods not exceeding one day. The meteorological characteristics of each individual day will obviously stamp that day as an infection day or not. The minimum frequency of observation which would seem to be desirable is consequently one observation per day.

Changes of a biological nature resulting from more or less abrupt changes of environment will not immediately show to a degree permitting evaluation of any kind; but either the single and simple establishment of a fact (a "+ or —" observation or a "yes or no" observation) or precise counting of lesions, diseased leaflets *etc.*, will be required for assessment of whether or not the intensity of attack has increased.

3.4.1 *Sampling*

The application of counts makes high demands on the system of sampling. At first glance this may seem to be a disadvantage as compared with the practice of evaluating the situation according to a grading system, since in the latter case no sample is needed: the whole field serves as such. Counting, however, is too elaborate to be applied to a whole field.

Random sampling systems for counting purposes must be rejected, though at any event counts can only be rendered practiable by sampling. But the number of lesions or blighted leaves varies from plant to plant and from stalk to stalk so that, when applying a random test method, differences found on two consecutive observation days are most likely to be attributed to chance.

In order to make sure that an increase in the number of lesions, for instance, is not a freak of chance, the same leaflets should be counted every time.

In this case the problem was solved by pre-selection of observation objects according to the *grid method.* An imaginary grid of lines, or a trellis, is superimposed on the test field. The plants standing at the intersections of the imaginary grid lines will then become the observation plants. No observations (counts) are done on other plants. In this way the number of plants under observation is successfully restricted while at the same time an even distribution of the observation plants over the area is secured.

If a good impression of the progress of disease incidence is to be obtained, a grid must provide a density of observation plants justifying conclusions. Should the *mesh width* of the observational network chosen be too coarse – for instance, in order to avoid too elaborate work – then it will be impossible to follow the spread of the organism from day to day. Use was therefore made of a better way of cutting down the time needed for observation work: observation was restricted to *preselected parts* of the observation plants.

Fig. 22 shows how the grid method was applied at *Bennekom* in 1960.

3.4.2 *Symptom observation*

Observation of the symptoms of a disease, is "one step nearer the infection stage and thus one step nearer the disease organism/weather relationship than is damage observation" (DE WEILLE, 144). The passage cited is more readily

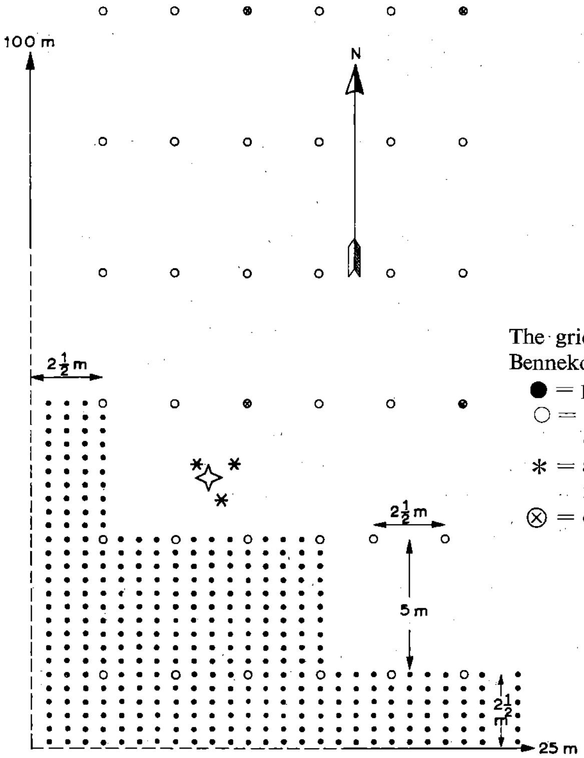

Fig. 22
The grid system for sampling, applied at Bennekom, 1960.

● = plant
○ = observation plant for counts of diseased leaves
* = additional obs. plants around artificial inoculum source (star).
⊗ = obs. pl. for leaf spot counts.

understood if it is realized that the occurrence of the earliest visible symptoms is separated from the corresponding infection data by the incubation period only. Since we have some knowledge concerning incubation periods it is possible to relate increments in daily symptom numbers to presumable infection dates. It will be clear that observation and evaluation of damage do *not* make this possible.

The experiments here described were concerned with two kinds of symptom observation, which might be called "coarser" and 'finer" or rough and more accurate. In Fig. 22 on p. 73 the plants selected for the rougher type of observation, *viz.* daily *counts of diseased leaves*, are indicated by circles. Beginning 2½ m from the southern and western borders of the experimental field the observation plants were to be found at 5 m mutual distance in every 4th row, so that the mesh width was 5 m × 2½ m. All selected plants were marked by a tonkin garden stick. Diseased leaves were counted on one preselected stalk of each observation plant, those selected being marked by a red ring. By registering the results of the daily counts the *progress* of the disease was chronicled.

Three additional observation plants were chosen in the near proximity of the artificial inoculum source in order to register the first generation of the organism in the crop as early as possible. The source was refreshed regularly until a primary disease focus was noted.

The more precise work was confined to every third observation plant in both directions. The plants selected for daily *counts of young lesions* (cf. BJÖRLING, 9), are indicated in Fig. 22 on p. 73 by a small cross in the circle. The mesh width for this kind of observation, meant to depict the *intensity* of attack in the various infection periods, was 15 m × 7½ m. Counts of primary necrotic spots constitute an elaborate kind of work. They were therefore performed on one leaflet, namely the top leaflet of a selected leaf marked by a yellow ring. When this top leaflet had yellowed the next one was used, and so on until the observer passed to a higher leaf, *etc.*.

As the season advanced it became increasingly difficult to interpret the symptom data. The rapidly growing and finally unlimited masses of inoculum often gave rise to a situation in which the (variable) incubation periods overlapped. Microphenological observation, which is to be recommended in any case, should be made in conjunction with the observation of symptoms lest the clear picture of epidemic development be disturbed later in the season.

The mesh width for diseased leaf counts performed at *de Bilt* in 1960 was 2 m × 2 m. There were 4 additional observation plants around the artificial source of iniculum. Counts of young lesions were carried out at a mesh width of 6 m × 6 m.

In 1961 the mesh width at Bennekom amounted to 4½ m × 2½ m for the rough and 13½ m × 7½ m for the exact observation; at de Bilt the corresponding measures were 5 m × 2½ m and 15 m × 7½ m. In both cases three additional observation plants had been selected around the artificial inoculum source.

3.4.3 *Phenological observation*

Phenology deals with the occurrence of phases in plant and animal life. Within the framework of this study the object of recording phenological observations of *Phytophthora infestans* is to determine the dependency of its recurring phases on environmental factors outside the laboratory, *i.e.* in relation to weather conditions.

In Chapter II it was shown that the prevalence of the environmental factor(s) needed to induce a new phase in the life cycle of Phytophthora is a matter of some hours, so that microphenological observations should be taken *daily*. Phenological data can be related to symptom recordings made later on and *vice verse*.

The phases to which such observation may apply are, firstly, those *visible* to the naked eye: sporulation and, in a way, the first appearance of lesions, the small "pin points". Secondly there are phases *outside the host tissue*, observable through the microscope. Mycelial development within host tissue is not very suitable for observation on a daily routine basis.

In the research here described the following microphenological observations were made:

1. sporulation, observed *macroscopically*
2. the presence of detached spores on the leaves }
3. germination } observed *microscopically*
4. where possible: penetration, infection }

The observation mentioned under 2, 3 and 4 is facilitated by the *leaf print* technique, a simplified form of the collodion film procedure described by BJÖRLING & SELLGREN (10).

Prints of the upper leaf surface showing all small objects lying upon the leaf, including *Phytophthora* conidia, are made by painting the leaf with a 6% collodion solution (in an alcohol/ether mixture). After the liquid is brushed on to the leaves it is allowed to dry up, either partly or completely, whereupon the collodion is detached from the foliar surface as a film. It is advisable to tear the film off the leaf as early as possible lest it become lumpy. The detached film, with leaf side uppermost, is laid upon an object slide to which it is stuck by means of an alcohol/ether mixture. It takes some experience to find the right way of working. If too little of the liquid is used the film will not flatten along the slide; too much will cause the film to dissolve. After it has spread out the cell wall structures will then be found to have disappeared. The same may happen if drops of the fluid fall *upon* the film; the right way of working is to lay the film down upon a thin film of liquid on the object slide. Then it should be left to solidify. When ready, microscopic examination will show a true picture of the leaf surface as though it were the cuticle itself under scrutiny. The shape of the epidermal cells, the plant hairs and, if present, stomata are clearly visible and so are all kinds of small objects which must have lain upon the leaf: pollen grains, dust or soot particles, yeast cells, *etc.*.

The replicas can be stored until it is convenient to study them. Then they are examined under water, glycerol or, in case the print is too lumpy and has to be made supple, in 60% alcohol. Addition of methylene blue to the collodion and of eosine to the fluid applied when examining the replicas microscopically may enhance the visibility by strengthening the contrasts. In the author's research the daily prints were stored in the laboratory so that their examination could be started after the field trials were over.

Very lumpy replicas were examined under long (18 × 36 mm) cover slides.

The phenomena observed in the leaf prints were the presence of (probably) healthy or (probably) dead conidia, germination of conidia and the presence of zoospores and even (although this is mainly a matter of chance) infection.

The *presence* of probably healthy conidia indicates the occurrence of a *spore flight*. Their absence however does not prove there was no flight but may mean that the investigator had not been lucky enough to catch spores. The presence of apparently dead sporal material indicates earlier spore flights or a spore flight followed by adverse conditions with respect to the conidia.

The possibility of "missing" the conidia was minimized by making the leaf prints from leaves situated under a sporing leaf or otherwise (in wind direction; weather vane) next to such a leaf.

It may be remarked that conidia found in a leaf print made at 10 o'clock (the usual time) of a certain day may originate from a spore flight that had occurred two days earlier or at least the preceding day. In this connexion it cannot be sufficiently emphasized how important it is that microphenological observations be made in conjunction with daily counts of symptoms on the grid plants.

Direct and indirect *germination* of *Phytophthora* conidia were very frequently encountered in the replicas. In the cases in which rain had fallen in either of the two places, Bennekom or de Bilt, but not in the other place, germination was not found in leaf films made in the dry place. It was found, however, in the field where rainfall had occurred.

Even *penetration* of hyphae into the epidermis could definitely be ascertained in a number of films. This is not possible in those replicas in which cell structures have vanished during preparation unless *appressoria* are found, swellings of the germ tubes, formed directly before the cuticle is pierced. These are not rare in the case of direct germination.

Microphenological observation does not produce numerical results. Whereas symptom observation leads to data in a numerical form the phenological work leads to + and — results. By studying both kinds of data together, in conjunction with physical ones a rather accurate picture of epidemic development is obtained.

3.4.4 *Determinations of germinative capacity*

The laboratory experiments described in Chapter II showed the sensitivity of *Phytophthora* conidia to external factors. Loose conidia proved to be sensitive to the radiation regime, attached ones to air humidity.

In order to check the progression of the germinative capacity (K) of the attached conidia so that knowledge be obtained with respect to (the days of) maturation and decline of K in the field, samples of sporal material were harvested in the field and subsequently germinated in the laboratory. The methods applied have already been described on p. 39.

As was to be expected, the values of K obtained in the samples differed widely from day to day.

3.5 Results

The various phases in the life cycle of the fungus are closely related to parallel stages in epidemic development. They are summed up in Table 13.

Phase in life cycle	Kind of observation in which noticed	Corresponding epidemiological dates
sporulation	visual observation of new conidial generations	formation nights
maturation	determination of K	maturation days
detached phase (survival)	examination of collodion films	spore flights
germination	examination of collodion films	germination days
penetration	examination of collodion films	infection days
incubation	counts of "pin points"	extension periods
extension of mycelium	counts of diseased leaves	epidemics

Table 13

Relationship between recurring biological phases (left) and dates on which epidemiological developments occur (right). Middle: observations playing a part in determining right hand set of data. Later stages can also help to determine moments of occurrence of earlier ones.

3.5.1 *Some definitions*

Some of the concepts stated in Table 13 under "epidemiological dates" should perhaps be defined more closely.

Formation nights are nights in which considerable amounts of fresh *inoculum* are produced (by sporulation).

Maturation days are characterized by an increase of the germinative capacity of newly formed inoculum; this increase largely takes place during the hours before noon.

Germination days are, of course, days on which an appreciable part of the newly matured inoculum germinates after having been detached from the plants upon which it had been formed and subsequently conveyed by air currents to other plants as a *spore flight*.

The term *infection days* is also clear: days on which not only germination but also *penetration* into host tissue, *i.e.* infection, takes place.

Extension periods are periods characterized by a considerable increase in the numbers of (very) young necrotic lesions on the foliage, just visible to the naked eye, "pin points", as they are sometimes called. The first extension day will invariably occur z days (z = incubation period) after the corresponding infection date. In this context it should be borne in mind that in most cases (see p. 5) $3 \leqslant z \leqslant 7$ (days).

The intensification of the degree of disease incidence recorded on extension days is not visible in an over-all view, so it cannot possibly be expressed in estimates of the intensity of attack according to grading systems (cf. p. 98) (examples: lit ref. 1, 2, 144).

Epidemics (or epiphytotics) are the visible manifestation of further progress of mycelial growth in the leaves, ultimately finding expression in a marked extension of the blackened leaf parts as well as the number of those spots. If the meaning of the current use of the term epidemic is fully realized it will also be realized that the dates indicating the onset of epidemics depend on the discernment of the individual observer, his personal way of interpreting his scale and, of course, also on the frequency of his observing the field.

In the research here described the inaccuracy inherent in this kind of epidemical data was obviated as much as possible by applying counts and the sampling method described on pp. 72–74.

The ultimate results of the biological *observation* per season and per test field are to be found on the following two tables.

3.5.2 *Biological field data*

The biological data are given in tables 14 and 15, where they were restricted to the "period covered by inventory graph" (see p. 71, table 12).

3.5.3 *Formation nights*

On comparing the data obtained from the observation of sporulation with air humidity data obtained in the standard meteorological screens and in the crop, a close relationship was found to exist between sporulation and the saturation deficit (s.d.) of the atmosphere in the crop. There is no such *close*

(caption on p. 83)

Table 14	Bennekom							de Bilt						
Dates, 1960	fo.	ma.	ge.	in.	ex.	ep.		fo.	ma.	ge.	in.	ex.	ep.	
July 1	++	+	+	+				++	+	+	−(+)			
2	+	−						++	−					
3	−							−						
4	−							−						
5	+	+	+	+			i	+	+	+	+			i
6	+	+	+	+				++	+	−				
7	++	−						++	+	+	+			
8	++	++	+	+			i	+	++	+	+			i
9	++	+	−					++	+	−				
10	+	+	+	+			i	++	++	+	+			i
11	++	−						−						
12	++	−						+	−					
13	+	−						+	−					
14	−							−				+		
15	++	+	+	+				++	−(+)	+	+		+	
16	+	−						++	+	+	−(+)		+	
17	++	++	+	+			i	+	++	+	+		+	i
18	++	−						++	−				+	
19	++	+	−(+)	+				++	++	+	+		+	
20	+	+	+	+			i	−					+	i
21	−				+	+		−					+	
22	+	−			+	+		+	−			+	+	
23	++	−				+		++	−				+	
24	++	−				+		++	−			+	+	
25	−				+	+		−					+	
26	−				+			−				+	+	
27	++	+	+	+	+			+	+	+	−(+)	+	+	
28	++	+	+	+			i	++	++	+	+	+		i
29	+	+	−					−						
30	+	++	+	+			i	+	++	+	−(+)	+		i
31	++	++	+	+			i	+	++	+	+		+	i
Aug. 1	+	+	−		+			+	+	−		+	+	
2	++	−			+			++	−(+)	+	+		+	
3	−				+			++	−				+	
4	+	−			+			−(+)	−					
5	++	−			+			++	−					
6	++	++	+	−(+)	+			+	+	+	−(+)		+	
7	++	−			+			−(+)	−					
8	++	−						+	−					
9	+	+	+	+				+	+	+	+			
10	−(+)	++	+	+			i	+	++	+	+			i
11	++	++	+	+	+		i	++	++	+	+			i
12	++	++	+	+			i	+	++	+	+			i
13	−							−						

(Continued)	Bennekom							de Bilt						
Dates, 1960	fo.	ma.	ge.	in.	ex.	ep.		fo.	ma.	ge.	in.	ex.	ep.	
14	−							+	+	−(+)	−			
15	++	++	+	+			i	−(+)	++	+	+			i
16	++	+	+	+				++	+	+	+			
17	++	−						++	−					
18	+	++	+	+			i	−(+)	++	+	−(+)			i
19	+	−						−						
20	+	++	+	−(+)			i	+	++	+	−(+)			i
21	++	+	−(+)					+	+	−(+)	−			
22	+	−						−						
23	+	−						−				+		
24	−							+	+	−(+)	−			
25	+	+	−(+)	+			i	++	+	−(+)	+			i
26	+	+	+	+			i	+	+	+	+			i
27	++	+	+	−(+)				++	+	−(+)	−(+)			
28	++	+	+	+			i	+	++	+	+			i
29	++	+	+	+			i	++	+	+	+			i
30	+	++	+	+			i	+	++	+	+			i
31	++	++	−(+)	−			i	+	+	+	+			i
Sept. 1	++	++	+	+			i	+	++	+	+			i
2	++	+	+	+			i	++	+	+	+			i
3	+	+	+	+			i	+	+	+	+			i
4	+	−(+)	+	+				−						
5	++	+(−)	−(+)	+				++	−					

Table 15	Bennekom							de Bilt						
Dates, 1961	fo.	ma.	ge.	in.	ex.	ep.		fo.	ma.	ge.	in.	ex.	ep.	
June 6	−													
7	+	+	−											
8	−													
9	++	−												
10	++	−												
11	−													
12	−													
13	−													
14	−													
15	++	−												
16	−													
17	−							−						
18	−							−						
19	++	−						++	−					
20	+	−						+	−					
21	++	−						++	−					
22	−							+	+	+	+			
23	++	−						++	−					
24	++	−						++	−					
25	++	−						++	−					
26	+	−						−(+)	−					
27	++	+	−(+)	+				++	+	−(+)	−			
28	++	−						++	−					
29	++	−						++	−					
30	−							++	−					
July 1	+	−						−(+)	−					
2	−(+)	−						−(+)	−					
3	++	+	−(+)	−				++	++	+	−(+)			
4	+	+	+	+			i	+	+	+	+			i
5	++	−						++	−					
6	++	−						++	−					
7	++	−						++	−					
8	−(+)	++	+	+			i	−(+)	++	+	+			i
9	++	+	+	−(+)			i	++	+	+	+			i
10	++	++	+	+			i	++	++	+	−(+)			i
11	++	++	−					++	+	−				
12	++	+	+	+				++	−					
13	++	+	+	+			i	++	+	+	+			i
14	++	+	−(+)	−				++	+	−				
15	−							+	+	+	+			i
16	++	++	+	+				++	++	+	+			i
17	++	+	+	−(+)				++	+	−(+)	−(+)	+	+	
18	++	+	+	+			i	++	+	−(+)	−			i
19	++	+	+	+			i	++	++	+	+			i

(Continued)	Bennekom							de Bilt						
Dates, 1961	fo.	ma.	ge.	in.	ex.	ep.		fo.	ma.	ge.	in.	ex.	ep.	
20	++	++	+	+				++	++	−(+)	−			
21	−							−(+)	++	−(+)	−			
22	++	+	+	+				++	+	−(+)	−			
23	++	+	−(+)	−				++	+	−(+)	−			
24	++	−						++	−					
25	−							+	+	−(+)	−			
26	+	+	+	+				+	+	+	+			i
27	+	+	−			+		−						
28	++	+	+	−(+)				+	−					
29	++	+	+	+				+	+	+	+			i
30	++	+	−(+)	−(+)				++	+	−				
31	++	−						++	−					
Aug. 1	++	−				+		++	−				+	
2	++	+	+	+		+		++	++	+	+		+	
3	++	−				+		+	−				+	
4	−				+	+		−						
5	++	+	+	−(+)		+	i	+	++	+	+			i
6	++	+	−(+)	−		+		+	+	+	−(+)			
7	++	−			+	+	i	+	−					
8	+	+	+	+		+	i	−				+		
9	−					+		−(+)	−			+		
10	++	+	−		+	+		++	−				+	
11	−				+	+		++	−				+	
12	++	+(−)	−(+)		+	+		++	−				+	
13	++	+	−(+)	+	+	+	i	+	+	−(+)	+		+	i
14	++	+	+	+	+	+		−					+	
15	−					+		−					+	
16	+	+	+	+		+		−					+	
17	+	−				+		++	−				+	
18	++	++	+	+		+	i	++	++	+	+		+	i
19	−(+)	++	+	+		+	i	−(+)	+	+	+		+	i
20	++	+	−(+)	−		+		++	+	−(+)	−		+	
21	+	++	+	+		+	i	++	++	+	+		+	i
22	+	+	+	+		+	i	++	+	+	+		+	i
23	++	−				+		++	−				+	
24	−(+)	++	+	+	+	+	i	++	++	+	+		+	i
25	++	+	+	+	+	+	i	++	+	−(+)	−		+	i
26	++	+	+	−(+)	+	+		++	+	−(+)	−		+	
27	++	−			+	+		++	−				+	
28	++	−						++	−			+	+	
29	−							++	−				+	
30	−							+	−				+	
31	++	++	+	+				++	++	+	+			

(Continued)	Bennekom							de Bilt						
Dates, 1961	fo.	ma.	ge.	in.	ex.	ep.		fo.	ma.	ge.	in.	ex.	ep.	
Sept. 1	++	+	+	+				++	+	+	+			
2	++	–			+			++	–					
3	++	+	+	–(+)	+			++	+	+	+			
4	++	+	–(+)	–	+			++	+	+	+			i
5	++	+	+	+			i	+	+	+	+	+	+	i
6	+	++	+	–(+)			i	+	++	+	–(+)	+	+	i
7	++	++	+	+			i	++	++	+	+	+	+	i
8	–							+	+	+	+			
9	–							++	+	+	+			
10	++	–						++	–					
11	+	++	+	+				++	++	+	+			
12	++	+	–(+)	–				++	+	–				
13	–							–						
14	–							+	++	+	+			
15	+	–						++	+	–				
16	–							+	–					
17	++	–						++	–					
18	++	–						++	–					
19	–(+)	–						–						
20	++	–						++	+	+	+			
21	–							++	+	–				

Tables 14 & 15

Epidemiological phases according to the physical criteria and in almost complete accordance with the results obtained by means of leaf prints. Columns "extension" and "epidemic" were derived from counts; + indicates that the relevant phenological stage was accomplished; – indicates that it was not; ++ stands for abundant sporulation (s.d. $\leqslant$ 0.3 mm) or significant maturation (no a.m. sunshine at all). Per line 1 boundary case was allowed: formation –(+) means: s.d. at 3 h. $>$ 0.4 mm, but at 6 h. $\leqslant$ 0.3 mm; maturation +(–) means sunsh. dur. = 2.0 h.; id. –(+) means sunsh. dur. = 2.1 h.; germination or infection –(+) means: precipitation not in "model" period (cf. pp. 93–94) but in 3-hourly period preceding or following it; i denotes probable infection date as derived from leaf print.

fo. = formation; ma. = maturation; ge. = germination;
in. = infection; ex. = extension; ep. = epidemic.

relationship with the analogous screen data.

A careful study of the available body of climatological data revealed that the occurrence of a low s.d. or a high r.h. in the crop is not very consistently correlated with the simultaneous, previous or later occurrence of a corresponding level of humidity outside the crop. Nor does an increase or a decrease of the air humidity in the crop consistently correspond to a simultaneous or systematically earlier or later increase or decrease of the humidity measured in the screen (cf. p. 11).

The data very convincingly showed that *screen measurements are no decisive measure for biological events* taking place in the phytosphere.

In this connexion it is significant that relationships between air humidities at different levels (POST, 107, 105, & RICHEL, 107; HIRST, 57, *etc.*) invariably apply to mean values averaged over longer or shorter periods (see, *e.g.*, Fig. 1, p. 10) and not to the more or less *momentary* values so decisive for the development of an organism like the blight fungus (cf. pp. 10–11).

Air humidity measurements by POST & RICHEL (107), intended to represent the situation in the crop, were even taken in a standard screen placed *beside* the potato field at a height of 40 cm. Working in that way they found correlations between the 24 hours' *means* of r.h. at both levels of observation.

When examining the data it became clear that significant sporulation is closely linked with the *nocturnal* incidence in the crop of a very low saturation deficit. In the experiments the s.d. values were computed from hygrograms, so that all air humidity data referring to the phytosphere are based on hygrograph readings. For a considerable part the almost proverbial inexactitude of hygrograph recordings was obviated by applying a method of reading especially suited to r.h. values exceeding 90% (see pp. 101–103). Every time a straight horizontal line (as part of the humidity curve) or a very slowly falling one (cf. BLEEKER, 11: p. 26) was recorded, this was used as the 100% standard level for the surrounding part of the hygrogram (in as far as it indicated r.h. $\geqslant 90\%$).

Working in this way a significant relationship was found to exist between the formation of inoculum and the apparently more or less critical s.d. level of 0.4 mm Hg (= 0.53 mb) or less. Abundant sporulation was found to occur at an s.d. of 0.3 mm (= 0.4 mb) or less.

The quantity s.d. was chosen for its being more conservative than the quantity r.h., which is almost completely meaningless without statement of the temperature. Since the crop temperature range pertinent to the nocturnal hours of the seasons did not appear to be very wide, the s.d. was treated as a quantity independent of T (for further explanation see p. 102).

The saturation deficits had been computed for specified moments of each day with intervals of 3 hours, *viz.* for 0, 3, 6, 9, 12, 15, 18 and 21 h. C.E.T.. The s.d. at 0, 3 and 6 h. C.E.T. was related to sporulation.

There were 72 collodion leaf prints made on days of which the 0, 3 and 6 o'clock s.d. was known. This collection was used for testing a number of air humidity criteria (on a s.d. basis). The intention was to find a climatological criterion selective enough to permit the determination of inoculum formation nights without examining a leaf print or the like. For some prints had been lost, while others had turned out badly and were less suited to microscopical examination. On the other hand in some cases the incidence of spores in a collodion film is due to sporulation at an earlier date. In a few cases this could be shown. It will be clear that the use of leaf prints at least involves *some* failures. These are inherent in the working method.

A simple mathematical procedure was applied for determining the best possible rule for the occurrence of sporulation and for threshing out the misleading leaf prints.

Seventy-two leaf prints made in 1960 and 1961 at both Bennekom and de Bilt were examined. They were divided into 3 classes, *viz.* (1) samples without conidia, (2) samples with very few conidia and (3) samples with many conidia. For statistical reasons the first two classes had to be combined; separately, they were both too small. Two classes thus remained, *viz.* (a) no or a few conidia; (b) many conidia.

First test

Frequency tables of the occurrence of a and b were composed with the help of the s.d. at 0 h., 3 h. and 6 h. C.E.T., respectively. The humidity classes were p[s.d. $\leqslant$ 0.4 mm (0.53 mb)] and q[s.d. $>$ 0.4 mm]. Additional frequency tables were composed for the s.d. at 0 h. & 3 h. and the s.d. at 3 h. & 6 h.; the humidity classes were P (s.d. $\leqslant$ 0.4 at both times) and q (s.d. $>$ 0.4 at one or both of the specified times. Finally a frequency table was added for the s.d. at 0 h. & 3 h. & 6 h., the humidity classes being p(s.d. $\leqslant$ 0.4 at all three times) and q(s.d. $>$ 0.4 at one, two or all three specified times). These tables are given in Table 16.

t (C.E.T.):	0 h.		3 h.		6 h.		0 & 6 h.		3 & 6 h.		0, 3 & 6 h.	
	p	q	p	q	p	q	p	q	p	q	p	q
a:	10	16	15	11	12	14	9	17	9	17	5	21
b:	39	7	43	3	44	2	37	9	43	3	38	8

Table 16
A simple test of a humidity criterion for sporulation. For explanation: see preceding text.

In Table 16 the marked character of the original class "no conidia" is considerably obscured by the addition of the more neutral class "few conidia".

Obviously the division of the biological classes over the two physical environmental categories is not completely attributable to chance since, in mathematical terms, a and b do not seem to follow a binomial or a "normal" distribution.

This normal distribution could not be expected since sporulation is known to depend on the humidity of the air, high humidity being necessary for the inoculum to be formed (Chapter II, p. 33). Normal distribution of a and b would have indicated that the p & q-classification was based on a non-applicable criterion. It may therefore be assumed that a p & q-classification is the more likely to be the best possible one the more the a & b-distribution appertaining to it diverges from the normal one, provided the boundary value between p and q is the right one, which could not be doubted in this case.

If, for example, p had been described as r.h. $\leqslant$ 10% and q as r.h. > 10%, all values of a and b would have been found to lie in class q! In a case like the one dealt with here, the maximum frequency within a and that within b have to lie in different classes; ideally (errorless sampling) a should completely occupy class q; b should lie in class p.

In order to obtain an impression of the extent to which the various frequency distributions depart from the binomial one the classical χ^2-test was applied. In this case the test starts from the null hypothesis that a and b are distributed *by chance* (over p and q), free from any causality. The values of the quantity χ^2 give an indication as to the extent to which the null hypothesis is valid. The pertinent values of the exceedance probability P show whether or not the hypothesis should be rejected. The test is described in several statistical text books, so that only the results will be discussed here.

The values of χ^2, given in Table 17, are very significant. The pertinent values of the exceedance probability P are very small in all cases and amount to *ca.* 0.01 per cent or less. As a matter of fact the data found confirm the influence of the s.d. upon spore formation. The P-values show that the null hypothesis is not valid and that none of the criteria tested can be rejected. Since the number of degrees of freedom amounts to 1 in all cases, mutual comparison of the χ^2-values does not seem unjustified.

C.E.T.→	0h.	3h.	6h.	0h. & 3h.	3h. & 6h.	0h. & 3h. & 6h.
Values of χ^2	16.62	14.08	27.23	15.40	28.02	31.16
degrees of freedom	1	1	1	1	1	1
P	0.01	0.015	$\leqslant$ 0.01	0.01	$\leqslant$ 0.01	$\leqslant$ 0.01

Table 17
Results of the χ^2 test of s.d. criteria for sporulation; the exceedance probability P of each value of χ^2 is expressed in percentages.

Indication is now duly obtained that the s.d. measured at 6 h. C.E.T. is of the utmost importance, though account should be taken of the s.d. in the preceding hours. Criteria not containing the s.d. at 6 o'clock are less significant than those which do include that quantity.

Second test

Since there are clear indications that, though inoculum is formed at a s.d. of 0.4 mm Hg, abundant sporulation requires still lower deficits of 0.3 mm or less, (see p. 84), a χ^2 test was also applied in which the distribution of the biological classes a (no spores or a few) and b (substantial sporulation) over 3 physical categories {p (s.d. < 0.4 mm), p′(s.d. $= 0.4$ mm) and q (s.d. > 0.4 mm)} was investigated. The set times to which the saturation deficits apply and their combinations were identical to those in the first test.

For computing χ^2 the class p′ was omitted since in the theoretically "expected" distribution, *i.e.* the distribution based on the adopted null hypothesis, no more than 5 cases occur, which constitutes a statistically undesirable situation. Visually, the picture now became yet more marked than in the first test. The results are given in Table 18. The significance of these data is, again, extremely great. In all cases P is well below 0.01 per cent.

C.E.T. →	0h.	3h.	6h.	3h. & 6h.	0h. & 3h.	0h. & 3h. & 6h.
Values of χ^2	23.05	19.31	29.62	24.38	35.19	31.77
degrees of freedom	1	1	1	1	1	1
P	$\ll 0.01$	< 0.01	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$

Table 18
Result of the second χ^2-test of s.d. criteria for sporulation.

Again, the χ^2-sum for testing the s.d. criterion at 6 o'clock is more significant than the corresponding quantity for testing it at earlier hours.

On comparing Tables 17 and 18 we see that an air humidity criterion for sporulation should at least incorporate the s.d. in the crop at 6 h. C.E.T.. It will also be noticed that all significances increased after isolating class p′(s.d. $= 0.4$ mg Hg)(in the 2$^{\text{nd}}$ test).

In consequence hereof it was deemed justifiable to adopt the following criteria for completing the column "formation" in the tables 14 and 15 (pp. 79–83):

for ++ (abundant sporulation): s.d. at 0 h., 3 h. and 6 h. resp. $\leqslant 0.4$, $\leqslant 0.3$ and $\leqslant 0.3$ mg Hg;

for + (sporulation): s.d. at 0 h., 3 h. and 6 h. resp. $\leqslant 0.5$, $\leqslant 0.4$ and $\leqslant 0.4$ mg Hg;

for — (no appreciable sporulation): all other cases.

After careful examination of an inventory list of all cases, comprising some 200, in which a s.d. of 0.5 mm was not surpassed at the three "critical" moments 0, 3 and 6 h. C.E.T., it became clear that it is not necessary to take into account the 0 h. data. After their deletion the minus-cases remained the same. This is in complete accordance with what Table 18 suggests and does not conflict with the data shown in Table 17.

Tentative conclusion

Since we have not yet made it clear that the humidity *measured* is equal to the humidity really *prevalent* in the crop at the same moment or, in other words, since we are not yet informed about the possible errors of observation due to the applied procedure of reading and/or the instrumental drawbacks inherent in the use of the often denounced hygrographs (see pp. 101–103), the criterion found should be expressed in cautious, or, at least tentative terms.

It may be stated that in the four field experiments

1) **sporulation was duly observed if at 3 h. and 6 h. C.E.T. the s.d. values computed from hygrograms obtained in the crop did not surpass 0.4 mm Hg (0.53 mb);**
2) **sporulation was abundant if at 3 h. and 6 h. C.E.T. the s.d. values computed from hygrograms obtained in the crop did not surpass 0.3 mm Hg (0.4 mb);**
3) **no appreciable sporulation was observed if at both specified times the analogous values exceeded 0.5 mm (0.67 mb).**

3.5.4 *Maturation days*

With regard to the study of the maturation of blight inoculum the procedure which was so successful in the case of sporulation was adopted once more. After previous thorough examination of the available biological (prints and germination samples) and physical data two kinds of criteria were tested, *viz.* s.d. criteria and *a.m.* sunshine duration criteria. Thereafter the best criteria of either kind were compared reciprocally in order to trace the most significant and most useful criterion indicating maturation.

First series of tests

When testing the s.d. criteria the author was, again, faced with the difficulty that two of the original classes of biological data, namely (1) "no maturation" and (2) "maturation uncertain", had to be combined for the same reason as described earlier (too small numbers in the binomial chance distribution). The classes over which the s.d. categories were distributed now became

(a) no maturation or maturation uncertain;
(b) maturation observed (concluded from germinations).

Frequency tables of the same kind as in Table 16 (p. 85), were composed for a good many different levels of s.d. at 6 h. (1 table; 84 cases ($n \equiv (a+b) = 84$)), 9 h. (4 tables; $n = 84$), 12 h. (5 tables; $n = 84$), 6 & 9 & 12 h. (5 tables; $n = 83$) and 9 & 12 h. C.E.T. (7 tables; $n = 83$). The extensive statistical material will not be published in extenso. The method applied was equal to that described on pp. 85–87.

The exceedance probabilities indicated a significant relationship in nearly all cases. Only the various s.d. levels at 6 h. C.E.T. constituted an exception. The frequency tables for the various scrutinized s.d. levels at 12 h., 6 & 9 & 12 h. and 9 & 12 h. C.E.T. led to P-values down to 0.1 %, the latter value corresponding with the highest χ^2 value, *viz.* 10.97, at one degree of freedom.

Much higher values of χ^2 and much lower ones of P were obtained from frequency tables of the s.d. at 9 h. C.E.T., the bulk of which is not published here. If no maturation is supposed to occur above an s.d.-level of y mm Hg and the sporal material is supposed to mature at a s.d. $\leqslant$ y, the statistical results obtained are as follows (Table 19).

$y \rightarrow$	1.3	1.4	1.5	1.6
χ^2	23.36	19.50	15.98	15.30
degrees of freedom	2	2	2	2
P	< 0.01	< 0.01	ca. 0.04	ca. 0.04

Table 19
Result of the best series in a test of s.d. criteria for maturation of the inoculum; y = tentative critical s.d. level at 9 h. C.E.T.; y in mm Hg, P in %; number of cases n = 84.

s.d. at 9 h. C.E.T. (mm):	$\leqslant 1.3$	> 1.3
no maturation:	0	5
maturation uncertain:	7	13
maturation observed:	50	9

Table 20
Frequency table corresponding to y = 1.3 in Table 19.

At (s.d. =) $y < 1.3$ mm the frequency distribution tables definitely lost their discriminative character.

The results indicate that maturation of sporal material is by no means a matter of chance, which already looked very improbable after a casual glance at frequency distributions like the one shown in Table 20.

In order to be somewhat on the safe side it may be assumed that extensive maturation of blight inoculum may be expected if the saturation deficit value at 9 h. C.E.T. computed from hygrograms obtained *in the crop* does not surpass 1.5 mm Hg.

Second series of tests

The significance of the duration of bright *sunshine before noon* was tested with the help of 157 cases. In 21 cases maturation did not occur, in 30 cases it could not be established with certainty and in 106 cases it was found to occur. The factor sunshine was tested in view of both its impact on the microclimate (BRUNT, 24) and the results of recent irradation experiments (pp. 49–51).

Lumping the 21 and the 30 cases together in the frequency tables a set of χ^2-values was obtained. Those χ^2-values appeared to be very much alike for a range of critical levels of a.m. sunshine duration varying from $1\frac{1}{2}$ hour to 2 hours. These results are given in Table 21. Though it is too difficult to make a choice, all data have one property in common: they give evidence that maturation and sunshine are not independent of each other. If no maturation is supposed to occur at a sunshine duration $>$ y, – y expressed in tenths of hours –, and the sporal material is supposed to mature at a sunshine duration $\leqslant$ y, the pertinent statistical results are as follows (Table 21).

y →	15	16	17	18	19	20
χ^2	46.98	49.32	49.99	48.99	48.23	47.75
degrees of freedom	1	1	1	1	1	1
P	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$

Table 21
Results of a test of sunshine duration criteria for sporal maturation; y = critical a.m. sunshine duration in tenths of hours; n = 157 (P is expressed in per cent).

A second test of the available data was performed after omitting the class "uncertain" from the frequency distribution tables, so that now the biological classes became
(a′) no maturation; (b) maturation observed.

Now the differences became all the more marked; Table 22 gives the results. and Table 23 shows the frequency distribution belonging to what at first glance seemed to be the best criterion. In this connexion some caution is desirable since, in grain, χ^2-values are not the proper quantities for indicating the "strength" of a criterion or, as it is called, the degree of association.

y →	15	16	17	18	19
χ^2	43.94	44.10	57.40	36.76	38.76
degrees of freedom	1	1	1	1	1
P	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$	$\ll 0.01$

Table 22
Results of the second test of a.m. sunshine duration criteria. Uncertain cases now left out of account; n = 127.

a.m. sunshine duration in 0.1 hours:	$\leqslant 17$	> 17
no maturation:	3	18
maturation observed:	91	15

Table 23
Frequency table corresponding to y = 17 in Table 22.

In order to be somewhat on the safe side it may now be assumed that extensive maturation of blight inoculum need not be expected when the duration of bright sunshine *before noon* exceeds 2 hours.

Besides, the impression is obtained that the morning sunshine duration criterion for the maturation of blight inoculum is superior to the analogous 9 o'clock saturation deficit rule. But since the values stated in Tables 21 and 22 are based on more cases (n = resp. 157 and 127) than those mentioned in Table 19 (n = 84), a valid judgment in this question should be based on a comparison of data having a bearing on identical sets of biological data (the "cases").

Such a mutual comparison was made.

A comparative test

For the purpose of comparing the indicatory merits of a humidity and a sunshine rule, the inventory list of maturation data that had been related to a.m. sunshine duration included no cases on which no reliable humidity datum was available when the various tests were carried out. This led to the deletion of nearly all data obtained at Bennekom in 1961, a season in which many Bennekom leaf prints had also yielded uncertain results. After deletion of these data (and of a few others) a more significant body of data resulted (Table 25). The following test data were computed (see Table 24).

$y \rightarrow$	20	17
χ^2	36.65	46.01
degrees of freedom	1	1
P	$\leqslant 0.01$	$\leqslant 0.01$

Table 24
Results of a third test of a.m. sunshine duration criteria. Same cases ($n = 84$) as in Table 19.

a.m. sunshine duration $\left(\frac{\text{hrs}}{10}\right)$:	$\leqslant 17$	> 17
no maturation or maturation uncertain:	3	33
maturation observed:	41	7

Table 25
Original frequency table corresponding to $y = 17$ in Table 24.

Table 24 primarily shows that a critical amount of a.m. sunshine duration of 2 hrs. (p. 90) was certainly a good choice. Secondly the impression is obtained that a sunshine criterion is superior to a humidity rule because the values of χ^2 in Table 24 exceed by far those summed up in Table 19. Since, however, χ^2-values are no exact measure for the real degree of association of the criteria compared a *test* is required. (For advice in this matter the help of dr. C. LEVERT, whose kind assistance is acknowledged with appreciation, was successfully implored.)

Such a test, described in several statistical text books, is the following one.

If values of a quantity x (here sunshine duration or s.d.) are divided into 2 categories p and q and if values of a quantity y (here K, expressed in %) are divided into 2 categories r and s (here resp. no maturation or maturation uncertain and maturation observed) the *colligation coefficient* of the frequency distribution of the 4 values found, *viz.* a, b, c and d, amounts to $A = (\sqrt{ad} - \sqrt{bc})/(\sqrt{ad} + \sqrt{bc})$. The extreme values of A are -1 (maximum negative association) and $+1$ (max. pos. assoc.).

	p	q
r:	a	b
s:	c	d

Actually, x (p, q) and y (r, s) should both follow the normal chance distribution if A is completely to satisfy the given formula. In practice, climatological parameters as s.d. (x) and sunshine duration (x) can be treated as normally distributed quantities. The values of K(y) cover the whole range from 0 to 100%, showing a very great natural variability, so that if x is accepted in the test, y should certainly not be repudiated. At any event calculation of A for both selected criteria will supply a better comparative impression of their merits than do χ^2-values. The more so because in each of the two cases the correlation coefficient can be approached by employing the formula $r \approx \sin \frac{1}{2}\pi A$. Comparison of two values of r may thus lead to a choice.

From Table 20 (p. 89) we compute: $$A_I = \frac{\sqrt{7 \times 9} - \sqrt{18 \times 50}}{\sqrt{7 \times 9} + \sqrt{18 \times 50}} = -0.78$$

From Table 25 (p. 91) we compute: $$A_{II} = \frac{\sqrt{7 \times 3} - \sqrt{33 \times 41}}{\sqrt{7 \times 3} + \sqrt{33 \times 41}} = -0.78.$$

Since $A_I = A_{II}$ it is evident that $r_I = r_{II}$, so that both criteria, in as much as revealed by the data at our disposal, are equally good from a stastical point of view. From a practical meteorological point of view however a definite choice is now justified: the sunshine criterion is preferred.

In fact the findings described in the above paragraph are very fortunate because we can now endeavour to step from the microclimate to a meteorological quantity tried in synoptic meteorology, *i.e.* a quantity with which meteorologists are conversant.

It may be concluded that there is considerable evidence that **an a.m. sunshine duration of 2 hours or more checks the maturation of blight inoculum and, in consequence thereof, checks the infection danger on a day characterized by such sunshine conditions.**

3.5.5 *Germination days*

With regard to the later phenological phases of the blight fungus, *viz.* germination and penetration (followed by the development in the host), the statistical research policy was changed. The only biological support for the stages mentioned was a number of leaf prints indicating that germination and/or infection had probably taken place the day before the film was made. In some cases however such a collodion film will show biological events that took place *e.g.* 2 days instead of 1 day before the print was produced.

As regards *e.g.* penetration into host tissue, for instance, lack of visual evidence of crop infection in a leaf print will certainly not prove that no infection happened. For that reason the "inventory" of the probable infection days was taken *unilaterally*, whereas the author returned to the *descriptive statistics* which had been successfully applied in the blister blight case (DE WEILLE, 137). The term unilateral stock-taking implies that only + cases are listed and no cases of "germination (or infection) not observed".

Meanwhile it is already known that in any case germination and infection are linked with precipitation and leaf wetness.

On the other hand macroscopic observation, *i.e.* counts of primary lesions and numbers of diseased leaves, will be useful for verifying the results obtained from the microscopical examination of leaf prints.

First test

Careful examination of *rainfall* data in conjunction with the probable germination dates (germination invariably assumed to have occurred on the day preceding the morning on which the sample was taken) supplied marked results.

There were 69 known (probable) germination days at de Bilt and likewise 69 at Bennekom (for the years 1960 and 1961 together). Of these 2 × 69 cases 49 at de Bilt and 48 at Bennekom were characterized by rainfall in the period from 9 to 15 h. C.E.T.. But though marked indications were thus obtained concerning the character of germination days there was also one series of 8 consecutive infection days (Bennekom, 1961) which could not possibly be explained by any simple rainfall rule.

The rainfall data had been obtained from pluviograph and pluvioscope recordings. Since fine drizzle and fog are not registered by those instruments, a second test was performed in which the data used for the first one were supplemented with data concerning drizzle and fog contained in the synoptic ww-code, as it is called. These data were taken from the official three-hourly reports made by the meteorological stations of de Bilt and Deelen (here applied to represent Bennekom).

Second test

By adding drizzle and fog data to those on rainfall, the cases left unexplained by the first test disappeared from the list.

As to the precipitation features of the different germination days the following cases were distinguished:

Case A: *model germination day*: precipitation in period 9–15 h.;
Case B: a day after a model day; in addition there was rain, drizzle and/or fog in the periods 6–9 h. and/or 15–18 h. C.E.T.;
Case C: a day after a model day, not characterized by the features described under B;
Case D: a day characterized by the features mentioned under B (precipitation in periods 6–9 and/or 15–18 h.), but not preceded by a model day.

By applying these four categories allowance was made for the imperfections inherent in the leaf print method.

Case	Brief description	frequency		
		de Bilt	Bennekom	dB and B'kom together
A	model day	55	55	110
B	1 day after model day; precipitation in periods 6–9 and/or 15–18 h.	8	9	17
C	1 day after model day; no precipitation in the above periods	4	3	7
D	Precipitation in the above periods; not 1 day after model day	2	2	4
	n:	69	69	138

Table 26
Results of an investigation for the purpose of finding a valid weather criterion for germination of *Phytophthora infestans*; data substantiate the choice of A (also see text).

The frequency distribution of the 4 cases is given in Table 26.

The results stated in table 26 verify the correctness of the precipitation criterion already found in the first test. *The term precipitation has to be conceived so, that it also covers* **drizzle** *and* **fog.**

A germination day is characterized by precipitation within the period between 9 and 15 h. C.E.T..

3.5.6 *Infection days*

The above-mentioned results obtained with the help of non-mathematical statistics were highly encouraging, so the same method was applied for the infection days.

As already pointed out (p. 92) the identification of infection dates by means of leaf prints only partly depends on chance. Therefore a unilateral inventory list of such cases was prepared.

From Chapter II it follows that crop infection is linked with *p.m.* precipitation and/or leaf wetness.

First test

By adding drizzle and fog data the unexplained case left by the first test, disappeared from the list. Adherence to the already established provisional criterion was improved.

With regard to the features of the different infection days, the following cases were distinguished:

Case E: *model infection day*: precipitation in period 12–18 h.;
Case F: a day after a model day; in addition rain, drizzle or fog occurred in the periods 9–12 h. and/or 18–21 h. C.E.T.;
Case G: a day after a model day, not characterized by the features described under F;
Case H: a day characterized by the features mentioned under F (precipitation in period 9–12 h.), but not preceded by a model day.

In the above way allowance was again made for the imperfections of the leaf print method, which *may* show crop infection one day late.

The frequency distribution of the 4 cases is given in Table 27.

		frequency		
Case	Brief description	de Bilt	Bennekom	dB and B'kom together
E	model day	42	40	82
F	1 day after model day; precipitation in periods 9–12 and/or 18–21 h.	2	1	3
G	1 day after model day; no precipitation in the above periods	2	2	4
H	precipitation in period 9–12 h.; not 1 day after model day	0	3	3
	n:	46	46	92

Table 27
Results of an investigation for the purpose of finding a valid meteorological criterion for crop infection to be accomplished by germinated blight conidia; data substantiate the choice of E (also see text).

The results given in Table 27 verify the correctness of the precipitation criterion already found in the first test. *The term precipitation embraces rain, drizzle and fog.*

Third test

On p. 67 mention was made of the *de Wit* leaf wetness recorder. Other types of wetness recorders are *inter alia* the "surface wetness recorder" (HIRST, 56), the "dew duration recorder" of WALLIN & POLHEMUS (133) and the *Bazier* thermo-humectograph. HEARN (49) stated that surface wetness recordings (in an orchard) by the HIRST apparatus conform to observations of r.h. ⩾ 90%, made in connexion with the 90% humidity rule by SMITH (114) (measurements in a screen). Since this statement is based on 10-day averages obtained outside the potato crop we should not be justified in drawing conclusions from it in view of potato blight.

At the K.N.M.I. infection data determined from leaf prints were considered in conjunction with *de Wit* leaf wetness data obtained *in the crop* (see Fig. 19 on p. 68).

Since only one wetness recorder was present in the years 1960 and 1961, the data obtained refer to de Bilt only.

There were 35 cases of observed probable crop infection. Each of those 35 cases was observed immediately (or sometimes 1 day) after a leaf wetness period of 13 hours or more. None of these periods of wet leaves occurred in the daytime only; all of them contained the midnight hour. The results thus stress the importance of leaf wetness for the entirety of phenological phases of *Phytophthora* outside the potato plant. Meanwhile it should be stated once more that, in contravention of the findings of HEARN (49), from case to case the recorded leaf wetness periods are unequal to the coincident periods of air humidity $\geqslant 90\%$. There is no such thing as a fixed coefficient to compute the one from the other. Averages are not valid for the individual cases (cf. p. 84).

That corresponds reasonably well to the statements made by ULLRICH (123). He found a leaf wetness period of 15 hours to be necessary for an infection wave to develop, this period of 15 hours being connected with rainfall; dew only moistens the uppermost leaves of the crop, whereas amounts of rain exceeding $\frac{1}{4}$ mm penetrate into the phytosphere, thus also wetting the lower leaves.

Since leaf wetness recorders are no precision instruments the difference between Ullrich's conclusion and the author's findings may be due in part to instrumental differences.

Fourth test

Although the fact of crop infection is primarily linked with wetness, the laboratory results and the tests with reference to maturation distinctly showed the importance of sunshine.

For that reason it was cursorily investigated what relationship could be found between sunshine and the dates of probable crop infection as obtained with the help of leaf prints. The 43 probable infection days at Bennekom and the 46 at de Bilt were related to 3 levels of total sunshine duration, *viz.* $\leqslant 2.0$ hrs., $\leqslant 3.0$ hrs. and $\leqslant 4.0$ hrs.. Lumping the two sets of data together, so that $n = 89$, the results were as follows:

70 out of these 89 cases occurred on days with 2 hours of sunshine or less;
80 out of these 89 cases occurred on days with 3 hours of sunshine or less;
83 out of these 89 cases occurred on days with 4 hours of sunshine or less.

All cases occurred 0, 1 or 2 days after a day with 2.1 hours or less of bright sunshine as measured with the Campbell-Stokes autograph.

The frequency data indicate that bright sunshine counteracts the accomplishment of infection. A duration of 2 hours is apparently unfavourable to the fungus, whereas a duration of more than 4 hours renders crop infection highly improbable. The conclusion may be drawn that *crop infection days of significance are deficient* in sunshine.

The results of the tests lead to the following conclusion.

Infection of the crop by already germinated conidia can be expected if precipitation occurs within the period between 12 and 18 h. C.E.T..

For the sequence of biological events leading to crop infection a leaf wetness period of at least 13 hours is required, whereas on infection days the total duration of bright sunshine is usually less than 2 hours and certainly less than 4 hours.

3.5.7 *Extension dates*

It has already been pointed out on pp. 72 and 74 why random sampling (Anon., 1, 3) and estimation of the severity of disease incidence (Anon., 2) were not carried out.

The results of counting *primary lesions* on pre-selected leaflets (p. 74) meanwhile did not fail to give an impression of the importance of some infection waves and appeared to be a satisfactory means of checking infection data derived from collodion films and of verifying previous conclusions.

Extension dates are the most marked dates in periods of extension of blight incidence (def.: p. 78). The marked dates selected from the list of *counts of primary lesions* were chosen as such on the grounds of some simple criteria. The cases were:

a. first infection of a previously uninfected pre-selected leaflet in the form of 2 or more young lesions;
b. the number of young lesions on an already blighted leaflet is at least doubled from one day to another; the doubled number should exceed 10;
c. otherwise very conspicious increase of the number of young lesions (pin points). This third criterion was rarely applied.

First test

The extension dates derived from the counts were studied in conjunction with the model infection days preceding them. In this test the precipitation criterion was applied: rain, drizzle or fog between 12 and 18 h. C.E.T..

There were 14 identified extension dates at de Bilt and 26 at Bennekom, so that n = 40; it appeared that:

23 out of these 40 cases occurred 3 days after a model infection day;
owing to persistence (cluster formation) in the occurrence of model days

24 out of the same 40 cases occurred 4 days after a model infection day;
meanwhile it can also be stated that

32 out of the same 40 cases occurred 5 days after a model infection day, whereas
28 out of the same 40 cases occurred 6 days after a model infection day.

As a matter of fact most cases of extension are represented in more than one of the above lines:

35 out of the 40 cases occurred 3–4 days after a model infection day;
1 out of the 40 cases occurred 6 days after the last preceding model infection day.

The aforementioned data confirm both the exactitude of the discussed precipitation rule for crop infection and the statement by NAUMOVA (96) concerning the incubation period.

Second test

There are many model days, more, for instance, than maturation days with a total duration of bright sunshine under 2 hours. Yet it will be evident that a model infection day in terms of precipitation is not valid if preceding criteria, *e.g.* that for maturation, have not been satisfied. In this connexion it will be apparent that the first test must have involved too many cases in one way or another. Since the model extension days often occur in small series of something like 4 consecutive days it is certainly not unlikely that only the first day of such a sequence should actually be taken into consideration because all days of the series may be associated with one and the same infection day. If so, the later days, the "followers", should be left out of account.

Omission of the followers halves the number of cases: n = 20. Now the following results remain:

16 out of these 20 cases occurred 3 days after a model infection day;
12 out of these 20 cases occurred 4 days after a model infection day;
19 out of these 20 cases occurred 5 days after a model infection day;
17 out of these 20 cases occurred 6 days after a model infection day.

This table should of course be understood in the same way as the preceding one.

Again most cases of extension are represented in more than one of the above lines; it appeared that
all cases occurred 3 – 4 days after the last preceding model infection day.

Third test

It goes without saying that later phases of *Phytophthora*'s life cycle are related to all preceding stages, though not all relationships will stand out in equally sharp relief. It is to be expected that, in a cycle of recurring phases, the various relationships will be slightly less marked in ratio to the distance between the examined stages.

It was, however, deemed of sufficient interest to test the connexion between extension days and sunshine duration (associated with maturation). A level of 2 hours total (bright) sunshine duration was adopted as criterion.

This third test involved all 40 cases already examined in the first one.

9 out of these 40 cases occurred 3 days after a day with <2 h. sunshine;
12 out of these 40 cases occurred 4 days after a day with <2 h. sunshine;
12 out of these 40 cases occurred 5 days after a day with <2 h. sunshine;
10 out of these 40 cases occurred 6 days after a day with <2 h. sunshine;
5 out of these 40 cases occurred 7 days after a day with <2 h. sunshine;
5 out of these 40 cases occurred 8–9 days after a day with <2 h. sunshine;
(8 or 9 were not registered if shorter intervals had also been found to precede the dates representing the cases involved).

Since the majority of the cases of extension are represented in more than one of the above lines the results must be summarized. It was found that

24 out of the 40 cases occurred 3–5 days after a day with <2 h. sunshine;
16 out of the 40 cases occurred $\geqslant 6$ days after the last preceding sunshine-deficient day (<2 h.).

These results are unsatisfactory. This should perhaps be ascribed to the fact that part of the extension days occur groupwise. In the various series of extension days the incidence of "followers" may as well be explained and circumscribed as the incidence of extension days on leaflets showing later responses to the fact of infection than did the leaflets whose new lesions were registered on the first date of the series. One and the same infection day is thus held responsible for the whole sequence of extension days.

Fourth test

In view of the above train of thought the test was repeated with the omission of the followers; $n = 20$. Now

8 out of these 20 cases occurred 3 days after a sunshine-deficient day (<2 h.);
10 out of these 20 cases occurred 4 days after a sunshine-deficient day;
10 out of these 20 cases occurred 5 days after a sunshine deficient day;
3 out of these 20 cases occurred 6 days after a sunshine-deficient day.

Since part of the cases are represented in more than one of the above lines, the results are summarized as follows:

16 out of the 20 cases occurred 3–4 days after a sunshine-deficient day;
4 out of the 20 cases occurred 5 days after the last preceding sunshine-deficient day.

These results are fairly well in accordance with the previously found maturation criterion (p. 92) and with the data given on p. 96.

Fifth test

Finally the extension data of de Bilt were scrutinized in conjunction with the available leaf wetness recordings. Only 10 cases could be studied, but fortunately enough they were in complete accordance with what was found with the help of the 35 cases of observed probable crop infection dealt with on p. 96. All extension dates were preceded by leaf wetness periods of at least 13 h.. All cases occurred 3–4 days after such a period. In 8 of the 10 cases there was a leaf wetness period both 3 and 4 days after extension was observed; in 7 cases a leaf wetness period $\geqslant$ 13 h. had also occurred 5 days earlier.

It can be concluded that the tests regarding the extension days, determined by counts of primary lesions on pre-selected observation leaflets, shed a favourable light on the results obtained with the help of leaf prints and other methods applied. The first leaf spots occurred 3 or 4 days after crop infection.

3.5.8 *Epidemics*

The term epidemic or epiphytotic is usually conceived as denoting a marked visible increase in the incidence of a disease. In this connexion an epidemic day is one on which the progress of the disease is marked, while an epidemic period embraces a sequence of consecutive epidemic days. It will be clear that for the purpose of forecasting blight outbreaks prolonged periods of attack are of greater importance than individual infection days which do not lead to very substantial damage.

In order to draw up an inventory of epidemical data some simple criteria were applied. The dates selected from the lists of *counts of diseased leaves* were considered as epidemical days in the following cases:

a. 2 or more diseased leaves appear on a previously healthy pre-selected stalk;
b. the number of diseased leaves on an already blighted stalk is at least doubled from one day to the next; the doubled number should exceed 10;
c. otherwise very conspicuous increase of the number of blighted leaves. This third criterion was rarely applied.

Over the years 1960 and 1961 48 epidemical days were registered at de Bilt and 34 at Bennekom. Out of these 82 cases

49 occurred 4 days after a model infection date;
49 occurred 5 days after a model infection date;
50 occurred 6 days after a model infection date;
3 occurred 7 days after the last preceding model infection day;
1 occurred 8 days after the last preceding model infection day;
1 occurred 9 days after the last preceding model infection day.

The cases noted in the last three lines referred to typical "followers".

Most cases of epidemical days are represented in the first two or three lines simultaneously. It is, therefore, of more importance to know that *70 out of the 82 observed epidemical days occurred 4 and/or 5 days after a model infection day.*

The persistence in the occurrence of epidemical days is striking. Far from being evenly distributed over the growing season, a considerable number of these days group themselves in typical more or less prolonged periods of attack, thus forming the notorious blight epidemics.

The following uninterrupted epidemical periods were observed at de Bilt:
15 –27 July 1960: 13 days;
31 July– 3 Aug. 1961: 4 days;
10 –30 Aug. 1961: 21 days;
5 – 7 Sept. 1961: 3 days;

at Bennekom:
21–25 July 1960; 5 days;
1–27 Aug. 1961: 27 days.

Combining de Bilt and Bennekom, the following periods will have to be taken into consideration for a meteorological approach:
15 –27 July 1960: 13 days;
31 July–27 Aug. 1961: 28 days; } see Ch. IV.
5 – 7 Sept. 1961: 3 days.

3.6 Notes on humidity measurements in the crop

Doubt has often been expressed with regard to the reliability of hygrograph measurements. One critic alleged, hygrograph recordings are extremely unreliable, especially in the region above 90 per cent.

This erroneous view proved to be attributable to misapprehension or abuse of a statement made by BLEEKER (11), who noticed that a hygrograph indication of 100% will slowly fall in the laboratory and in a constantly saturated atmosphere, until a level of 96% is finally reached. This statement is correct but does not inevitably imply that, in the crop, errors of 4 or more % r.h. are invariably made. Nor does it imply that the errors are greatest above 90% r.h..

It is therefore useful to consider some typical features of (good) hygrographs.

1. The long horizontal parts in the hygrogram depict saturation of the ambient air.
2. When very long, these trajects will slant down slightly to a level at which the lines on the paper slip indicate a value between 95 and 100%, usually closer to the latter. The whole of this straight line, whether slanting or not, represents an r.h. of 100%. By implication every individual point in the line does so.

   This in turn implies that, when hygrograms indicate a gradual rise of r.h. to, or a similar fall from, the level of saturation, the nearest point of the straight line should be used to adjust the adjacent lower values, at least inasmuch as values of more than 95 % or perhaps 90% are involved.
3. The reactions of hygrographs to the environment are slow. When the r.h. is quickly lowered in the laboratory, the instrument cannot be expected to respond instantly. In the crop, where the humidity regime does not show too rapid variations, a good hygrograph will not be far beside the truth as long as high air humidities are involved. A special advantage is that the indication of a hygrograph embodies, as it were, the humidity regime of, say, the last 10 minutes.

   The temporary presence of an observer will thus not immediately affect the hygrogram by his disturbing the ecoclimate.
4. Hygrographs in crops are not ventilated artificially, only naturally, so that at low wind speeds they record the situation just around the hair bundle, or they may record the bun-

dle's own surface wetness. The same applies to unventilated psychrometers, whose dry bulb might sometimes be dimmed in spite of the plastic roof above it. In such cases these instruments might represent the situation near a leaf surface, or its wetness, better than an Assmann psychrometer, which only measures the humidity of the air *between* the plants.

The above arguments together with the use of saturation defecits instead of relative humidities may be sufficient explanation of the mathematically very significant nature of some responses of *Phytophthora* to s.d. values computed from hygrograms.

The use of s.d. was already advocated by STEVENS (115) and LIVINGSTON (81) as a more satisfactory expression of atmospheric humidity than is r.h.. LIVINGSTON (81) pointed out that r.h. is not a satisfactory unit of comparison whenever more than one temperature is employed, whereas the "vapor pressure deficit" demands no correction for T. If r.h. is to have any real significance it is always necessary to take into account the temperature prevailing at the time. STEVENS (115) wrote that in s.d. the factor of T is included (because the maximum vapour pressure depends on T). In addition he stated that the rate of evaporation is much more nearly proportional to the s.d. than to the r.h..

Meanwhile the whole situation at T = 30° C differs from that at *e.g.* 3° C., but, in any case, the s.d. is a more conservative quantity than the r.h.. Moreover the author's s.d. values lay in a fairly narrow temperature traject between 5 and 15° C, where the saturation vapour pressure curve is not yet very steep. In most of the examined cases (s.d. $\leqslant$ 0.4 mm Hg) the pertinent r.h. amounted to 96% or more.

Since the saturation deficits employed had been derived from hygrograms a test was applied in order to check the reliability of such data.

For his epidemiological work POST (105, 106) had used hygrographs in conjunction with dry and wet bulb thermometers. The instruments were located in the crop. The hygrograph indications were compared regularly with the psychrometer readings. In 1956 a *Richard* hygrograph was used, in 1957 a *Fuess*. The data left by POST were examined thoroughly. Starting from the assumption, – a working hypothesis in itself –, that the humidities derived from psychrometer readings are correct, the departures of hygrograph data from corresponding psychrometer data were calculated. There were 217 pairs of data, 103 of them

r.h. according to hygrogram	departures from psychrometer data								
	Richard hygrograph; 1956					Fuess hygrograph; 1957			
	−2	−1	0	+1	u	−2	−1	0	+1
100	1		4			1		3	
99		1	5	1				3	
98			5		n		1	1	
97			3	1			2	1	
96		1	1	1			2		1
$\Sigma n = 24 + 15 = 39$	1	2	18	3	+	1	5	8	1

Table 28
Frequency distribution of departures in hygrograms of high air humidities recorded from r.h.- data derived from readings of (unventilated) psychrometers. Departures $u = r.h._{p(sychr.)} - r.h._{h(ygr.)}$

referring to the Richard and 114 to the Fuess instrument. The departures, (r.h.$_{p(sychr.)}$ − r.h.$_{h(ygr.)}$) = u, were summed up in frequency tables referring to different humidity regions in such a way that for the Richard the number of cases per table were about equal.

As we are primarily interested in the high humidities, only *their* frequency table is given in Table 28. The other frequency distribution tables showed that the hygrograph readings lose steadily in accuracy as the humidity region is lower. At low humidities the hygrographs gave (much) too low values. This phenomenon was particularly marked in the case of the Fuess, an instrument which was definitely worse than the Richard used in 1946. This is shown by the data given in table 29, which contains the computed mean deviations from psychrometrically obtained humidity values together with their standard deviation, so that here $\overline{\text{r.h.}_h} = \overline{\text{r.h.}_p} - \bar{u} \pm \sigma$. The greater differences (ū-values) are statistically significant: $\bar{u} > 3\,\sigma$.

humidity region in % r.h.$_h$	Richard 1956				Fuess 1957			
	n		ū	σ	n		ū	σ
96–100	24	r.h.$_h$ = r.h.$_p$	+ 0.04	± 0.13	15	r.h.$_h$ = r.h.$_p$	+ 0.40	± 0.17
87– 95	24	r.h.$_h$ = r.h.$_p$	− 1.08	± 0.33	18	r.h.$_h$ = r.h.$_p$	+ 0.17	± 0.63
79– 86	25	r.h.$_h$ = r.h.$_p$	− 2.80	± 0.50	17	r.h.$_h$ = r.h.$_p$	− 3.24	± 0.65
70– 78	24	r.h.$_h$ = r.h.$_p$	− 2.50	± 0.18	25	r.h.$_h$ = r.h.$_p$	− 5.56	± 0.77
< 70	6	(ū = 2.17; n too small)			39	ū much greater		

Table 29
Mean departures of hygrograph readings (in a number of humidity regions) from corresponding data obtained with the help of dry and wet bulb thermometers and their standard deviations. Data apply to measurements in potato crop.

Adding the above findings to the statistical significance of the s.d. criterion for sporulation, we can safely conclude that the results described on p. 88 are reliable.

3.7 Survey and conclusions

The results of the continuation in the field of the application of fundamental working methods previously applied in the laboratory enabled the investigator to find well-defined environmental criteria for the occurrence of each of the phenological phases of the potato blight fungus. The following survey may be useful.

1. Sporulation can be expected if the saturation deficit (s.d.) prevailing in the crop at 3 and 6 h. C.E.T. is 0.4 mm Hg or less. If the s.d. does not surpass 0.3 mm sporulation may become abundant.
2. If the duration of bright sunshine prevalent before noon (as measured by a Campbell-Stokes autograph) remains under 2 hours the newly formed inoculum is likely to mature.

3. If, in addition, precipitation occurs in the period between 9 and 15 h. C.E.T. the sporal material can germinate.
4. It may infect the potato crop if precipitation in any form (incl. drizzle and fog) occurs in the period between 12 and 18 h. C.E.T..

   We may conclude from 3 and 4 that afternoon rainfall (12–18 h.) is of great epidemiological importance (cf. item 5 on p. 64).

   The sequence of developments leading to crop infection is associated with a leaf wetness period of $\geqslant$ 13 hours and, as appears from the extension dates, with a total daily sunshine duration of less than 2 hours.
5. Three or four days after infection the first leaf spots occur; the number of diseased leaves will soon begin to increase.
6. This increase is observed partly on a number of scattered epidemical days and, to a considerable extent, in prolonged periods of such days, the major blight epiphytotics.

The above findings show the correctness of the presumed course of events in the field (p. 65), which was based upon laboratory results (pp. 62–63).

CHAPTER IV

BLIGHT FORECASTING

For practical reasons the criteria whose repeated fulfilment leads to large scale infection of a potato crop cannot easily be used for forecasting the said infection. Now that a good many infection dates are known, their occurrence is yet to be related to the preceding and the coincident weather situation.

The time has now arrived to shift to the empirical approach to the subject so strongly advocated by BOURKE (20). This transition is made possible by the fundamental knowledge now obtained.

It is of essential importance that forecasts of weather, including blight weather, be made by persons well versed in this field. It cannot be denied that this is pre-eminently a meteorological task. Meanwhile the epidemiologist should enable the meteorologist to acquit himself of this task by conveying to him (in a meteorological form) the necessary knowledge of what exactly must be forecast.

In this connexion it will be useful to study in the first and foremost place the meteorological conditions associated with the important blight periods mentioned on p. 101.

4.1 The meteorological character of significant crop infection days

In chapter III it became apparent that a *sequence of conditions* has to be satisfied before crop infection ultimately takes place. Each of the criteria was tested separately, not in conjunction with possible compliance with or contravention of rules valid for preceding phenological phases. It was found conceivable that the infection data indicated in Tables 14 and 15 on pp. 79–83 could diverge widely from those indicated by the leaf prints. After again scrutinizing all physical data in order to render the tables as accurate as possible, the infection dates derived from the collodion films were included in the tables; they were denoted by i. The accordance with the theoretical infection dates was very good, so that there is no doubt that the dates and periods now to be examined meteorologically are the correct ones.

4.1.1 *July, 1960*

On both experimental fields a very marked increase of disease incidence was observed from 15th to 27th July, 1960. No doubt the first important wave of epidemic spread was occasioned on 10th July, when substantial crop infection apparently took place (see Table 14, p. 79). The weather on that date should therefore be considered of the utmost significance.

Twelve (or more) hours prior to infection the weather situation was as represented in Fig. 23, the weather map of the 10th of July at 1 h. C.E.T.. From the Atlantic Ocean a depression, not yet occluded and thus still accompanied by a warm sector, moves in the direction of the low countries. In such a situation the precipitation activity of the warm front is significant. If it passes in the course of the morning, *rain is to be expected during the day.* The humidity of the relatively warm sub-tropical air behind the front will prevent wet foliage from drying up.

This warm air mass is followed by maritime air of polar origin. By its movement above the relatively warm water of the ocean this cold air had become more or less unstable.

Fig. 24 demonstrates the topography of the 500 mb level on 10th July at 13 h. C.E.T., which shows a westerly general upper air current. In this case the steering centre of the disturbance is situated in the surroundings of Ireland.

The situation at ground level at 13 h. C.E.T. is shown in Fig. 25. The warm front is passing the low countries with rain.

Meanwhile the warm air is followed by maritime polar air.

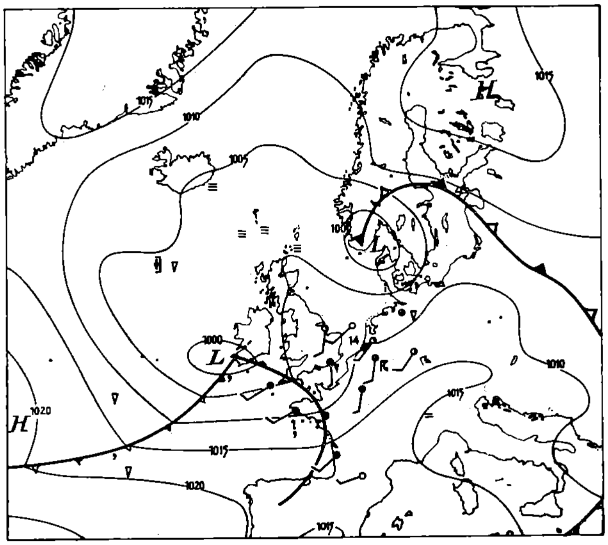

Fig. 23
Weather map of July 10, 1960, at 1 h. C.E.T.. Model situation type 1, at least 12 hours prior to crop infection.

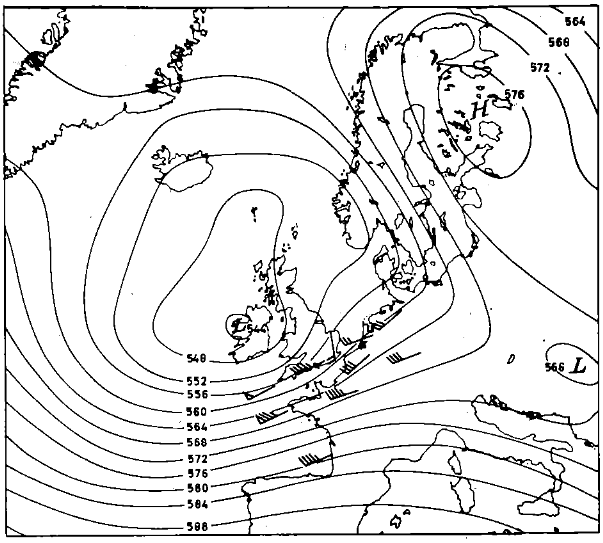

Fig. 24
Circulation pattern on an important crop infection day. Topography of the 500 mb level on July 10, 1960, 13 h. C.E.T..

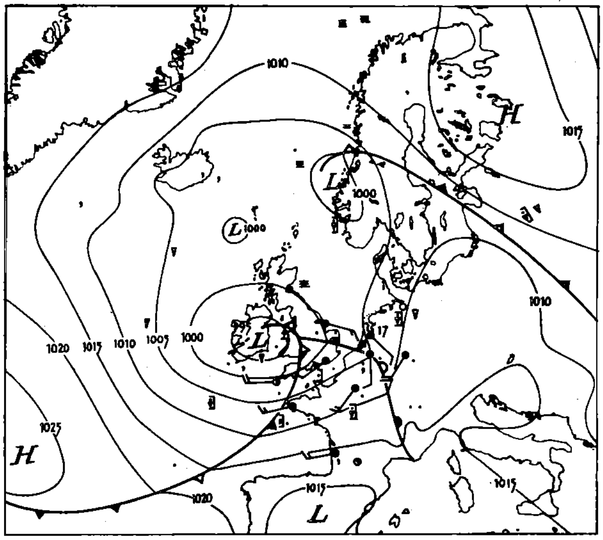

Fig. 25
Weather map of July 10, 1960, 13 h. C.E.T., showing situation leading to the onset of a blight epiphytotic immediately before substantial infection of the potato crop.

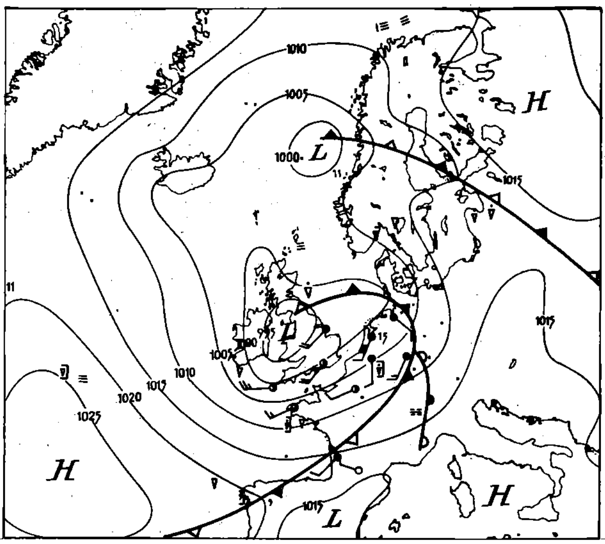

Fig. 26
Weather map of July 11, 1960, 1 h. C.E.T., showing post-infection weather situation. Front passage (and partial occlusion) have taken place.

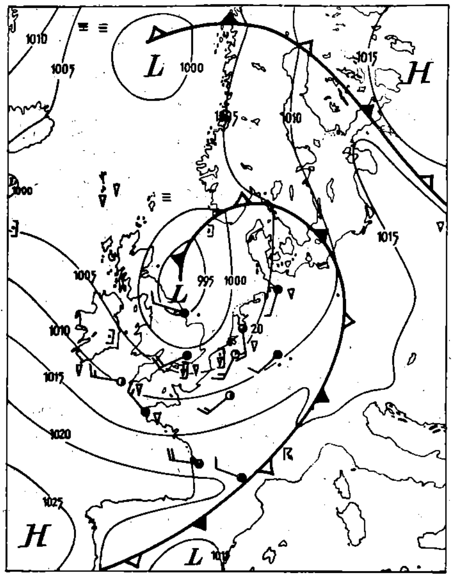

Fig. 27
Weather map of July 11, 1960, 13 h. C.E.T.. Occlusion completed.

When the cold front had crossed the Netherlands (see Fig. 26) the depression was meanwhile occluded. The occlusion obtained a cold-front character (see also Fig. 27).

The course of events shown in the Figs. 23–26 will be referred to as *model situation type 1:* **in connexion with a westerly to south-westerly upper air current** above the temperate zone **a warm front passes** the low countries *with precipitation.*

Crop infection ensuing the occurrence of this familiar constellation can be considered predictable.

A related situation, second in importance in its biological effect, though by no means insignificant for blight epidemiology and undoubtedly more frequent than type 1, is model situation *type 2* (Figs. 28–33). In type *2* daytime rainfall and moist air are also the predominant features of the situation, but a wave of warm air is not (directly) involved in the over-all picture. Infection days of this type are associated with an **occlusion, cold front or trough occasioning precipitation** while moving over the low countries **in connexion with a westerly to south-westerly upper air stream.** Newly occluded depressions for instance readily give rise to rainfall.

In Fig. 28 the circulation at the 500 mb level is given a whole day before crop infection commenced in weather situation type *2.* The sequence of events at

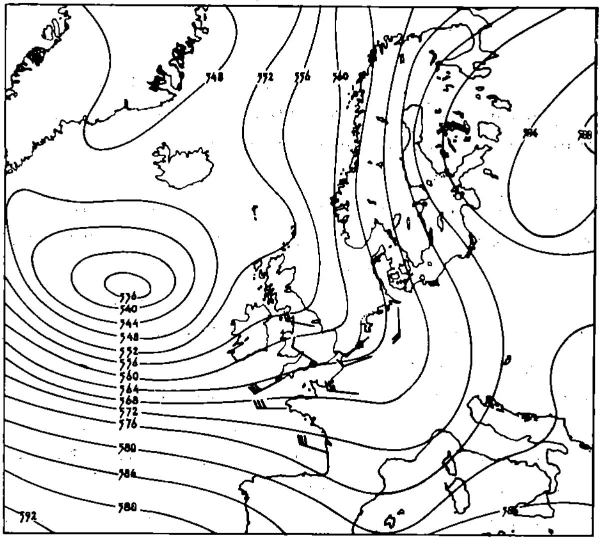

Fig. 28
Topography of the 500 mb level, showing circulation pattern at least 24 hours prior to crop infection. July 16, 1960, 13 h. C.E.T..

ground level may be different. In this context three different sub-types can be distinguished.

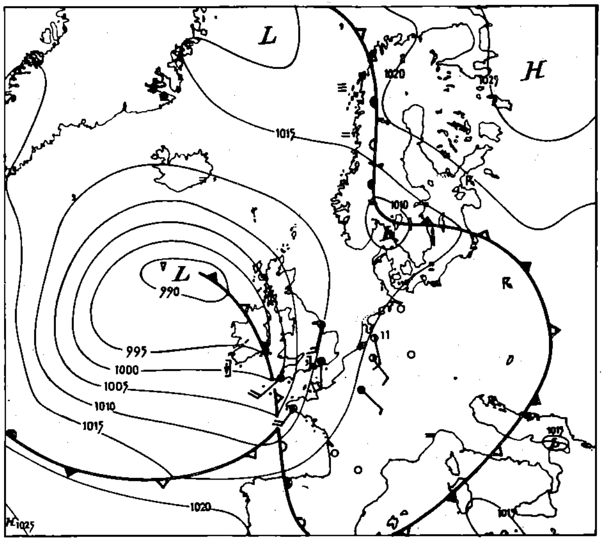

Fig. 29
Weather map of July 17, 1960, 1 h. C.E.T., showing situation type 2a, at least 12 hours prior to crop infection.

Figs. 29–31 for instance illustrate model situation *type 2 variate a*: **in a westerly to south-westerly air current** over Western Europe **an occlusion or cold front followed by maritime polar air passes** the low countries **with precipitation.**

The degree of crop infection is of course dependent on the humidity and rainfall conditions (see p. 103); the situation in the air *behind* the front is therefore held responsible for crop infection.

The general rough definition of model situation type *2* – amounting to a movement of moist maritime polar air – does not necessitate the distinct passage of an occlusion or cold front. Fairly far behind such a front and some days after its passage the conditions in the atmosphere may still or again be so, that the sequence of climatological criteria leading to crop infection are satisfied without any front passage taking place.

This rarer situation type of secondary significance is too important to be left out of account. It will be referred to as situation *Type 2 Variate b:* **a pronounced trough** at the surface and aloft in humid maritime polar air **moving** over the low countries **in an easterly direction.**

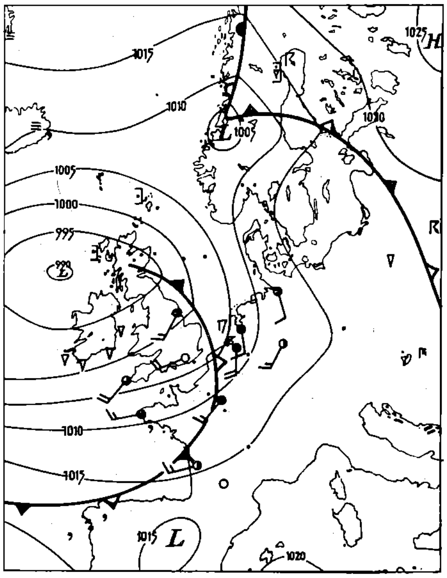

Fig. 30
Weather map of July 17, 1960, 13 h. C.E.T., showing situation leading to infection. Warm air already occluded.

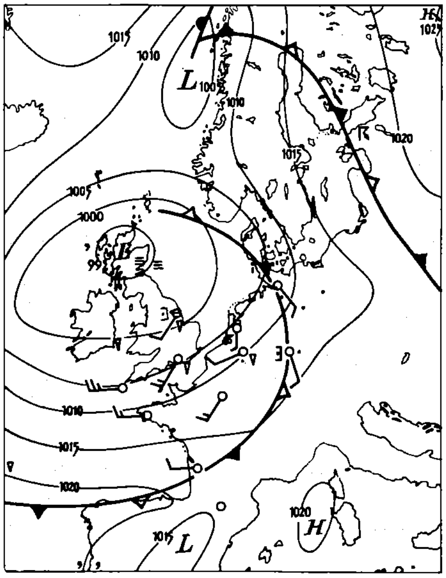

Fig. 31
Weather map of July 18, 1960, 1 h. C.E.T., showing post-infection weather situation. Front passage has taken place.

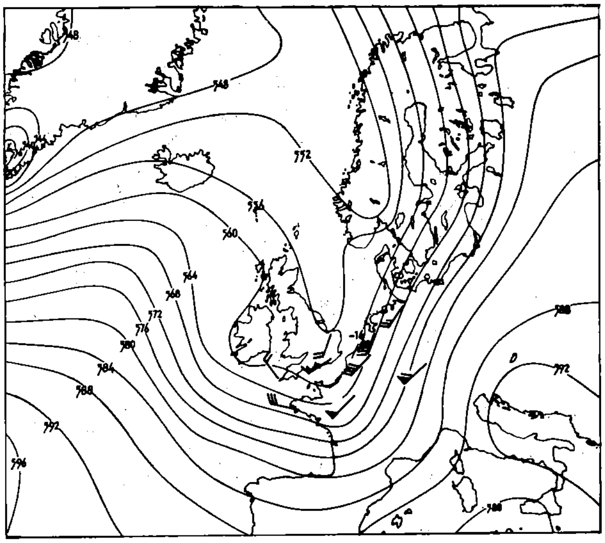

Fig. 32
Topography of the 500 mb level, showing circulation pattern at least 24 hours prior to crop infection. July 19, 1960, 13 h. C.E.T..

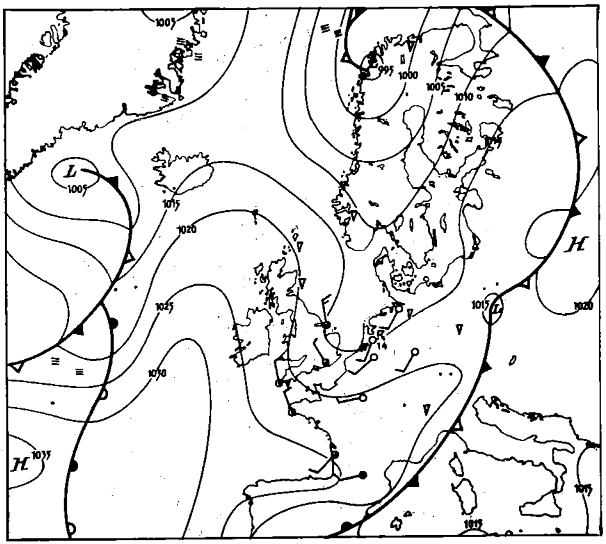

Fig. 33
Weather map of July 20, 1960, 1 h. C.E.T., showing situation type 2b, at least 12 hours prior to crop infection.

When such a trough is present the sky may remain distinctly cloudy or overcast for a considerable time.

On 20th July, 1960, infection took place at Bennekom though no front passage had occurred. The trough in the upper air was located in such a way that maritime air of polar origin flowed to the Netherlands from the south-west, thus passing France. Though in connexion with this situation showery weather was to be expected, it is difficult to predict under these conditions when and where rain showers will occur.

Fig. 33 shows the weather map of the night preceding the infection day. Twelve hours after the moment on which Fig. 33 has a bearing, de Bilt and Uccle reported overcast sky and showers.

A more infrequent variate of Type 2 is *2c*, in which unstable **maritime polar air is supplied from a western to north-western direction, bringing precipitation.** Then a centre of low pressure in the upper air is situated north, north-east or east of the low countries. The whole pressure pattern of 2b is moved, as it were, to a more eastern position, so that *no pronounced trough* is present above the Netherlands. This situation prevailed, for instance, in the second half of July, 1961. Cloudiness inherent to it will result in poor chances for wet foliage to dry up.

The findings to which the weather maps bear witness are in accordance with those of FØRSUND & FLAATTEN (36, 37), whose list of blight-inducing conditions included quasi-stationary fronts over the North Sea and Southern Norway, warm sectors with humid air over the country and the transport of maritime humid and unstable air from the west. A certain relationship also exists between the prevalence of the situations described in this chapter and the weather situations occurring in Eire 1 or 2 days earlier, as described by BOURKE (21) (see p. 13).

Rapid *nocturnal* passage of a cold front bringing precipitation during the night and/or early morning hours only is *not* sufficient for crop infection of any importance to be accomplished. Such a passage occurred, for example, in the night of July 21/22, 1960, when thunderstorms and rain showers of high intensity were observed. No infection took place on the cold day following the passage, *viz.* 22nd July.

With the exception of the sporulation criterion (the s.d. rule, p. 88) all criteria for crop infection were complied with at Bennekom on 25th July: model situation type *1*.

Only at Bennekom, and not at de Bilt, infection requirements were met on 27th July: situation type *2c*.

In both places infection was observed on the 28th July – type *1* – and 30th and 31st July: type *2a*.

4.1.2 *August, 1961*

The build-up of the significant blight epidemic in August 1961 started in much the same way as that of the epiphytotic just chronicled of July, 1960. No doubt the epidemic, the first visible signs of which were detected at de Bilt on 31st July and at Bennekom on 1st August, had been initiated on 26th July (cf. Table 15, p. 79) when a warm front, followed by a cold front, passed over the low countries in the usual manner: model situation type *1*. The circulation at the 500 mb level, 1 day prior to infection, is given in Fig. 34.

The 29th of July was an infection date associated with situation type *2b*; on 2nd (see Fig. 35) and 5th August all infection conditions were fulfilled in connexion with the prevailing situation type *2a*.

A series of later infection dates can also be described as above all of which can be classified as belonging to the specified standard situations 1 and 2 pertinent to westerly upper air currents. Repeating the examples already given does not make much sense. In this connexion an over-all test including all hitherto unmentioned cases of infection together with those already dealt with seems preferable (see pp. 117–120).

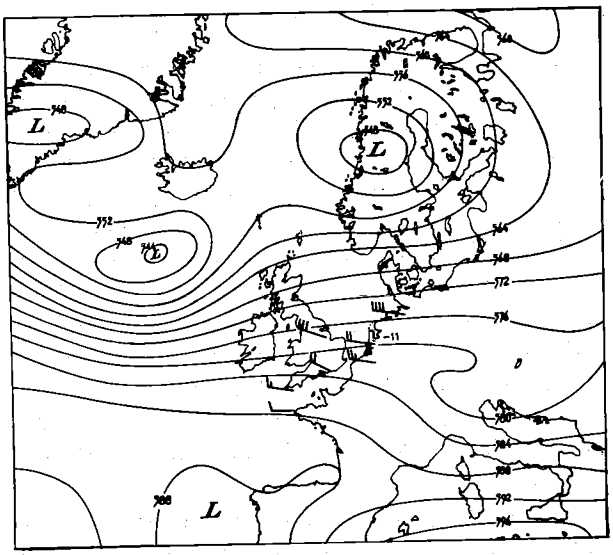

Fig. 34
Topography of 500 mb level, showing circulation pattern at least 24 hours prior to crop infection. July 25, 1961, 13 h. C.E.T..

4.1.3 *September, 1961*

At Bennekom an increase in blight incidence was observed on 2nd, 3rd and 4th September, 1961, whereas at de Bilt the intensity of attack was observed to increase on the 5th, 6th and 7th of that month. To a considerable extent the above observational results have to be ascribed to infection on 31st August and 1st September. A peculiarly divergent situation with fog

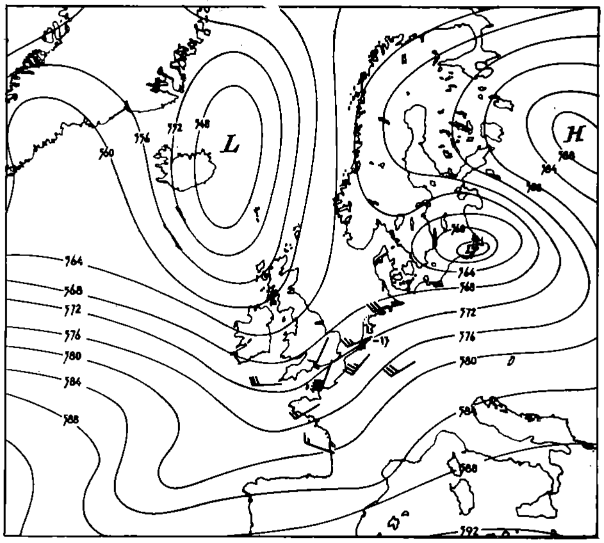

Fig. 35
Topography of 500 mb level, showing circulation pattern at least 24 hours prior to crop infection. August 1, 1961, 13 h. C.E.T..

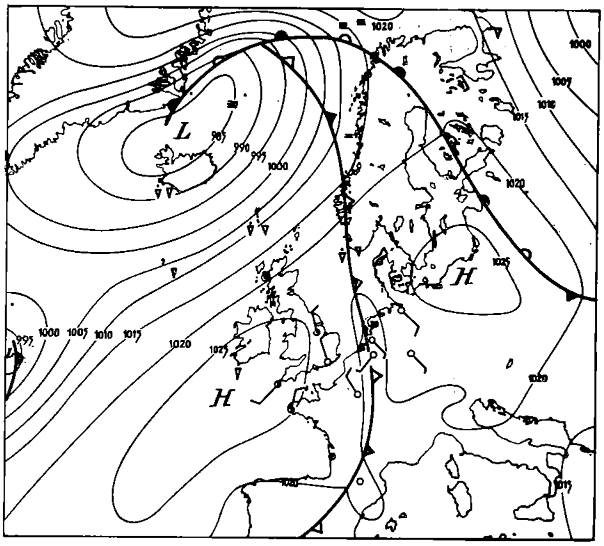

Fig. 36
Weather map of August 30, 1961, 13 h. C.E.T., showing situation type 3, at least 24 hours prior to crop infection due to fog instead of rain.

instead of rain must have initiated at least the minor attack at de Bilt. The economic significance of so late an epiphytotic not being overwhelming (LARGE, 79), it could have been passed over in silence were it not for the *inconformity* of the case. No blight epiphytotic could ever have developed had the situation of Figs. 36 and 37 occurred 1 month earlier.

The occurrence of infection days characterized by fog tallies with statements by FØRSUND & FLAATTEN (36, 37), who mention foggy weather as an special kind of weather giving rise to crop infection in Norway. That this weather type indeed requires individual description is readily apparent from the Figs. 36 and 37.

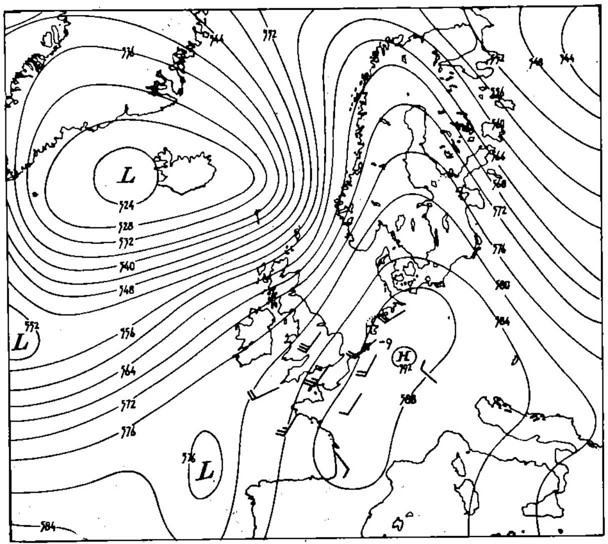

Fig. 37

Topography of 500 mb level, showing circulation pattern at least 24 hours prior to crop infection due to persistent fog. August 30, 1961, 13 h. C.E.T.

Fig. 36 shows the weather situation in question, – *type 3* –, 1 day prior to crop infection. According tothe German "Großwetterlage" classification this is situation HM (high pressure over Central Europe). The high pressure above the continent blocks the air circulation (Fig. 37).

Two cells of high pressure are separated by an old front which is losing its significance; this dividing line, a weak convergency line, is situated in the environment of the Netherlands. The situation is fairly persistent; the air mass is stagnant. Frontal convergence may give rise to the occurrence of very moist air. In this relatively stable moist air flowing slowly to the low countries the formation of low stratus clouds and fog is to be expected. Strong nocturnal outgoing radiation is no longer easily counterbalanced by sunshine; stratus clouds and fog are not readily dissipated at that time of the year since sunshine intensity has already appreciably decreased. The absence of drying conditions in the field will favour crop infection.

In the after-season the probability of the incidence of fog situations like this one is not inconsiderable.

Crop infection on 5th and 7th September 1961 was due to the occurrence of situation type *2a*, followed by *2b* (and, finally, on the 8th, *2c*).

It is hoped that knowledge of the synoptic situation of the Figs. 23–37 may prove useful for crop infection forecasting.

It may be concluded that, in addition to knowledge of the climatic requirements for blight development summed up on pp. 103–104, **weather maps constitute a most important aid in predicting crop infection by the potato blight fungus.**

4.1.4 *A comprehensive test of the synoptic models*

In order to obtain an impression of the validity of the synoptic models aimed at taking the place of the climatological model developed in Chapter III, inventory lists were drawn up of the dates on which the specified synoptic model situations prevailed and those on which crop infection occurred according to the climatological sequence of criteria. The intention was to evaluate

a. the number of cases in which compliance with both the climatological and the synoptic models occurs simultaneously;
b. the number of cases in which infection is "missed" by the synoptic model;
c. the number of cases in which infection fails to take place in spite of the occurrence of a synoptic model situation: "false alarms".

Table 30

Date(s) 1960	model sit. type	infection	
		B'kom	De B.
1–7		+	−(+)
5–7	1	+	+
5 to 6–7	2a		
6–7	2c	+	−
7–7	2b	−	+
8–7	2b	+	+
10–7	1	+	+
11–7	2b	−	−
13 to 14–7	2a	−	−
15–7	2b(+c)	+	[+]
17–7	2a	+	+
18–7	2c	−	−
19–7	2b	[+]	+
20–7	2b	+	−
21 to 22–7	2a	−	−
25–7	1	−	−
27–7	2c	+	−(+)
28–7	1	+	+
30–7	2a	+	−(+)
31–7	2a	+	+
9–8	2b(+c)	+	+
10–8	2b	[+]	+
10 to 11–8	1		
11–8	2a	+	+
12–8	2b	+	+
15–8	2b	+	[+]
16–8	2b	+	+
18–8	1(+2a)	+	−(+)
20–8	2a	−(+)	−(+)
22 to 23–8	2a	−	−
25–8	2a	[+]	[+]
26–8	2b	+	+
27–8	2b	−(+)	−(+)
28–8	2b	+	+
29–8	2a	+	+
30–8	2a	+	+
31–8	2a	−	+
1–9	1	+	+
2–9	1	+	+
3–9	2a	+	+
4–9	2a	[+]	−
5–9	2b	[+]	−
1961			
27–6	2a	[+]	−

Table 30, cont. Date(s) 1960	model sit. type	infection		Date(s) 1961	model sit. type	infection	
		B'kom	De B.			B'kom	De B.
2 to 3–7	2a			15–8	2a	–	–
3–7	2c	–	–(+)	16–8	2a	+	–
4–7	2a	+	+	16 to 17–8	2a	–	–
7 to 8–7	2a			18–8	1	+	+
8–7	1	[+]	[+]	18 to 19–8	2a		
9–7	2a	–(+)	+	19–8	2b	[+]	[+]
10–7	1	+	–(+)	21–8	1	+	+
12–7	2a	+	–	22–8	2a	+	+
13–7	2b	+	+	24–8	1	[+]	+
15–7	2b	–	+	25–8	2a	+	–
16–7	2b	+	+	26–8	2a	–(+)	–
17–7	2c	–(+)	–	27–8	2a	–	–
18–7	2c	+	–	31–8	3	+	+
19–7	2c	+	+	1–9	3	+	+
20–7	2c	+	–	3–9	2a	[+]	+
21–7	2c	–	–	4–9	2a	–	+
22–7	2c	+	–	5–9	2a	+	+
26–7	2a	+	+	6–9	2a	–(+)	–(+)
28–7	2a	–(+)	–	7–9	2b	+	+
29–7	2c	+	+	8–9	2c	–	+
2–8	2a	+	+	9–9	3	–	+
5–8	2a	–(+)	+	10–9	3	–	–
8–8	2a	+	–	11–9	3	+	+
10 to 11–8	2a	–	–	11 to 12–9	2a	–	–
13–8	2a	[+]	[+]	14–9	2a	–	+
14–8	2a	+	–	20–9	3	–	+

Table 30

List of the dates on which the specified synoptic situations occurred and lists of infection dates drawn up irrespective of the former column.

[+]: one of the criteria pertinent to development prior to penetration was not completely satisfied (see Tables 14 & 15, p. 79): suboptimal data.

–(+): penetration conditions marginal (see p. 83).

Re a): Coincidence of the occurrence of the climatological and the synoptic model is the rule. If the 10 cases of nocturnal front passage, which is no valid criterion, are left out of account, in 76 of the remaining 84 cases in which one of the synoptic models had occurred infection conditions had been fulfilled in at least one of the two test fields. The sub-optimal cases of infection are all included.

Re b): Only once did infection take place without any of the described weather models being present. On 1st June, 1960, the whole situation was similar to type *2c*, but the north-westerly airflow over the low countries came directly from the polar region. Since a direct break-through of northerly cold air is certainly not conducive to blight development (BOURKE, 21) and since in other – equal – cases no infection has ever been observed, the author ventures on the supposition that on 1^{st} June, 1960, the intensity of crop infection had not been of any importance.

Re c): In 7 of the 83 cases mentioned under b) no infection occurred in spite of the prevalence of a synoptic model situation associated with potato blight.

The cases dealt with in the above paragraphs are summed up in Table 31.

Measure of occurrence of infection conditions	Occurrence of weather situation type					
	1	2a	2b	2c	3	other situation
+ +	7	11	9	2	3	
+ [+]	1	1	4			
[+] [+]	1	2	1			
+ −(+)	2	3		1		1
+ −	1	7	3	5	2	
−(+) −(+)		2	1			
[+] −		2	1			
−(+) −		2		3		
− −	1	2	1	2	1	
	+	+	+	+	+	+
85 cases	13	32	20	13	6	1

Table 31

Frequency table of the occurrence of different specified weather situations in conjunction with simultaneous occurrence (or absence) of crop infection conditions;

+ +: all conditions fulfilled in both places;

+ [+]: in one of the 2 places conditions were marginal for one of the pre-penetration stages;

− (+): penetration conditions marginal.

See also tables 14, 15 and 30.

If the fact that some cases of infection are more or less boundary cases is not taken into account and if the weather type 2 is not subdivided, the merits of the synoptic models show to full advantage: see Table 32.

It being inconceivable that frequency distributions like those given in Table 32 are attributable to chance and not to weather, a statistical test was not carried out.

Tables 31 and 32 support the view that model situation type *1* constitutes the most significant situation favouring the epidemic spread of blight. Examination of Tables 14 (pp. 79–80), 15 (pp. 81–83) and 30 (pp. 117–118) and several

Occurrence of (climatological) crop infection conditions	Frequency of the occurrence of model synoptic conditions of specified types			
	1 (movement of warm maritime air)	2 (movement of cold maritime air)	3 (fog)	4 (other conditions)
+ + (in both places)	11 } 12	37 } 60	3 } 5	1
+ − (in one place)	1	23	2	
− − (in one of the two)	1	5	1	
	+	+	+	+
85 cases	13	65	6	1

Table 32
A simplified version of Table 31, demonstrating the efficiency of the synoptic models for indicating epidemiologically critical days.

notes made during the field experiments also show that the most important epiphytotics are associated with the occurence of type *1*.

Whereas the prevalence of situation type *1* initiates blight attacks of major intensity it also initiates a sequence of sunoptic situations significant for the further spread of blight. The occurrence of type *1* is invariably followed by that of type *2*. The visually observable persistence in the occurrence of infection dates is thus easily explained by the persistence in the prevalence of weather types conducive to blight development. This tallies with the generally known fact that there are typical spells of blight weather, a fact already mentioned on earlier occasions.

In a really predictive blight forecast system the most careful attention should therefore be given to the occurrence of the fairly easily predictable synoptic model situation type *1*.

4.2 The proposed disease forecast system

Any system forecasting crop infection by a downy mildew such as the blight fungus should start from the principle – which is of general validity – that for that infection a clearly defined sequence of likewise clearly defined environmental requirements must be met. This series of critical conditions, here summarized on pp. 103–104, may be called the *climatological model*. So the *first proposition* is: *let this* or, for other downy mildews, a similar **climatological model** *be the* (scientific) *basis for the forecast system.*

Although the consecutive fulfilment of the criteria together constituting the climatological model situation may be a crop infection requirement of general validity, it is not very feasible to forecast in detail all individual constitutive factors, the more so because some of them can only be measured in the crop. By being alive to the possibility that a relationship exists between the climatological model as a whole and certain synoptic situations it may yet prove to be possible to profit by the know-how of the experienced forecaster after having established this relationship.

So the *second proposition* is: *a relationship should be sought between the occurrence of the climatologial model situation and coincident* **synoptic model** *situations.* This paper reports how this was done in the Netherlands. The described models also hold good for neighbouring regions but may not be applicable to continental areas.

The *third proposition* is: *the occurrence of significant synoptic model situations favouring disease development be* **forecast** if possible.

The *fourth* and last *proposition* is: *forecasts of an infection situation should be* **communicated to the growers** *at the earliest opportunity and in the quickest manner.* Such communications could be issued by an official plant disease forecast service linked with the weather service and associated or collaborating with the plant protection authorities.

For practical application of the blight forecast method the following rules may be adopted.

1. Infection forecasts start after 0-date (see pp. 18–22).
2. Spray warnings are issued, – *i.e.* the probability of crop infection is announced –, as soon as the prevalence of synoptic model situation *1* can be forecast.
3. If blight weather 5 to 7 days after the warning still persists through the prevalence of one of the other specified model situations, a further warning is issued. (The interval chosen can be made conditional on the epidemiologically perilous nature of the prevailing synoptic model situation, *e.g.* 5 days for type 1 and 7 days for type *2* var. *b.*)
4. If no blight forecast has been issued for a week because there simply was no blight weather and a new wave of infection becomes predictable, a warning is issued in any case, regardless of whether the initiating model situation belongs to type *1* or not. After the occlusion of warm air before a front system reaches the low countries the initiating situation is usually *2a.*
5. These rules should be handled in the most flexible way. Whenever deemed justified, additional warnings may be issued provided the weather situation is in accordance with one of the synoptic models. In this way account can be taken of the practical opportunities of spray application, which might have been impracticable on previous very rainy days. Account can even be taken

of the wash-off effect of intense rainfall in respect of spray residues on the foliage. And account must of course be taken of the free week ends. After prolonged sunny periods the first warning(s) may be omitted because of a general lack of inoculum, which would otherwise make spraying a waste of money.

The fungicidal character of prolonged dry sunny periods is very important for the practical operation of a blight warning service. The agronomist who has to judge the necessity of warnings should in each individual case ask himself: "If I were a potato grower myself, would I then spray or not in to-day's circumstances?" (SCHARRINGA, 112). In the dry season of 1959 the number of warnings could have been reduced to one (in the beginning of that season) had this simple procedure been applied. The various front passages then took place *without precipitation*, thus lengthening the sunny period and postponing the following warning, which would otherwise have been broadcast on the occurrence of a synoptic model situation. Then rainfall held off again, *etc.*.

The above considerations show that a well-operating plant disease forecast service is neither the exclusive domain of the meteorologist nor that of the plant pathologist. Both have to play their part according to their own competence.

Table 30 proved that a sound basis for a blight forecast service has now been obtained. But yet the table does not give complete satisfaction. The data it provides are very precise but yet dissatisfactory in that there are too many indications of infection dates. The insignificant minor attacks should not be warned against in practice.

When during the last few years forecasts were issued by making use of the climatological model, which contains a sunshine criterion, no excessive warnings were issued. The insignificant infection cases were not warned against and the crop protection results were optimal.

The synoptic models presented in the preceding pages do not give a great deal of information with respect to the *sunshine* factor. It was therefore attempted to add different sunshine criteria to the models. Various limits were set, whereupon the complex criteria thus obtained were tried out with the help of Tables 14 and 15 (pp. 79–83). Setting the 2-hour limit appertaining to the original climatological model left a significant body of data. An additional criterion combining the synoptic model situation with the occurrence of a total (daily) sunshine duration which was *measured at de Bilt* and did not surpass 4 hours, turned out, however, to sieve out a moderate number of minor cases of infection. A striking agreement was now attained with the dates of *observed* infection according to microscopical examination of leaf prints. This catches the eye when comparing Tables 14 and 15 with Table 33.

Table 33 was derived from Table 30 (pp. 117–118) by deleting the dates with sunshine duration >4 hours.

In a similar way Tables 34 and 35 are analogous to Table 32 and 23, respectively.

Date(s) 1960	mod. sit. type	infection		Date(s) 1961	mod. sit. type	infection	
		B'kom	De B.			B'kom	De B.
1–7		+	−(+)	27–6	2a	[+]	—
5–7	1	+	+	3–7	2c	—	−(+)
7–7	2b	—	+	4–7	2a	+	+
8–7	2b	+	+	8–7	1	[+]	[+]
10–7	1	+	+	9–7	2a	−(+)	+
15–7	2b	+	[+]	10–7	1	+	−(+)
17–7	2a	+	+	12–7	2a	+	—
19–7	2b	[+]	+	13–7	2b	+	+
20–7	2b	+	—	15–7	2b	—	+
25–7	1	—	—	16–7	2b	+	+
28–7	1	+	+	19–7	2c	+	+
30–7	2a	+	−(+)	20–7	2c	+	—
31–7	2a	+	+	21–7	2c	—	—
9–8	2b	+	+	22–7	2c	+	—
10–8	2b	[+]	+	26–7	2a	+	+
11–8	2a	+	+	29–7	2c	+	+
12–8	2b	+	+	2–8	2a	+	+
15–8	2b	+	[+]	5–8	2a	−(+)	+
18–8	1(+2a)	+	−(+)	13–8	2a	[+]	[+]
25–8	2a	[+]	[+]	14–8	2a	+	—
26–8	2b	+	+	16–8	2a	+	—
28–8	2b	+	+	18–8	1	+	+
29–8	2a	+	+	19–8	2b	[+]	[+]
30–8	2a	+	+	21–8	1	+	+
31–8	2a	—	+	24–8	1	[+]	+
1–9	1	+	+	25–8	2a	+	—
2–9	1	+	+	26–8	2a	−(+)	—
3–9	2a	+	+	31–8	3	+	+
4–9	2a	[+]	—	3–9	2a	[+]	+
				4–9	2a	—	+
				5–9	2a	+	+
				6–9	2a	−(+)	−(+)
				7–9	2b	+	+
				8–9	2c	—	+
				9–9	3	—	+
				11–9	3	+	+
				14–9	2a	—	+

Table 33
List of the dates on which the specified synoptic situations occurred while at the same time the total daily amount of bright sunshine did not surpass 4 hours, as well as lists of the infection data pertinent to those dates. Cf. Table 30 on pp. 117–118.

Measure of occurrence of infection conditions	Occurrence of compliance with aggravated meteorological model					
	type					other conditions
	1	2a	2b	2c	3	
+ +	7	10	8	2	2	
+ [+]	1	1	4			
[+] [+]	1	2	1			
+ −(+)	2	3				1
+ −		7	3	3	1	
−(+) −(+)		1				
[+] −		2				
−(+) −		1		1		
− −	1			1		
	— +	— +	— +	— +	— +	— +
66 cases	12	27	16	7	3	1

Table 34
Frequency table of the occurrence or absence of crop infection conditions in cases in which the aggravated meteorological model requirements were met. Cf. Table 31.

The data thus obtained indicate that when reaching a decision on the question of whether or not to issue a warning against blight in a given case, due consideration should be given to the prospects concerning the expected amount of sunshine or, in other words, to cloudiness.

If, for example, front passage is expected to be followed bij substantial clearing up in the afternoon, no warning should be issued.

Application of the additional criteria of course increases the demands made on the forecaster. But by tightening up the rules we fall into line with the practical operation of the Netherlands blight warning service in the last few years. The feasibility of infection forecasts was then shown, as will be demonstrated in the last pages of this treatise.

4.3 Communication techniques

Although the occurrence of the familiar synoptic model situations *1* and *2a*, which are responsible for most of the blight weather, can be predicted without too much difficulty, the spraying time left after a spray warning has been issued is not so great that time can be lost in issuing the actual warning. For that reason the post card method (p. 5) cannot be given serious consideration. Better means of communication are radio (and t.v.) and telephone.

Occurrence of crop infection ↓	Frequency of dates on which the aggravated meteorological model requirements were met						
	type						other conditions
	1		2		3		
+ + (in both places)	11	11	32	49	2	3	
+ − (in one place)	0		17		1		1
− − (in neither place)	1		1				
		+		+		+	+
66 cases	12		50		3		1

Table 35
A simplified version of Table 34, demonstrating the favourable effect of tightening up the synoptic models with the help of an additional sunshine criterion. Cf. Table 32.

4.3.1 *Radio service*

In the Netherlands blight warnings can be given in radio braodcasts at 5.45, 6.40 and 12.30 C.E.T.. A short description of the working method was given on pp. 7–8. Since, as stated there, the methodic loss of time involved in the use of this means of communication lies between ½ and 17½ hours it remains regrettable that no messages can be broadcast in the late afternoon, though the development of synoptical models to take the place of the original climatological model will facilitate early forecasting.

4.3.2 *Telephone services*

The two regional telephonic warning services already functioning in the Netherlands (see p. 5) embody the most ideal way of avoiding loss of time in issuing blight forecasts. A spoken warning is recorded on a tape which is put on a reply-machine, an automatic answering-device such as that used for giving the time signal, the standard-A or the weather review. By dialling a certain number the grower immediately gets the latest epidemiological news.

Warning services of this kind can issue important new messages at any time. The greatest drawback adhering to the radio warning service, namely the lack of information in the afternoon and evening, is thus obviated.

4.4 Recent experiences regarding forecasts

In a previous publication (143) it was claimed by the author that the application of *real* disease forecasts would not only reduce the number of "doubtful cases", but also that the total number of spray applications to be given during one season would become relatively small.

Meanwhile it should be borne in mind that the two growing seasons dealt with in this paper refer to decidedly wet seasons with much blight weather. In such seasons an advantage consisting in one or two spraying rounds less as compared with the classical spray application in regular 10-day rounds is the utmost that can be achieved. Apart from the fact that applying the spray at the ideal moment is an advantage in itself, a well-operating warning service particularly pays off in the relatively drier seasons.

In 1959 several seed potato growers in het Bildt, a municipality of the province of Friesland, sprayed their crop 7 times because they did not trust the system of late warnings then still in force. In fact they sprayed 6 or 7 times too often.

On the other hand control measures in 1961 were started at an unusually early date because much of the infective material formed in the blight year 1960 had survived the very mild winter of 1960–1961, so that blight development in 1961 led to an extraordinarily early build-up of new inoculum.

In general the growing season will not be that extreme. On the grounds of a simple survey of the weather maps of a series of potato seasons SCHARRINGA (112) concluded that the application of blight forecasts does result in saving labour and chemicals by reducing the number of rounds.

In 1961 predictive warnings were given on an experimental basis. While the radio service still broadcast warnings based on the fulfilment of the first rule of POST (105, 106) and the expected fulfilment of the second rule, the experimental forecasts were phoned to the offices of the Plant Protection Service, which tested the forecasts on their regional test fields, where the results of spray application after K.N.M.I. forecasts were compared with those obtained from spraying according to the POST rules, those from spraying in regular 10-day rounds, and those from untreated plots.

The results obtained when spraying according to forecasts equalled those achieved by spraying at regular intervals as regards the yield of the treatment plots but were attained in *fewer application rounds*. The other treatments yielded worse results. In 1961 similar results were obtained.

The basis for the 1960 and 1961 forecasts was a tentative *climatological model* embracing the following items:

1. a prolonged nocturnal period of high air humidity is continued in the morning;
2. a sunless or sunshine-deficient day must follow;
3. precipitation occurs by or after mid-day.

The synoptical model had not yet been defined.

The forecasts were indeed issued prior to the official warnings. No forecasts were issued within one week after their predecessor. Table 36 gives the dates of both categories of messages. In addition, infection dates, derived from Table 33, are also given. The results of the tentative forecasts were certainly not discouraging.

Had our knowledge then been what it is now, and leaving Sundays out account, warnings would have had to be issued on 23/6, 4/7, 10/7, 16/7, 24/7, 8/8 and 17/8.

Radio message 1960	Forecast 1960	Infection dates	
25–6	23–6	24–6	
29–6		1–7	5–7
9–7	7–7	7–7	10–7
11–7		8–7	15–7
18–7	16–7	17–7	20–7
		19–7	
28–7	27–7	28–7	30–7
1–8			31–7
10–8	9–8	10–8	21–8
		11–8	15–8
18–8	17–8	18–8	25–8

Table 36
Official warnings and non-official tentative infection forecasts in 1960. Infection dates are identical to those given in Table 33 on p. 123.

In 1961 semi-official predictive warnings prudently made their way into the broadcasts, where forecasts were issued in so-called clear cases. As a precautionary escape measure the POST rules were kept ready to hand.

No official statement had been made to the growers in advance and, by way of precaution, the forecasts were worded in the following careful terms: "Growers of potato varieties susceptible to blight who have not sprayed their crop for a week or more are advised to do so now since is not unlikely that infection of the crop will be resumed within the next few days".

For growers who had not sprayed their crop for a week, forecasts were sometimes issued within one week of the preceding one.

Table 37 shows that the results were encouraging. A forecast on 26th July, which was valid for only a part of the country, was not broadcast but was used for experimental purposes (spray application in some of the test fields of the Plant Protection Service). This case was not considered a clear one. The forecast of 21st August was not broadcast again since the majority of the late potatoes had been harvested, were about to be harvested, had already had their haulms killed by herbicidal application or were about to be treated with the herbicide·

Radio message	Kind of message	Infection dates
12–6	forecast	No infection data; the POST rules were fulfilled
4–7	compliance with POST rules + forecast for coming days	4–7 9–7 8–7 10–7
10–7	id.	12–7 (15–7) 13–7 (16–7)
13–7	forecast	15–7 19–7 16–7 20–7
5–8 *)	id.	5–8
10–8	id.	13–8 (16–8) 14–8
14–8	id.	16–8 19–8 18–8 21–8
21–8 not broadcast	id.	24–8 26–8 25–8

*) 3 & 4–8: message broadcast on behalf of agricultural consultants: haulm of blight susceptible earlies should be killed (through herbicidal application).

Table 37
Radio messages of the blight warning service broadcast in 1961.

Tables 36 and 37 show that predictive warnings do not result in excessive spray application. By critical spray timing the intervals between two successive application rounds are shortened to, say, 6 days without increasing the total number of rounds. There are indications that the number of rounds can be reduced by involving the factor *wind speed* in the considerations, whereas the *post-infection temperature* is important with respect to the *severity* of an epiphytotic. These factors will constitute a subject for further research. The growing seasons of 1960 and 1961 have not yielded enough data for the author to venture a conclusion in this respect.

In 1962 potato blight forecasting on a routine basis was officially adopted by the K.N.M.I., thus superseding the POST method. The method became operative in the same year and was successfully applied throughout the season.

It is generally recognized in the Netherlands that transition from the older system to real forecasts does not involve any particular risk since no one really profited by the previous systematically late warnings. The *observed* infection period, observed with the help of "rules" or now with models, can still be made use of should the forecaster fail.

4.5 Survey and conclusions

By relating the fulfilment of the series of conditions together constituting the *climatological model* of an infection day (pp. 103–104) to the pertinent synoptic situations as given in common weather maps it proved feasible to specify synoptic situations giving rise to crop infection. First in importance are movements of warm maritime air from the west; second in importance are movements of relatively cold maritime air from west or southwest. Less important are situations characterized by cold maritime air coming in from a north-westerly direction or by fog.

The following *synoptic model* situations were distinguished.

1. Movement of relatively warm maritime air over the low countries in conjunction with a westerly to south-westerly upper air current; *precipitation.*	type 1: a warm front passes (with rainfall);
2. Movement of relatively cold maritime air over the low countries in conjunction with a more or less westerly upper air current; *precipitation.*	type 2: 2a: in a W to S-W air current an occlusion or cold front is followed by the passage of maritime polar air; 2b: a pronounced trough moves in easterly direction; 2c: maritime polar air flowing from W to N.W. direction;
3. Fog situation;	type 3: persistent fog at the end of the season. Described on p. 116: situation HM.

Tests of the meteorological models support the conclusion that weather maps constitute a most important aid in predicting blight infection.

It was shown that:

1. only *nocturnal* occurrence of a model situation does not justify infection forecast;
2. on significant infection days there are no more than 4 hours but usually less than 2 hours of bright sunshine.

Taking account of rainfall and sunshine prospects, blight forecasting was successfully applied. In 1962 the predictive working method – still based on a tentative climatological model – was officially adopted in the Netherlands.

SUMMARY

Various kinds of blight warning systems are described in Chapter I. The disadvantage of systems based on the observation of critical periods – which are only *noted* and not forecast – is that the warnings are issued when infection has already partly or completely taken place. The action of fungicides is only a prophylactic one; curative means are not (yet) known. *Forecasts* of crop infection are therefore advocated.

Laboratory experiments shed light on the reactions of the blight fungus to environmental conditions, especially radiation conditions (Chapter II). A survey of the results is given on pp. 62–63.

With the help of these findings assumptions were made as to the behaviour of the blight fungus in the field (p. 64). The assumptions were tried out in field tests (Chapter III). A survey of the results is given on pp. 103–104. The sequence of conditions to be met within the crop for appreciable infection to be accomplished, also called the *climatological model*, could be specified. This model is in accordance with the said assumptions.

In an attempt to render the system of infection forecasting suitable for use by the weather service, the occurrence of the climatological model was related to coincident synoptical situations (Chapter IV). Some meteorological model situations were described. The occurrence of the climatological model conditions is distinctly associated with the specified *synoptic model situations* summed up on p. 129.

It is shown that synoptic weather maps can be successfully used for predicting blight epiphytotics. The method developed at the K.N.M.I. is now officially in use in the Netherlands: predictive blight warnings have become a reality.

SAMENVATTING

HOOFDSTUK I: Na een beknopte inleiding omtrent de verwekker en de bestrijding van de aardappelziekte wordt nader ingegaan op de betekenis van waarschuwingssystemen.

Daar de ziekte chemisch slechts *voorbehoedend* kan worden bestreden, d.w.z. voor de besmetting van het gewas plaats vindt, moet men van een desbetreffende waarschuwingsdienst verlangen dat dan ook die infektie wordt voorspeld. Hier echter falen de gebruikelijke systemen, waarvan een aantal wordt besproken. Zij *signaleren* de infektie slechts op grond van hun zgn. regels en slaan daarna pas alarm. De waarschuwing komt dan in feite te laat. De wijze van berichtgeving, – post, radio of telefoon –, beïnvloedt de mate waarin waarschuwingen te laat komen. Door de waarschuwingsduur te bekorten en telefoondiensten in te schakelen werd in Nederland reeds vooruitgang geboekt. Een waarlijk voorspellend systeem blijft echter nodig.

Eer men tot voorspellen in staat is moet men beschikken over gedetailleerde kennis omtrent de invloed van de uitwendige faktoren op de parasiet in elke (fenologische) ontwikkelingsfase. Het probleem wordt derhalve *op fundamentele wijze* benaderd (DE WEILLE, 144). Na verkrijging van voldoende fundamentele kennis weet men eerst nauwkeurig wàt er moet worden voorspeld. Dan volgt aansluitend de empirische meteorologische benadering om te weten te komen, hòe dit te doen.

HOOFDSTUK II: Laboratoriumproeven werden genomen ter verkrijging van een zo goed mogelijk inzicht in de kringloop van *Phytophthora infestans*. In het bijzonder werd aandacht besteed aan de reacties van vaste en losse conidiën op de luchtvochtigheid en op zichtbare en ultraviolette straling. De toegepaste hulpmiddelen en werkwijzen worden uitvoerig besproken. Het te onderzoeken sporenmateriaal moet aan strenge eisen voldoen (DE WEILLE, 142) om zoveel mogelijk een statistich *homogene populatie* te vormen.

Uit de verschillende proeven, tesamen met wat reeds bekend was, verkrijgt men het volgende beeld.

1. Conidiën, *vastzittend* aan het substraat met hun dragers, zijn ten zeerste gevoelig voor *lage luchtvochtigheid.* Hoe groter het verzadigingsdeficit (v.d.), hoe sneller het verlies van potentiële kiemkracht. Voor losse conidiën geldt dit niet zozeer.
2. Pas (in het donker) gevormde conidiën hebben ’s morgens vroeg nog een heel

geringe kiemkracht (K). In geheel of bijna verzadigde lucht neemt K geleidelijk toe: er treedt *rijping* op. Des middags of nog later bereikt K een topwaarde, tenzij afgenomen waterdampverzadiging van de lucht een voortijdige daling van K met zich meebrengt.
In onverzadigde lucht treedt geen rijping op.

3. In de loop van de ochtend laten veel conidiën los van hun dragers. Tegen twaalven is het sporengehalte van de atmosfeer op zijn hoogst; na 5 uur n.m. zijn de conidiën in de lucht zeldzaam geworden (HIRST, 54).
4. *Losse* conidiën zijn niet zozeer gevoelig voor een verzadigingstekort van de lucht als wel voor *ultraviolette straling* (u.v.). Lage doses kunnen stimulerend werken; grotere, die 1.000.000 ergmm^{-2} te boven gaan, zijn fungicide. Deze gegevens gelden alleen voor *langgolvig* u.v. ($2900\ \text{Å} < \lambda < 3900\ \text{Å}$) zoals voorkomend in ons zonlicht (kortgolvig u.v. zoals voortgebracht door hoogtezonnen en germicide lampen werkt veel sterker).
5. Inmiddels is de kiemkracht van het nog *vastzittende* deel der conidiëngeneratie de topwaarde gepasseerd. In de loop van de nacht en de vroege ochtend neemt K af: *verval* van de generatie.
6. Onder daartoe gunstige vochtigheidsomstandigheden kan zich in de zojuist genoemde nacht weer een nieuwe conidiëngeneratie hebben gevormd. Conidiën vormen zich nl. niet in belangrijke mate bij een verlichtingssterkte $\geqslant 400$ lux, zodat in het licht vooral veel steriele dragers worden gevormd.
7. Daar de nieuwe generatie begint te rijpen als het verval van de voorgaande zich voltooit, vertoont K bij vastzittend inoculum in verzadigde lucht een kenmerkende periodiciteit met een minimum in de vroege morgen en een maximum na twaalven.
8. Voor kieming van de conidiën is vloeibaar water nodig.

HOOFDSTUK III: Op grond van voorgaande 8 punten werd een vermoedelijk verloop van een model-infektiedag opgesteld. De juistheid van dit *klimatologische model* werd in veldproeven getoetst, waardoor tevens tot een meer nauwkeurige omschrijving der criteria voor de afzonderlijke fasen der kringloop werd gekomen. Aangenomen werd dat gewasinfektie na de middag plaats vindt en dat zonneschijn een belangrijke rol speelt.

Door biologische precisie-waarnemingen, dagelijks verricht, konden verscheidene vormingsnachten en rijpings-, kiemings- en infektiedagen worden bepaald. Zulke gegevens werden tesamen verwerkt met gegevens omtrent natuurkundige grootheden. De toegepaste werkwijzen worden uitvoerig besproken.

De uitkomsten zijn als volgt.

1. *Sporevorming* van betekenis treedt op wanneer *in het gewas* om 3 en 6 h. M.E.T. het *v.d.* $\leqslant$ 0,4 mm kwikdruk (0,53 mb) is. Overvloedig is de sporulering bij v.d. $\leqslant$ 0.3 mm Hg (0,40 mb).

2. *Rijping* treedt op, wanneer 's morgens de *zonneschijnduur* de 2 uren niet te boven gaat.
3. Wanneer bovendien tussen 9 en 15 h. M.E.T. neerslag (incl. motregen en mist) optreedt, kan *kieming* plaats vinden.
4. Neerslag tussen 12 en 18 h. M.E.T. leidt tot *besmetting* van het gewas door de gekiemde sporen.

Deze gewasinfektie hangt ook ten nauwste samen met een bladnatperiode $\geqslant 13$ uren en met een totale zonneschijnduur $\leqslant 2$ uren. Bij een zonneschijnduur > 4 uren vindt geen besmetting van enige betekenis plaats (zie daarvoor hoofdstuk IV).

Drie of vier dagen na een dergelijke *model-besmettingsdag* worden de eerste jonge bladvlekjes aangetroffen.

Aangetoond werd dat, mits de juiste afleestechniek wordt toegepast, hoge luchtvochtigheden met een goede hygrograaf betrouwbaar kunnen worden gemeten.

HOOFDSTUK IV: Van enkele belangrijke epidemieën werd van dag tot dag het verband nagegaan tussen het vóórkomen van het klimatologische model en de bijbehorende synoptische situatie. De volgende meteorologische modeltoestanden blijken op te treden:

	type
1. westelijke tot zuidwestelijke stroming in de bovenlucht; betrekkelijk warme (subtropische) maritieme lucht stroomt over ons land; *neerslag.*	1: een warmtefront trekt over (met neerslag).
2. min of meer westelijke stroming in de bovenlucht; betrekkelijk koude (polaire) maritieme lucht stroomt over ons land; *neerslag.*	2: drie varianten die elk neerslag veroorzaken: 2a: in een westelijke tot zuidwestelijke stroming trekt een occlusie of koufront over, gevolgd door maritieme polaire lucht; 2b: een uitgesproken trog beweegt zich oostwaarts; 2c: maritieme polaire lucht wordt aangevoerd uit westelijke tot noordwestelijke richting.
3. mistsituaties	3: aanhoudende mist. Van deze pas aan 't eind van het seizoen optredende mogelijkheid wordt op blz. 116 de situatie HM beschreven.

De toestanden 1 t/m 2c nemen in de gegeven volgorde af in belangrijkheid, d.w.z. in gevaarlijkheid voor het gewas. Type 3 doet zich bij de teelt van vroege en middelvroege rassen doorgaans niet voor.

Besmetting van het gewas met aardappelziekte doet zich blijkens het onderzoek voor, wanneer een der geschetste situaties *overdag* optreedt, vooral bij een geringe totale direkte zonneschijnduur (zeker <4 h., liefst <2 h.).

Aangetoond wordt dat voorspelling van gewasbesmetting praktisch uitvoerbaar en ook gunstig is. In 1962 werd dan ook officieel tot het verstrekken van voorspellende radio-waarschuwingen overgegaan.

RÉSUMÉ

I^er^ CHAPITRE: Quelques systèmes d'avertissements contre le mildiou de la pomme de terre sont brièvement discutés. L'auteur traite le désavantage des systèmes usuels qui *signalent* les "périodes critiques" selon leurs règles. Ils annoncent bien les éruptions visibles de la maladie mais non l'infection précédente qui en est la cause. A vrai dire de tels avertissements viennent trop tard. Aussi l'auteur préconise-t-il la *prédiction* des infections au lieu de celle des éruptions visibles.

II^me^ CHAPITRE: Des expériences de laboratoire montrent que, – dans l'alternance naturelle du jour et de la nuit –, les conidiophores peuvent toujours se former, tandis que les conidies ne peuvent se former due dans l'obscurité. L'atmosphère doit être (presque) saturée. La sporulation s'achève dans l'obscurité, la *maturation* se produit le matin, c.à.d. que le pouvoir germinatif K augmente jusqu'à ce qu'un maximum soit atteint dans l'après-midi ou plus tard (voir fig. 15, p. 58). L'air doit encore être saturé ou presque saturé. Tant que les conidies tiennent encore aux sporophores, un déficit de saturation (d.s.) peut arrêter la maturation après quoi K diminue plus vite que dans de l'air saturé (fig. 17, p. 61), dans lequel K diminue jusqu'à un niveau nuisible dans les premières heures du deuxième matin. Alors, une nouvelle génération de conidies commence à maturer. De cette façon K montre une certaine *périodicité*, une marche journalière.

Des conidies détachées sont moins sensible au d.s., mais le sont davantage à la radiation solaire ultra-violette (u.v.) qui décide si le pouvoir germinatif déjà acquis sera oui ou non conservé (fig. 13, p. 51), C'est le matin que ces conidies sont dégagées du substrat. Vers midi, le nombre de conidies libres est le plus grand; après 17 h., elles deviennent rares dans l'atmosphère (HIRST, 54).

III^me^ CHAPITRE: Un *modèle climatologique* des jours d'infection fut dessiné pour pouvoir déterminer les dates d'infection à l'aide d'observations météorologiques dans la phytosphère. Ce modèle, qui se base sur les données de laboratoire, contenues dans chapitre II, fut éprouvé au moyen d'expériences faites dans des champs. En appliquant des observations biologiques de haute précision, le modèle climatologique put être décrit plus exactement.

Les résultats s'énoncent comme suit: le critère pour

1. *sporulation* significative: à 3 h. et à 6 h. (H.E.C.) un d.s. $\leqslant$ 0,4 mm Hg (0,53 mb);
   sporulation abondante: à 3 h. et à 6 h., (H.E.C.) un d.s. $\leqslant$ 0,3 mm Hg (0,40 mb);

2. *maturation* des conidies: avant midi une durée d'ensoleillement $\leqslant 2$ h.;
3. *germination*: précipitation entre 9 h. et 15 h. (H.E.C.);
4. *infection*: précipitation entre 12 et 18 h. (H.E.C.).

IV^{me} CHAPITRE: Pour quelques épiphytoties importantes le rapport entre l'apparition du modèle climatologique et les situations synoptiques accessoires fut étudié. Les situations-modèles météorologiques en question sont les suivantes:

	type	
1. courant de direction ouest à sud-ouest dans les hautes couches de l'atmosphère; *précipitation.*	1:	un front chaud traverse (avec précipitation);
2. courant de direction plus ou moins ouest dans les hautes couches; *précipitation.*	2a:	dans le cas d'un courant d'ouest à sud-ouest, une occlusion ou un front froid traverse, suivi d'air maritime polaire;
	2b:	un creux barométrique se déplace dans la direction de l'est;
	2c:	de l'air maritime polaire est transporté de direction ouest à nord-ouest;
3. des situations de brouillard.	3:	brouillard persistant. Voir p. 116; seulement à la fin de la campagne.

Le degré du danger que les situations décrites constituent pour les plantes diminue selon l'ordre indiqué.

Les plantes sont infectées quand une des situations données se produit pendant *le jour*, surtout en combinaison avec une faible durée journalière d'ensoleillement direct (p. ex. < 2 h.).

Depuis 1962 la méthode de prédire les infections des plantes est officiellement appliquée par l'Inst. Royal Météorologique des Pays-Bas.

REFERENCES

1. Anonymous — The measurement of plant diseases in the field. Trans. Brit. mycol. Soc. 26: 172–173; **1943.**
2. Anonymous — The measurement of potato blight. Trans. Brit. mycol. Soc. 31: 140–141; **1947.**
3. Anonymous — Disease measurements in plant pathology. Trans. Brit. mycol. Soc. 31: 343–345; **1947.**
4. Bary, A. de — Die gegenwärtig herrschende Kartoffelkrankheit, ihre Ursache und ihre Verhütung; 75 pp. Förstner, Leipzig, **1861.**
5. Bary, A. de — Recherches sur le développement de quelques champignons parasitaires. Ann. Sci. nat., Sér. 4, (20): 5–148. Paris, **1863.**
6. Bary, A. de — Researches into the nature of the potato-fungus, Phytophthora infestans. J. Bot. 5: 105–126; 149–154. Lond., **1876.**
7. Beaumont, A. — On the relation between the stage of development of the potato crop and the incidence of blight (Phytophthora infestans). Ann. appl. Biol. 21: 23–47; **1934.**
8. Beaumont, A. — The dependence on the weather of the dates of outbreak of potato blight epidemics. Trans. Brit. mycol. Soc. 31: 45–53; **1947.**
9. Björling, K. — Biological and technical notes on spraying against potato blight. Eur. Potato J. 1, (2): 1–4; **1959.**
10. Björling, K. & Sellgren, K. A. — Deposits of sporangia and incidence of infection by Phytophthora infestans on upper and lower surfaces of potato leaves. Acta agric. scand. 4: 375–386; **1955.**
11. Bleeker, W. — Leerboek der meteorologie II. Meten en schatten van meteorologische grootheden; 98 pp. Thieme & Cie, Zutphen (Neth.), **1942.**
12. Bochow, H. — Der Einfluß der Witterung auf das Auftreten der Kraut- und Knollenfäule [Phytophthora infestans (Mont.) de Bary] und die sich daraus ergebenden Möglichkeiten für die Einrichtung eines Warndienstes zur Durchführung prophylaktischer Maßnahmen. Wiss. Z. Univ. Rostock 4, (1): 47–66; **1955.**
13. Bochow, H. & Ræuber, A. — Untersuchungen über den Einfluß niederer Temperaturen auf den Krautfäuleerreger Phytophthora infestans de By. Nachr.-Bl. dtsch. Pfl.-schutzdienst (6): 120–123; **1956.**
14. Boer, H. J. de — De hoeveelheid ultraviolet licht in de globale straling te de Bilt. K.N.M.I. (Roy. Neth. meteor. Inst.), Wet. Rapp. (59-6), 14 pp.; **1959.**
15. Bonde, R. & Schultz, E. S. — Potato refuse piles as a factor in the dissemination of late blight. Maine agric. Exp. Stat., Bull. (416): 229–246; **1943.**
16. Bonde, R. & Schultz, E. S. — Potato refuse piles and late blight epidemics. Maine agric. Exp. Stat. Bull. (426): 233–234; **1944.**
17. Bonde, R. & Schultz, E. S. — Control of late blight tuber rot by killing the tops with weed killing materials. Maine agric. Exp. Stat., Bull. (426): 235–236; **1944.**

18. Bonde, R., Tobey, E. R. & Plummer, B. E. Late blight and early blight. Maine agric. Exp. Stat., Bull. (442): 145–146; **1946**.

19. Bourke, P. M. A. Potato blight and the weather: a fresh approach. Irish meteor. Serv., Techn. Note (12), 11 pp.; **1953**.

20. Bourke, P. M. A. The forecasting from weather data of potato blight and other plant diseases and pests. W.M.O. (World meteor. Organiz.), Techn. Note (10), 48 pp.; **1955**.

21. Bourke, P. M. A. The use of synoptic weather maps in potato blight epidemiology. Ir. meteor. Serv., Techn. Note (23), 35 pp.; **1957**.

22. Bourke, P. M. A. Modern meteorology and epidemiology of plant diseases. Proc. 4th int. Congr. Crop Protect. (2): 169–174. Brunswick, **1959**.

23. Bourke, P. M. A. Meteorology and the timing of fungicide applications against potato blight. Int. J. Bioclimatol. & Biometeor. (Oegstgeest, Neth.) 3, Pt. 2 Seet. E, 8 pp.; **1959**.

24. Brunt, D. Some factors in micro-climatology (abstr.). Nature 157: 828; **1916**.

25. Butler, J. & Jones, S. C. Plant pathology: 514–524. MacMillan & Co., Lond., **1949**.

26. Clayson, A. M. & Robertson, N. F. Some observations on the early stages of potato blight attacks. Pl. Pathol. 6: 123–127; **1957**.

27. Cook, H. T. Forecasting late blight epiphytotics of potatoes and tomatoes. J. agric. Res. 78: 545–563; **1949**.

28. Crosier, W. Culture of Phytophthora infestans. Phytopathology 23: 713–720; **1933**.

29. Crosier, W. Studies in the biology of Phytophthora infestans (Mont.) de Bary. Cornell Univ., Agric. Exp. Stat., Mem. (155), 40 pp.; **1934**.

30. Dogniaux, R. Étude du climat de la radiation en Belgique. Kon. meteor. Inst. Belg., Contr. (18), 54 pp.; **1954**.

31. Doorn, A. M. van Onderzoekingen over het optreden en de bestrijding van valse meeldauw (Peronospora destructor) bij uien. Thesis, Wageningen, 63 pp.; **1959**. Also in T. Pl.-ziekten 65: 193–255; **1959**.

32. Dufrenoy, J. Les conditions qui permettent l'infection des pommes de terre par le Phytophthora infestans. Ass. franc. sci., 5th sess.: 250–251; **1932**.

33. Everdingen, E. van Het verband tussen de weersgesteldheid en de aardappelziekte (Phytophthora infestans). T. Pl.-ziekten 32:129–140; **1926**.

34. Everdingen, E. van Über die Zusammenhang zwischen Wetter und Kartoffelkrankheit (Phytophthora infestans). Bioklimatol. Beibl. (2): 111–116; **1935**.

35. Farlow, W. G. The potato rot. Bull. Bussey Inst. (4): 319–338; **1875**.

36. Førsund, E. & Flaatten, H. K. Experiments of forecasting late blight epiphytotics in Norway. Eur. Potato J. 1, (2): 5–8; **1958**.

37. Førsund, E. & Flaatten, H. K. The interrelationship between climate and outbreak of late blight epiphytotics. Meld. Norges Landbr.-høgskole (Vollebekk) 38, (6), 61 pp.; **1959**.

38. Gäumann, E. Pflanzliche Infektionslehre. 2nd ed., 681 pp. Verl. Birkhäuser, Basel, **1951**.

39. Geiger, R. Das Klima der bodennahen Luftschicht. 3rd ed., 460 pp. Vieweg & Sohn, Brunswick, **1950**.

40. Glaerum, O. Forsøk med poteter og en undersøkelse over potetenes og torråtens avhengighet av vaerlag og høideforhold. Beretn. St. Forsøksgård Møistad 1931: 1–55; **1931.**

41. Goossen, H. Krautfäulebekämpfung und Regen. Mitt. dtsch. landwirts-Ges. 73: 739–740; **1958.**

42. Goossen, H. & Eue, L. Verteilung, Regenbeständigkeit und Umlagerung von Spritz- und Sprühlbelägen im Kartoffelbestand. Höfchen-Briefe. 8: 67–86; **1955.**

43. Gottlieb. D, The physiology of spore germination in fungi. Bot. Rev. 16: 229–257; **1950.**

44. Grainger, J. Host nutrition and attack by fungal parasites. Phytopathology 46: 445–456; **1956.**

45. Grainger, J. Blight – the potato versus Phytophthora infestans. Agric. Rev. 3, (5): 10–26; **1957.**

46. Grümmer, G. Ausbruch und Verlauf der Krautfäule-Epidemie in Greifswalder Kartoffelbeständen während der Jahre 1952–1957. Wiss. Z. Univ. Greifswald 7, (1/2); **1958.**

47. Harrison, A. L. The relation of weathering to epiphytotics of late blight on tomatoes. Phytopathology 37: 533–538; **1947.**

48. Heald, F. D. Manual of plant diseases. 2nd ed., 953 pp. McGraw Hill, N. York/Lond., **1933.**

49. Hearn, J. M. The duration of surface wetness. Meteor. Mag. 90: 174–178; **1961.**

50. Heigel, K. Der Benetzungsschreiber nach Woelfle. Erfahrungen und Meßergebnisse. Meteor. Rdsch. 15: 111–114; **1962.**

51. Hiebel, K. Erfahrungen mit der praktischen Auswertung der Phytophthora-Testparzellen im Landkreis Bad Kissingen von 1955 bis 1958. Pfl.-Schutz (Munick) 11: 119–121; **1959.**

52. Hill, L. Die Messung der biologisch aktiven ultravioletten Strahlen des Sonnenlichtes. Strahl.-Therapie 34: 117–128; **1929.**

53. Hirst, J. M. An automatic volumetric spore trap. Ann. appl. Biol. 39: 257–265; **1952.**

54. Hirst, J. M. Changes in atmospheric spore content: diurnal periodicity and the effect of weather. Trans. Brit. mycol. Soc. 36: 375–393; **1953.**

55. Hirst, J. M. The early history of a potato blight epidemic. Pl. Pathol. 4: 44–50; **1955.**

56. Hirst, J. M. A simplified surface-wetness recorder. Pl. Pathol. 6: 57–61; **1957.**

57. Hirst, J. M. New methods for studying plant disease epidemics. Outlook Agric. 2: 16–26; **1958.**

58. Hirst, J. M. & Stedmann, O. J. The effect of height of observation in forecasting potato blight by Beaumont's method. Pl. Pathol. 5: 135–140; **1956.**

59. Hirst, J. M. & Stedmann, O. J. The epidemiology of Phytophthora infestans. I: Climate, ecoclimate and the phenology of disease outbreak. Ann. appl. Biol. 48: 471–488; **1960.**

60. Hirst, J. M. & Stedmann, O. J. id. II: The source of inoculum. Ann. appl. Biol. 48: 489–517; **1960.**

61. Hyre, R. A. Meteorological data correlated with potato and tomato late blight in northeastern United States. (Abstr.). Phytopathology 42: 481; **1952.**

62. Hyre, R. A. Progress in reporting late blight of potato and tomato. Pl. Disease Rep.-er 38: 245–253; **1954.**

63. Hyre, R. A. & Bonde, R. Forecasting late blight in northern Maine. Am. Potato J. 32: 119–125; **1955.**

64. Hyre, R. A. & Horsfall, J. G. Forecasting potato blight in Connecticut. Pl. Disease Rep.-er 35: 423–431; **1951.**

65. Jaivenois, A. Les avertissements concernant le mildiou de la pomme de terre (Phytophthora infestans). Rev. agric. (Bruss.) 12: 715–717; **1959.**

66. Jensen, J. L. Moyens de combattre et détruire le Peronospora de la pomme de terre. Soc. agric. (franç.). Mém. 131: 31–156; **1887.**

67. Johannes, H. Beitrag zur Epidemiologie der Phytophthora infestans I. Einführung und mikroklimatische Untersuchungen. Z. Pfl.-Krankh. & Pfl.-Schutz 60: 289–307; **1953.**

68. Jones, L. R. The onion mildew. Vermont Exp. Stat., Ann. Rep. 10: 61–62; **1897.**

69. Jones, L. R., Giddings, N. J. & Lutman, B. F. Investigations of the potato fungus Phytophthora infestans. Vermont agric. Exp. Stat. Bull. (168), 108 pp.; **1912.**

70. Katterfeld, N. O. Zur Biologie der Peronospora Schleideni Ung. (Russ.; w. German abstr.). Bolezni Rastenij (Leningr.): 71–87; **1926.**

71. Keay, M. A. Delayed sporulation of Phytophthora infestans on infected potato shoots. Pl. Pathol. 2: 68–71; **1953.**

72. Kimball, H. H. & Hand, I. F. Bleaching of methylene-blue-acetone-water solutions by ultraviolet radiation. Bull. Nat. Res. Council (61): 123–125; **1927.**

73. Large, E. C. Field trials of copper fungicides for the control of potato blight. I. Foliage protection and yield. Ann. appl. Biol. 32: 319–329; **1945.**

74. Large, E. C. The interpretation of progress curves for potato blight and other plant diseases. Pl. Pathol. 1: 109–117; **1952.**

75. Large, E. C. Potato blight forecasting investigation in England and Wales, 1950–1952. Pl. Pathol. 2: 1–15; **1953.**

76. Large, E. C. Methods of plant disease measurement and forecasting in Great Britain. Ann. appl. Biol. 42: 344–354; **1955.**

77. Large, E. C. Potato blight forecasting and survey work in England and Wales, 1953–1955. Pl. Pathol. 5: 39–52; **1956.**

78. Large, E. C. Losses caused by potato blight in England and Wales. Pl. Pathol. 7: 39–48; **1958.**

79. Large, E. C. Disease losses in potatoes. Proc. Nutrit. Soc. 20: 15–20; **1961.**

80. Limasset, P. Recherches sur le Phytophthora infestans (Mont.) de Bary. Ann. Epiphyt. 5: 21–39; **1939.**

81. Livingston, B. E. The vapor tension deficit as an index of the moisture condition of the air. Johns Hopkins Univ., Circ. (293): 170–175; **1917.**

82. Löhnis, M. P. Onderzoek naar het verband tussen de weersgesteldheid en de aardappelziekte (Phytophthora infestans) en naar de eigenschappen, die de vatbaarheid der knollen voor deze ziekte bepalen. Med. Wet. Comm. Adv. & Onderz. Volkswelvaart & -weerbaarh., 129 pp.; **1924.**

83. Marshall Ward, H. Illustrations of the structure and life-history of Phytophthora infestans, the fungus causing the potato disease. Quart. J. microsc. Sci. 27: 413–425; **1886.**

84. Mastenbroek, C. Over de differentiatie van Phytophthora infestans (Mont.) de Bary en de vererving van de resistentie van Solanum demissum Lindl. Thesis, Wageningen, 121 pp.; **1952**.

85. Melhus, I. E. The perennial mycelium of Phytophthora infestans. Centr.-Bl. Bakteriol., Parasitenk. & Inf.-Krankh. 39: 482–488; **1913**.

86. Melhus, I. E. Germination and infection with the fungus of the late blight of potato. Agric. Exp. Stat. Univ. Wisconsin, Res. Bull. (37), 64 pp.; **1915**.

87. Melhus, I. E. Hibernation of Phytophthora infestans in the Irish potato. J. agric. Res. (Washington) 5: 71–102; **1915**.

88. Morstatt, H. Die jährlichen Ernteverluste durch Pflanzenkrankheiten und Schädlinge und ihre statistische Ermittlung. Ber. Landwirtsch. (Berlin) 9: 433–474; **1929**.

89. Müller, K. O. Untersuchungen über die Kartoffelkrautfäule und die Biologie ihres Erregers. Arb. Biol. Reichsanst. 16: 197–211; **1929**.

90. Müller, K. O. & Griesinger, R. Der Einfluß der Temperatur auf die Reaktion von anfälligen und resistenten Kartoffelsorten gegenüber Phytophthora infestans. Angew. Bot. 24: 130–149; **1942**.

91. Müller, K. O. & Haigh, J. C. Nature of "field resistance" of the potatoes to Phytophthora infestans de Bary. Nature 171: 781–783; **1953**.

92. Müller, K. O. & Munro, J. The reaction of virus-infected potato plants to Phytophthora infestans. Ann. appl. Biol. 38: 765–773; **1951**.

93. Murphy, P. A. The bionomics of the conidia of Phytophthora infestans (Mont.) de Bary. Sci. Proc. Roy. Dublin Soc. 16: 442–446; **1922**.

94. Murphy, P. A. & McKay, R. Further experiments on the sources and developments of blight infection in potato tubers. J. Dep. Lands & Agric. 25: 10–21; **1925**.

95. Naumova, N. A. On forecasting the appearance of Phytophthora infestans on the potato. Plant Protect. (Leningr.) 3: 51–54; **1935**. [Russ.; abstr. in Rev. appl. Mycol. 15: 522; **1936**].

96. Naumova, N. A. Krankheiten der landwirtschaftlichen Pflanzen; 2nd ed.; Moscow, **1952**. Cited by Ullrich, 122.

97. Nugent, T. J. When is the right time to spray? Food Packer 30: 34–36; **1949**.

98. Oort, A. J. P. Onwaarschijnlijkheden bij het ontstaan van plantenziekten – epidemieën. Versl. Kon. Ned. Akad. Wet. 69: 129–132; **1960**.

99. Orth, H. Der Einfluß der Luftfeuchtigkeit auf das Keimverhalten der Sporangien von Phytophthora infestans (Mont.) de Bary, der Erreger der Kartoffelkrautfäule. Z. Pfl.-Krankh. & Pfl.-Schutz 47: 425–447; **1937**.

100. Orth, H. & Lehmann, H. Über Degenerationserscheinungen bei Phytophthora infestans. Züchter 7: 12–16; **1935**.

101. Orton, C. R. Meteorology and late blight of potatoes (abstr.). Phytopathology 6: 107; **1916**.

102. Peterson, L. C. The overwintering of Phytophthora infestans (Mont.) de Bary under Long Island conditions. Am. Potato J. 24: 188–197; **1947**.

103. Pethybridge, G. H. Considerations and experiments on the supposed infection of the potato crop with the blight fungus (Phytophthora infestans) by means of mycelium derived directly from the planted tubers. Sci. Proc. Roy. Dublin Soc. 13: 12–27; **1911**.

104. Poeteren, N. van Een waarschuwingsdienst voor het optreden van aardappel-

ziekte. Versl. & Med. Pl.-ziektenk. Dienst (Wageningen) (53), 8 pp.; **1928**.

105. Post, J. J. Een nieuw onderzoek naar de samenhang tussen het weer en het optreden van aardappelziekte. Verslag van het eerste proefjaar (1950). K.N.M.I. (Roy. Neth. meteor. Inst.), Wet. Rapp. (57-6), 18 pp.; **1957**.

106. Post, J. J. Id. Verslag van het tweede en derde proefjaar (1957 en 1958). K.N.M.I., Wet. Rapp. (59-5), 57 pp.; **1959**.

107. Post, J. J. & Richel, C. De mogelijkheden tot reorganisatie van de waarschuwingsdienst voor aardappelziekte. Landbouwk. T. 63: 77–95; **1951**.

108. Post, J. J. & Richel, C. De waarschuwingsdienst voor de aardappelziekte. Tuinbouw 6: 133–134; **1951**.

109. Ræuber, A. & Bochow, H. Über die Bedeutung der Sporenfluges von Phytophthora infestans für den Warndienst. Nachr.-Bl. dtsch. Pfl.-schutzdienst (1): 6–11; **1957**.

110. Reddick, D. Potato blight. Am. Potato J. 5: 285–288; **1928**.

111. Rentschler, H. C., Nagy, R. & Mouromseff, G. Bactericidal effect of ultra-violet radiation. J. Bacteriol. 41: 745–774; **1941**.

112. Scharringa, M. Adelantos recientes en el campo de la previsión de ataques de Phytophthora infestans sobre papas. Fitosanitarias (La Plata) 2. In the press; **1964**.

113. Shipley, A. Onion disease at Bermuda. Roy. Gardens, Kew (Lond.), Bull. (19): 1–23; **1887**.

114. Smith, L. P. Potato blight forecasting by 90 per cent humidity criteria. Pl. Pathol. 5: 83–87; **1956**.

115. Stevens, N. E. A method for studying the humidity relations of fungi in culture. Phytopathology 6: 428–432; **1916**.

116. Sutcliffe, R. C. Predictability in meteorology. Arch. Meteor. Geophys. & Bioclimatol. 7: 3–15; **1954**.

117. Thomas, W. D. Factors influencing the epidemiology of late blight on potatoes. Thesis. Univ. Minnesota; **1947**.

118. Thran, P. Phytophthora–Warndienst. Kartoffelbau 3: 129–130; **1952**.

119. Thurston, H. D., Knutson, K. W. & Eide, C. J. The relation of late blight development on potato foliage to temperature and humidity. Am. Potato J. 35: 397–406; **1958**.

120. Uhlig, S. Untersuchungen zum Problem der Phytophthora–Warnungen. Ber. dtsch. Wetterdienst 5, (37), 27 pp.; **1957**.

121. Uhlig, S. Die meteorologischen Voraussetzungen für die Ausbreitung der Kartoffelkrautfäule. Kartoffelbau 9: 86; **1958**.

122. Ullrich, J.: Die Biologie und Epidemiologie von Phytophthora infestans (Mont.) de By. Nachr.-Bl. dtsch. Pfl.-schutzdienst 9: 129–138; **1957**.

123. Ullrich, J. Die Tau- und Regenbenetzung von Kartoffelbeständen. Ein Beitrag zur Epidemiologie der Krautfäule (Phytophthora infestans). Angew. Bot. 32: 125–146; **1958**.

124. Ullrich, J. Ursachen und Verlauf der Kartoffelkrautfäule-epidemien. Kartoffelbau 9: 85; **1958**.

125. Ullrich, J. Grundlagen und Möglichkeiten der Prognose des Auftretens von Pflanzenkrankheiten und Schädlingen. Mitt. biol. Bundesanst. Land- & Forstwirtsch. (Berl.-Dahlem) 97: 149–156; **1959**.

126. Vassy, A. Radiosonde spéciale pour la mesure de la répartition verticale

de l'ozone atmosphérique. J. sci. Météor. 10: 63–75; **1958**.

127. Vowinckel, O. Die Anfälligkeit deutscher Kartoffelsorten gegenüber Phytophthora infestans (Mont.) de By. unter besonderer Berücksichtigung der Untersuchungsmethoden. Arb. biol. Reichsanst. Land- & Forstwirtsch. 14: 588–641; **1926**.

128. Waggoner, P. Distribution of potato blight around inoculum sources. Phytopathology 42: 323–328; **1952**.

129. Wallin, J. R. Field studies on the development and survival of Phytophthora infestans sporangia on potato and tomato plants (abstr.). Phytopathology 42: 482; **1952**.

130. Wallin, J. R. The production and survival of Phytophthora infestans on tomato and potato plants. Phytopathology 43: 505–508; **1953**.

131. Wallin, J. R. & Hoyman, W. G. Forecasting potato late blight in Dakota. Bimonthly Bull. N.-Dakota Exp. Stat. 16: 226–231; **1954**.

132. Wallin, J. R. & Hoyman, W. G. Influence of post-inoculum air temperature maxima on survival of Phytophthora infestans in potato leaves. Am. Potato J. 35: 769–773; **1958**.

133. Wallin, J. R. & Polhemus, D. N. A dew recorder. Science 119: 294–295; **1954**.

134. Wallin. J, R. & Samson, R. W. Forecasting late blight in Indiana from mean temperatures and cumulative rainfall data (abstr.). Phytopathology 42: 482; **1952**.

135. Webster, A., Hill, L. & Eidinow, A. Measurement of ultra-violet light by means of an acetone methylene-blue solution. Lancet, (206): 745–747; **1924**.

136. Weille, G. A. de De fungicide werking van licht van verschillende golflengten t.a.v. blister blight. Ber. Alg. Proefstat. A.V.R.O.S. (Medan, Indon.) (1); 1956. Also in Bergcultures (Jakarta) 26: 149–157; **1957**.

137. Weille, G. A. de Blister blight control in its connexion with climatic and weather conditions. Thesis, Bogor (Indon.), **1957**. Also in Commun. Res. Inst. S.P.A. (Medan), Gen. Ser. (70), 116 pp.; **1960**. And in Arch. Tea Cult. (Bogor) 20, (1): 116 pp.; **1960**.

138. Weille, G. A. de Possibilities offered by the use of sunshine data for the purpose of forecasting epidemics of fungous plant diseases. Proc. 4th int. Congr. Crop Protect. (Hambg.) 1: 209–210; **1957**.
Also in Ber. Alg. Proefstat. A.V.R.O.S. (Medan) (8) (Dutch) & 9 (Engl.), 6 pp.; **1957**.

139. Weille, G. A. de The adaptation of tea cultivation to the occurrence of blister blight. Commun. Res. Inst. S.P.A. (Medan), Gen. Ser. (72), 32 pp.; **1960**. And in Arch. Tea Cult. (Bogor) 20, (1), 32 pp.; **1960**.

140. Weille, G. A. de Blister blight (Exobasidium vexans) in tea and its relationship with environmental conditions. Neth. J. agric. Sci. 8: 183–210; **1960**.

141. Weille, G. A. de L'influence de la radiation ultra-violette proche sur le pouvoir germinatif des conidies de Peronospora arborescens (Berk.) de By. T. Pl.-ziekten 67: 417–433; **1961**.

142. Weille, G. A. de An analysis of the variability of the germinative power of conidia in a number of fungi belonging to the Peronosporales. T. Pl.-ziekten 69: 115–131; **1963**.

143. Weille, G. A. de Laboratory results regarding Phytophthora infestans and their significance in the epidemiology of blight. Eur. Potato J. 6:

121-130; **1963**.

144. Weille, G. A. de Some remarks regarding biological observations in behalf of agrometeorological investigations concerning the epidemiology of plant diseases and pests. Arch. Meteor. Geophys. & Bioklimatol. (Vienna) 13: 114–136; **1963**.

145. Whetzel, H. H. Onion blight. Cornell Univ., Agric. Exp. Stat., Bull. (218): 138–161; **1904**.

146. Wiltshire, S. P. The correlation of weather conditions with outbreaks of potato blight. Quart. J. Roy. Meteor. Soc. 57: 304–316; **1931**.

147. Yarwood, C. E. The relation of light to the diurnal cycle of sporulation of certain downy mildews. J. agric. Res. (Washington) 54: 365–373; **1937**.

148. Yarwood, C. E. Onion downy mildew. Hilgardia 14: 595–691; **1943**.

149. Zaag, D. E. van der Overwintering en epidemiologie van Phytophthora infestans; tevens enige nieuwe bestrijdingsmogelijkheden. Thesis, Wageningen, **1956**. Also in T. Pl.-ziekten 62: 80–156; **1956**.

150. Zaag, D. E. van der De overwintering van Phytophthora infestans. Pootaardappelhandel 10 (1): 13–16 & (2): 5–8; **1956**.

151. Zachos, D. G. Un cas d'attaque de mildiou de la pomme de terre en rapport avec les facteurs météorologiques de l'année 1949. Ann. Inst. phytopathol. (Benake, Greece) 4: 17–18; **1950**.

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