KONINKLIJK NEDERLANDS METEOROLOGISCH INSTITUUT

MEDEDELINGEN EN VERHANDELINGEN

No. 97

G. A. DE WEILLE

AN APPROACH TO THE POSSIBILITIES OF FORECASTING DOWNY MILDEW INFECTION IN ONION CROPS

1975 Prijs f 17,50

STAATSDRUKKERIJ / 'S-GRAVENHAGE

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PUBLIKATIENUMMER K.N.M.I. 102-97

U.D.C.: 551.509.39 :
551.586 :
581.5
632.4 :
632.911 :
632.914 :
632.92 :
635.25 :
635.263 :

VOORWOORD

Interdisciplinair onderzoek met betrekking tot de wisselwerking tussen het levende organisme en zijn fysische omgeving geniet in toenemende mate de aandacht. Daar steeds meer wetenschappelijke vakgebieden betrokken raken bij deze soort interdisciplinaire aanpak is het te begrijpen dat het werken in ploegverband allerwege wordt nagestreefd.

Individuele pogingen om op dit interdisciplinaire terrein belangrijke problemen tot een oplossing te brengen worden dan ook steeds zeldzamer. Het is daarom verheugend, dat in de onderhavige studie door Dr. Ir. de Weille over de valse meeldauw in uien nog zo'n poging is gedaan.

De Hoofddirecteur van het

Koninklijk Nederlands Meteorologisch Instituut,

(DR. M. W. F. SCHREGARDUS)

PREFACE

Interdisciplinary research into the interrelationships between the living organism and its physical environment is enjoying increasing attention. As more and more scientific specializations become involved in this kind of interdisciplinary endeavour it is understandable that there is a wordwide call for team work.

For that reason attempts by individual scientists to tackle important problems in this interdisciplinary field become gradually more scarce. It is gratifying, therefore, that in the present study on downy mildew in onions Dr. de Weille has made such an attempt.

The Director in Chief of the
Royal Netherlands Meteorological Institute,
(DR. M. W. F. SCHREGARDUS)

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CHAPTER I

GENERAL CONSIDERATIONS

1.1 Introduction

Downy mildew in onions, caused by the fungus *Peronospora destructor* (Berk.) Casp., an organism akin to the causative fungus of potato blight, is one of the plant diseases characterized by a very distinct weather relationship. In addition, its economic importance is certainly great enough to justify biometeorological research aimed at a judicious exploitation of this disease – weather relationship.

1.1.1 *The significance of downy-mildew epidemics*

Downy mildew constitutes a distinct menace to onion crops. In 1943, Yarwood (54) writes that the losses caused by it may vary from none to total failure. For the period 1920 to 1936 he mentions losses of 0 up to 70 per cent in different years. In Finland, Jamalainen (22) reports high percentages of mildewed plants in lots of *multiplier onions* and yields that are correspondingly poor, even negligible. This is written in 1952. In the Netherlands, progress has then been made in the field of downy mildew control, but yet Van Doorn (10) still states the returns of a spring-sown onion crop to have been diminished by 10% in case of moderate and by 30% in case of severe infection in the years before 1952. Later developments in the field of chemical control brought better means to bear on the disease (Van Doorn et al., 11), but not to the extent that it was vanquished.

According to FAO data (1, 2) on 1959-'60, the Netherlands then produced 162 000 (metric) tonnes of onions on about 6 000 ha (1) whereas they imported (in 1959) 15 500 tonnes and exported 135 800 tonnes (2).

At the moment these lines were written (ult. Febr., 1970) the auction price of untrimmed onions amounted to about *f* –,57 per kg. This implies that at the production level stated by the FAO (1) each per cent loss of crop will cost the growers approximately *f* 900 000,– or *f* 150,– per ha. Further commercial losses amounting to, say, *f* 600 000,– (shop prices were as high as *f* 1,– p.kg.) will be partly compensated by trade in commodities replacing onions. In conclusion, it may be assumed that 1% crop loss can be estimated to cost *f* 1 000 000,–.

1.1.2 *The control of downy-mildew epidemics*

In the field, the occurrence of downy mildew is characterized by sudden, sometimes almost explosive outbreaks relieved by periods of varying duration in which the spread of the disease comes to a nearly complete stand-still. This conspicuous variation in intensity of attack has, for many years already, been known to relate to weather conditions. Muggy weather strongly favours build-ups of disease incidence as was already reported at the turn of the century (Whetzel, 51).

1.1.2.1 Under muggy conditions, when the fungus flourishes and multiplies best, the crop badly needs preventive *chemical protection*, which is usually applied in the form of a spray. Unfortunately, copper compounds like the classical Bordeaux mixture and the more modern copper sprays so useful in the control of potato blight fail to give adequate fungicidal protection against Peronospora. Nowadays the scourge is quite successfully kept under control with the help of macozeb, maneb or zineb, nebulized in quantities of 3 kg/ha, contained in 150 l of liquid per ha, admixed with a spreader or agglutinant. This method is still generally applied. Applications are discontinued in the beginning of August. No fungicides are applied in the last 4 weeks preceding harvesting.

Van Doorn et al. (11) communicated that the crop should be treated for the first time before downy mildew becomes noticeable on main crop onions. Spraying is repeated every 7 to 10 days according to the weather conditions prevailing. In continued investigations Van Doorn (10) tried to define more specifically the exact times of application.

Meanwhile, Van Doorn et al. (11) had already found that, in their 1953 tests, weekly zineb application resulted in an average gain of crop amounting to 25%. Fortnightly spray application still increased production by 20% as compared with untreated lots.

1.1.2.2 Downy-mildew control can also be achieved by *non-chemical* means like plant selection and ameliorated cultural practices. In the latter connection it should be avoided to plant or to sow onions in poorly drained low parcels, so-called 'down spots' (cf. Whetzel, 51). Nor should this be done at shaded sites, for instance alongside an orchard or a maize field. Sowing and planting too densely also favours the disease. A similar effect can be occasioned by too high nitrogeneous fertilizer applications (Van Doorn et al., 11).

Summing up the above, the conclusion can be drawn that the origination of a humid micro-climate into which sunshine has no free access must be prevented.

1.1.2.3 *Sanitary measures* are also taken. It is known that primary infection foci usually spring from a 'secondary diseased' or 'systematically diseased' plant growing from a bulb containing hibernated mycelium. It goes without saying that such infected bulbs carrying over the disease from one year to another have to be rogued out where and whenever possible. The avoidance of growing main crop onions near planted (hibernated) onions grown for seed production is another precaution taken in order to keep the infestation within bounds (Van Doorn et al., 11).

As the carry-over of overwintered fungal material to a new crop takes place through bulbs, systematical propagation by means of bulbs as is or was practised in some countries with topset or multiplier onions (Newhall, 31; Jamalainen, 22) implies systematical maintenance of downy mildew. Seed disinfectants having no effect on downy mildew in bulbs, the latter author recommends a warm-water treatment of onion sets for 1½ hours at 40 °C, which kills the mycelium. In the Netherlands, warm-water treatment or temporary storage in warm air of cured onion sets has been applied successfully in shallot cultivation (Bruinsma, 8).

Peronospora not normally being carried over by seed, propagation by seed is usually preferred in commercial onion cultivation.

1.1.3 Historical notes

Since the organism causing the downy-mildew disease of onions and allies was first described and named by Berkeley (5) as early as 1841 (he called it Botrytis destructor) much research has been conducted for the ultimate purpose of its control.

It was soon found out that the weather-dependent dissemination of the disease during the growing season is by airborne conidia, but the role of the oospores or resting spores has for a long time puzzled the phytopathologists. In 1904 Whetzel (51) communicated that the oospores found germinating in decaying leaves complete the annual life history of the parasite. It was already known at that time that mycelium passes the winter in bulbs (Trelease, 37; Dudley, 15; cf. fig. 3). Whetzel (51) questioned the correctness of the view that this mycelium initiated the annual build-up. We now know that it is mainly in the form of perennial mycelium that Peronospora destructor not only lives over the winter (Katterfeld, 25; Murphy & McKay, 29; Yarwood, 54) but also perpetuates its incidence in the field. There is no strong evidence that oospores play a major part in the mildew's carry-over, nor is there any strong evidence for seed transmission (Katterfeld, 25; Murphy & McKay, 29; Hiura, 21; Cook, 9; Yarwood, 54), either through oospores or through mycelium.

However, oosporal infection cannot be completely disregarded (Murphy & McKay, 30; Van Doorn, 10), since systematically diaseased plants do indeed exist in sown plantations.

In this treatise we shall highlight in particular on the manifold meteobiological aspects of the spread of downy mildew through conidial infection.

In the Netherlands, the SNUiF (Stichting Nederlandse Uien Federatie, the Netherlands Onion Growers Foundation) conducted its first downy mildew control field test in 1939. Later field investigations were made by the PD (Planteziektenkundige Dienst, Plant Protection Service) (1949-1953) and the IPO (Instituut voor Planteziektenkundig Onderzoek, Institute for Phytopathological Research) (1952-1958), both at Wageningen. The IPO research was conducted by Van Doorn (10), assisted by the SNUiF and the KNMI (Koninklijk Nederlands Meteorologisch Instituut), who took care of replicate test fields and local observations.

Van Doorn brought the problem of timing spray applications according to weather conditions to a partial solution contained in his disseration (10). Since Dr. Van Doorn was no longer in the position to continue this work it was agreed that the present author was to assume this task. He did so in co-operation with the SNUiF.

In 1965 the laboratory and field tests were brought to an end. The results are given in Chapters III and IV.

1.2 The fungus and its hosts

1.2.1 The fungus

The causative organism of the downy mildew disease in onions and related species, *Peronospora destructor*, belongs to the order Peronosporales of the Oomycetes, an important group of the Lower Fungi or Phycomycetes. This order is characterized by a sexual stage in which oospores or resting spores are formed and by a vegetative stage during which asexual zoosporangia releasing zoospores or swarm spores, or conidia, germinating with a germ tube, develop. In Peronospora destructor and other downy mildews vegetative propagation is by conidia.

1.2.1.1 The *mycelium* consists of non-septate hyphae growing intercellularly in the parenchyma of the invaded parts of susceptible Allium species. Branched and coiled haustoria, sometimes seen wrapped around the nucleus (Whetzel, 51), absorb water and nutrients form the host cells, thus nourishing the mycelium, meanwhile causing the cells to die.

1.2.1.2 On certain moist days diseased parts of onion plants are externally covered by a dense whitish mouldy growth, discernable from other similar aerial fungal growths by its pale violet tinge.

After a few days the parts on which this mouldy growth has occurred become chlorotic, at last contrasting with the surrounding green parts by a distinct yellow colour. Most yellow leaf areas cocur near the apex of the leaves. The areas often expand in a concentrical way: new mouldy growth is then seen along the boundaries of the necrotic area; this zone becomes yellowhish etc.. The chlorotic areas are found on seed stalks as well as on leaves. Finally they decay, causing leaves and stalks to topple over.

If no muggy weather occurs, the incidence of chlorotic lesions may precede the occurrence of the hyaline growth, which will be observed at the fringes of the yellowish areas as soon as the muggy conditions show up.

It will be clear to the biologist, but not self-evident to the meteorological reader, that in this *clinical picture* the yellow plant areas are the parts already severely colonized by mycelium (see 1.2.1.1) and that the whitish growth at their fringes is constituted by sporophores bearing conidia.

Fig. 1 Conidiophores and conidia.

The conidiophores (fig. 1) are dichotomously branched aerial hyphae emerging in small groups from stomatal openings. The branches extend at acute angles; the ultimate branches are acute (Heald, 17) and bear one vegetative spore or conidium. These start their existence as little swellings at the tips of the branches, enlarge until the size of mature spores is reached and are then separated from the branch by a thin wall. This process is completely vegetative.

1.2.1.4 The *conidia* (fig. 1) are egg-shaped, quite sharply pointed at one end. Nearly colourless in the author's research work, they are discribed by Whetzel (51) as being pale violet, with very thin walls, 45 to 58 × 20 to 25 μ in size.

Their numbers are enormous. Shipley (36) stated that on onion leaves there are 70 000 stomates to every sq. in., whilst on badly infested leaves from at least 1 in 10 of these stomates a conidiophore (or two or three of them) protrude(s). With 20 conidia per conidiophore this means 140 000 p. sq. in.. Newhall (31) arrived at 100 000 p. sq. in.. Repeatedly wiping a crop of conidiophores off a leaf he found that three times a new crop formed within 48 hours.

1.2.1.5 When ripe, the conidia are easily released from their stalks and can be blown about to healthy plants by the slightest breeze. The mass of airborne conidia involved is referred to as *spore flight*.

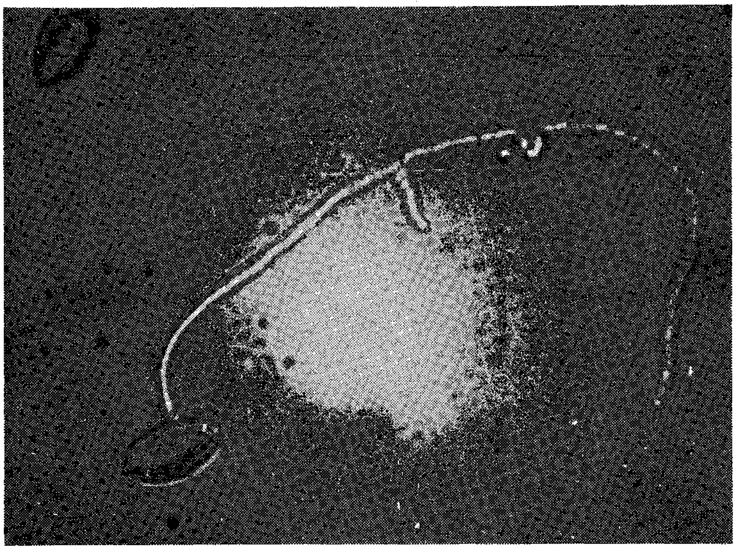

Fig. 2 Germinating conidium.

1.2.1.6 *Germination* of conidia can follow if they chance to alight on an onion plant and, in addition, chance to fall into a rain drop or film of liquid water clinging to the foliar surface. In water, the spore produces a thread-like germination tube (fig. 2).

1.2.1.7 This seeks a stoma. If the leaf remains wet long enough the stoma is reached by the apex of the growing tube, which then penetrates into the intercellular spaces: *infection* is accomplished.

1.1.2.8 After a lapse of time called *incubation period* the new mycelium is able to send out aerial hyphae and thus the life cycle is repeated. The incubation period will last 10 to 20 days (Van Doorn, 10), usually 11 to 17 days.

1.2.1.9 The cycle expounded under the items 1.2.1.1 through 8, whose biometeorological aspects

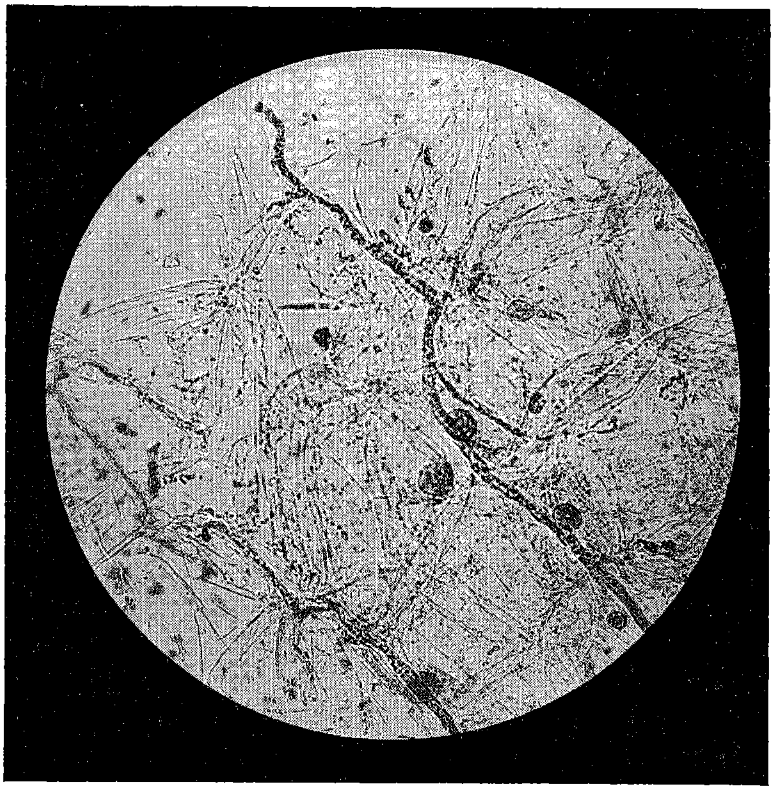

Fig. 3 Hyphae and oospores in diseased onion bulb (By courtesy of IPO, Wageningen).

will be dealt with in extenso in this treatise, is the asexual one. In 1.1.3 brief mention was made of the oospores, which have much less to do with the meteorological side of crop ecology.

These oospores are globose bodies, approx. 30 μ in diameter, scattered promiscuously through the tissues of the host plant (fig. 3); they arise from a union of two dissimilar unequal gametes, viz. the (female) oogonium and the (male) antheridium. (For particulars: see i.a. Heald (17); McKay (28) and Whetzel (51).) Equipped with a circa 4 μ thick wall usually strengthened by an additional protective layer adhering tenaciously to it and consisting of remains of the original oogonial sac, they remain viable for many years. Erratic germination was even observed in oogonial material up to 40 years of age (McKay, 28).

1.2.1.10 Unlike conidia, oospores can overwinter and do not readily germinate. They are also named *resting spores*. According to Berry & Davis (6) their formation is unpredictable. Epidemiologically, they are of questionable importance, but their contaminating the soil (Murphy & McKay, 30) may account for the occurrence of systemically diseased plants in lots of sown onions (Van Doorn, 10).

Moreover, oospores are not found in bulbs, whereas perennating mycelium does occur there (see also 1.1.3). Within its biometeorological framework this publication will centre on Peronospora's asexual cycle.

1.2.2 The hosts

The onion downy mildew only infects certain Allium species; beside the common onion (A. cepa) it also attacks shallots (Allium ascalonicum or A. cepa), Japanese bunching or 'Welsh' onions (A. fistulosum) and has been reported on leek, garlic and chives (McKay, 28; Jones & Mann, 24).

Special forms of the common onion, sometimes called seed onion, are multiplier (or 'potato') onions (A. cepa var. aggregatum or multiplicans), propagated by means of their laterals, referred to as multiplier onion sets, and top, topset, Egyptian or tree onions (A. cepa var. bulbiferum or proliferum), which have bulbiferous umbels and can propagate through their bulbils. The bulbils of one inflorescence are referred to as a top set.

In the Netherlands no top onions are grown. Beside the fairly important cultivation of common onions, some shallots are grown as a horticultural crop. In the shallot, according to Jones & Mann (24) a member of the aggregatum group, vegetative propagation is commonly practised: a single planted bulb produces a cluster of bulbs.

1.2.3 Onion cultivation

In the Netherlands onions are grown in different ways.

1.2.3.1 Spring-sown onions harvested in August or September are called *sowing-onions*. Very densely sown are the small silver-onions grown for the canning industry.

1.2.3.2 The above crops are annual. Maincrop onions are also grown according to a biennial scheme. In that case the onions are sown relatively densely but by far not nearly so dense as silver onions. The young *planting-onions* are stored during the winter, replanted next spring and harvested by the end of July.

1.2.3.3 It is less customary to sow in August in order that the young plants overwinter in the field. Next year they develop rapidly either on the spot or after having been transplanted and can be pulled relatively early. This winter cultivation has proved to be too risky, so that the onions marketed in the Netherlands usually derive from transplants.

1.2.3.4 Onions grown for seed, *seed onions*, are replanted early in spring in order to stimulate timely seed-stalk formation.

1.3 Warning systems

When sprays directed against onion downy mildew are applied at regular 7- to 10-day intervals 'according to the weather' as formerly recommended by Van Doorn et al. (11) this will amount to a total number of spraying rounds of up to 7 in sowing-onions and up to 12 in seed onions (Van Doorn, 10).

The cautious degree of flexibility still reluctantly advocated in the earlier publication quoted (11) has of course a bearing on the mildew's relationship with 'muggy' weather conditions already mentioned in 1.1.2. In 1.1.2.2 the conditions conducive to the disease were described as originating 'a humid micro-climate into which sunshine has no free access'. As we will see in Chapter IV both aspects of peronosporal environment are significant.

It stands to reason that attempts have been made to exploit knowledge of weather – disease relationships to the effect that warnings aimed at timely fungicidal application are issued on the basis of the degree of disease incidence in the field and disease-inducing weather conditions or either of the two.

Very much work has been done with regard to Phytophthora infestans, the fungus causing potato blight (De Weille, 47) and very little with reference to Peronospora destructor. And yet the two are akin, having so much in common that, if outbreaks of P. destructor occur at all, these will follow corresponding blight outbreaks after a 6-day period. The latter lapse of time results from the difference in duration between the incubation periods of the two fungi. Both outbreaks then stem from one and the same muggy infection day.

The idea originally underlying the quest for warning systems was that the application of climatological criteria, rules as they are called, characterizing weather conditions conducive to the disease and, in fact, inducing infection of the crop, leads to a more judicious timing of spray or dust applications than does spraying at regular intervals irrespective of the weather. Thus, the best degree of control was supposed to be coupled with savings in labour and fungicides ensuing from the omission of unnecessary spraying rounds.

1.3.1 The significance of warning systems

During the first half of our century a considerable number of warning schemes was developed, potato blight undoubtedly leading in this field. Their warnings were often called forecasts, since the fulfilment of their climatologically and statistically determined conditions is followed by an *outbreak* of the disease. So after having noted that the rules had been complied with, the plant pathologist could easily forecast the visible outbreak ensuing from the 'critical period.'

A spray warning was then issued stating critical conditions to have prevailed and that an outbreak could therefore be envisaged so that, if the last preceding spray had been applied so long ago that the crop could no more be considered to enjoy sufficient fungicidal protection, a new fungicidal treatment was recommendable.

The above kind of message is of the type criticized as late warnings in quite a number of lectures and articles produced by the author (e.g. 47, 49). The dogmatical correctness of this view can be readily recognized if we realize what the old-fashioned warning scheme does or did. It rings the alarm bell as soon as the conditions, n hours with a relative humidity (r.h.) over m% and a minimum temperature (T_n) above p° C, have been met. In fact, these rules, whose fulfilment is (supposed to be) followed by an outbreak, characterize the circumstances conducive to infection. The 'critical period' is in fact the infection period. If critical conditions have prevailed long enough for crop infection to have taken place, and the parasite is safe and sound inside the host plant we wish to protect, the agricultural forecaster begins to disperse warnings and, knowing the result of the infection wave, viz. the resultant outbreak, part of the incubation period is used for the dissemination of what is then called a plant disease *forecast*.

Unfortunately, predictions of this kind do not really help the grower. As the right way of combating plant disease consists in the application of a protective fungicidal residue *prior to* crop infection, optimum preventive spray application is only facilitated by forecasts of the accomplishment of crop infection or, if the rules are correct, forecasts of their fulfilment.

Dogmatically, classical warning systems observing and noting infection periods are of no avail but, fortunately enough, there is a marked persistence in muggy conditions, grouping infection days together in longer periods, so that, depending on the methodic loss of time involved in the means of dissemination (radio, telephone or postcards), crop infection during the later days in the series of critical dates can be prevented by spraying following the message.

Nevertheless, maximum efficiency can only be expected if we can arrive at a really predictive warning scheme giving rise to infection forecasts at such early moments as enable the grower to spray his onion crop prior to infection.

1.3.1.2 Apart from the scientific evaluation of warning schemes their *economic importance* is an item that should not be disconsidered, since, originally, economical thoughts gave rise to their development. Savings in labour and materials may perhaps not outweigh the ease of planned control rounds by a spraying-contractor, but saving an additional percentage of the yield by more efficient control due to better timing is certainly worth while if we realize that each per cent saved will entail an over-all profit of one million guilders (cf. 1.1.1 on p. 11).

1.3.1.3 Finally, there is a strong case for less spraying rounds if we consider the *pollution of the biosphere* caused by sprays. Most fungicides may not be as malignant as are many of the pesticides brought to bear on insects, but this should not withold responsible scientists from furthering any epidemiolocal progress by promoting epidemiological biometeorology in general.

1.3.2 Examples of warning systems

In his extensive treatise on potato blight (47: pp. 7-17), the author gave a survey of a good many warning schemes formerly or presently in use in several countries. With reference to Peronospora destructor there is no such bountiful variety of systems.

1.3.2.1 As appears from early reports by Van Doorn & Post (12, 13) the first Dutch warning scheme encompassed the following rules:

a. a day is critical if at 9.00, 12.00 and 15.00 h. GMT the relative humidity, measured in a standard meteorological screen at a height of 2.20 m, equals or exceeds 80 per cent,

b. the minimum temperature in the preceding night should not have been below the freezing point; more briefly:

a. at date p: at 9, 12 & 15 h. GMT: r.h. $\geqslant 80\%$

b. during night $(p-1)$ to p: $T_n \geqslant 0$ °C.

This tentative scheme, tested experimentally in 1957 with the help of a dummy warning system, did not stand comparison with customary spray application in weekly rounds in that savings in the number of applications were obtained at the expense of the degree of crop protection. Reportedly, the rules were not strict enough to cover marginal cases. Moreover, it was felt that they failed to reflect the ecoclimatic situation in very leafy crops (12) and that spraying on the day after the critical day implies risks.

For better identification of infection days hourly r.h. data were preferred to 3-hourly data, whereas analysis of critical periods expressed in such hourly values led to ameliorated criteria (Van Doorn & Post, 13).

1.3.2.2 On this basis a regular warning service was started in 1958. Forecasts were dispersed by radio and by one telephonic disease warning service (at Dordrecht).

According to the rules applied, infection is accomplished if an at least 10 hours' period with r.h. $\geqslant 90\%$ is followed by one of a 17 hours' duration and r.h. $\geqslant 75\%$. An interruption of the latter period of up to 4 hours with r.h. $< 75\%$ is allowed. Briefly:

$$\left.\begin{array}{lll} \text{a.} & \geqslant 10 \text{ hrs.} & \text{with r.h.} \geqslant 90\% \\ \text{b.} & \geqslant 13 \text{ out of 17 hrs.} & \text{with r.h.} \geqslant 75\% \end{array}\right\} \text{w} = 27 \text{ h.}$$

It must be noted that the total period of observation w, for all the improvement in precision gained, has become intolerably long, viz. 27 hours. Biologically, very much can take place in so long a period.

Van Doorn & Post (13) must have been aware of this, since the messages were advanced whenever feasible.

This is easily understood if we get acquainted with the way the warning service functions and, in addition, know that, as its designers communicated (13), infection periods will start between 16 and 3 h.

There were two separate regions for which warnings were issued, viz. the south-western clay area of Zealand and S.-Holland (r.h. data from 2 stations) and the northern part of N.-Holland (data from Alkmaar).

When applicable, at about 10 o'clock in the morning the critical humidity data were phoned to the KNMI. In most cases a message could then be inserted in next day's early agricultural radio broadcast at 5.45 and 6.40, viz. 36 h. after the infection period commenced. The methodic loss of time m, – the loss in time inherent in the method of communication, here the radio –, will thus amount to 9 hours ($\text{w} + \text{m} = 36$).

In cases in which during the consecutive evening, night and morning until ca. 12 o'clock the critical weather conditions had been met whereas the fixed r.h. threshold was unlikely to be crossed in the afternoon, a message was already inserted in the afternoon broadcast of 12.30, i.e. 20 hours after the onset of critical conditions. When doing so, a methodic loss of time was obviated, while w was reduced to 20 h. The message then ran like this: 'In North Holland (or the S.-W. clay area, or both areas) the present weather conditions are conducive to downy-mildew infection.'

1.3.2.3 Yet Dr. Post was not content. Mr. Van Doorn had found out that the infection period can be split up into its components *a* and *b* on other than statistical grounds. It appeared, at least according to Van Doorn & Post (13), that period *a* is for sporulation and spore germination and *b* for ingress: penetration of germ tubes through the stomatal openings.

In their 1958 experiments the two epidemiologists tried out a warning scheme immediately issuing a message after compliance with rule *a* (r.h. $\geqslant 90\%$ for $\geqslant 10$ h.), i.e. after ($t = w_a =$) 10 hours of high atmospheric humidity. Their instant-response spray experiments revealed that, while fungicidal application immediately after $w_a + w_b$ gave slightly less protection than spraying at weekly intervals, though this only slightly less favourable result was achieved at considerably lower costs, viz. in less rounds, spray application immediately after *a* yielded the best results.

As appears from 1.3.2.2 and 1.3.2.3 the Achilles' heel of the classical plant disease warning method, late alarm, had been discerned in a way. Once this weakness had been diagnosed the trend was bound to be in the direction of real disease forecasts forecasting the occurrence of infection-inducing conditions (cf. 1.3.1.1). The endeavours of the author's two predecessors in the field of epidemiology to advance the issuance of their warnings must therefore be considered an important move towards integrated plant disease control.

1.3.2.4 Van Doorn (10) was conscious of the fact that the last word in downy-mildew control had not been spoken. After Dr. Post had left the meteorological institute, – he was later succeeded by Dr. de Weille –, he continued the field research and also re-examined the existing body of epidemiological data. He arrived at new rules in which w was reduced to 17 h., viz. 11 h. for w_a and 6 h. for w_b. Heedful of the importance of the crop ecoclimate rather than the above-crop climate for the completion of the sporulation stage and the survival of newly-formed sporal material, he also introduced microclimatic quantities.

His rules, of which a is again followed by b, were:

a. $\geqslant 11$ h. r.h. $\geqslant 95\%$ in the crop at 10 cm (or $\geqslant 90\%$ at 2.20 m)

b. $\geqslant 6$ h. r.h. $\geqslant 80\%$ in the crop at 10 cm (or $\geqslant 75\%$ at 2.20 m).

By comparing series of observations in and above the onion crop it was established that the occurrence of the observed systematic difference in r.h. of about 5% is sufficiently consistent to justify the use of readily available standard screen data to replace corresponding microclimatic data.

The new criteria were utilized in 1960 and 1961 as an alternative for the semi-forecasts discussed under 1.3.2.3. The two methods were applied as expedient in view of the limited opportunities to get the messages broadcast (see 1.3.3).

1.3.3 Mode of communication

As fungous diseases can only be treated prophylactically there is a lasting quest for speedy information. Even in case warnings cannot be dispersed prior to crop infection and, in consequence thereof, dogmatically belong to the belated category, this pursuit of promptitude still makes sense. Important infection days rarely occur separately within a fair-weather period. Instead, owing to the marked persistence in the occurrence of precipitation, they are grouped within spells of wet weather. This implies that, even if the first day in a run of infection days is missed, a pushful communication system can be substantially beneficial in helping to reduce further build-up of an epiphytotic. By no means should a second critical day be allowed to occur without having been preceded by an early notice.

1.3.3.1 The quantity m (methodic loss of time, cf. 1.3.2.2) is inherent to the mode of communication. We already saw that w (period of observation) is inherent in the criterion or rule. Together they make up for the systematic dealy in communication embodied in the lapse of time between the onset of the attack and the alarm.

This consideration bars out the use of postcards or stencilled bulletins, which will be all the more clear if we realize that for the production of one levy of spores, its spread and the infection brought about by it less than a day's time is needed.

1.3.3.2 The lateness of radio messages is less prohibitive, and in the Netherlands radio broadcasts could have been an ideal means of disseminating warnings if disease forecasts could be inserted in arbitrary broadcasts of the news service (which is operated by the ANP (Gen. Neth. Press Agency). Unfortunately, the possibility of insertion is however restricted to the three agricultural broadcasts at 5.45, 6.40 and 12.30 CET. A better arrangement could not be achieved. If the messages, which are teletyped from the KNMI to Hilversum, arrive in due time, m can be as brief as half an hour. However, the gap after the 12.30 broadcast may cause m to attain values of up to 17½ hours.

1.3.3.3 So far, the best solution in this field has been that of the regional *telephonic warning services* supplying tape-recorded warnings in much the same way as the latest weather review is made available. The good growers know what number has to be dialled.

An any time of the day new messages can be issued and expired ones cancelled. Methodic loss of time is negligible.

1.3.4 The zero-date

The 0-date is the annual date marking the beginning of the chemical crop protection campaign. In principle, the development of the fungus, i.e. the amount of inoculum threatening the crops, should determine the date of issue of the first infection forecast. The application of this principle requires intensive investigation of the areas under onion cultivation.

The SNUiF considers preventive spraying at an early date an important safeguard. Therefore, the arrangement was made that the 0-date is announced each year by the SNUiF on the ground of the early development of sowing- and silver-onions and that, from that day on, the Horticultural Warning Service issues messages based on weather criteria until, finally, the SNUiF communicates, to the warning service, the closing date of the warning season, this, again, based on the development, viz. the mature condition of the crop.

CHAPTER II

BIOMETEOROLOGICAL CONSIDERATIONS

2.1 Prefatory notes

2.1.1 Introduction of a concept

Biometeorology has reference to the interrelationships of life and weather; similarly, bioclimatology refers to the analogous coherence of life with climate.

On the one hand biometeorology embraces the greater part of agrometeorology, on the other hand it forms part of the ecological sciences, in particular auto-ecology.

Ecology, in turn, considers and studies the organism within the framework of the ecosystem to which it belongs and within which this organism exerts influences and reacts to influences exerted by environmental factors of a biotic or abiotic nature. Attempts are made to quantify the effect of these environmental factors on the population dynamics of organisms. In this field, biometeorology exclusively deals with the biological effects of abiotic quantities (and, eventually, the modification of abiotic environment by living organisms), restricting itself to atmospheric environmental factors.

2.1.2 Definitions

There has been a good deal of argument about the meaning of several of the terms used in the above paragraphs. Ecological or 'biospheric' science has indeed made semantics hum.

According to Lowry (26), biometeorology is the science which investigates the interrelationships of atmospheric and biological processes.

This is clearly a bilateral matter, whereas the definition en vogue in the International Society of Biometeorology only states investigation of the effects of the atmospheric environment on organisms, a unilateral matter. In this restricted sense the word meteobiology would be more appropriate. Properly speaking, the reverse effect, including the genesis of crop microclimates, has a better title to the name biometeorology. But as the usage, or abuse, of this term to denote its counterpart, – or its complement in prof. Lowry's definition –, has already been hollied by international custom the author will follow Lowry (26) and will look upon meteobiology as an integrating part of biometeorology.

In biometeorological practice stress is sometimes laid on 'bio' rather than on 'meteo', whereas in agromet circles meteorology is usually emphasised in the concept agrometeorology, though not to the extent that the organism is disregarded (3: Ch. 1).

2.1.3 Scope

The scope of biometeorology is one of wide purport. Within that of this publication one aspect is of particular interest, namely the part played by the entirety of meteorological conditions as a matrix for (phasic) development of organisms, be they crop plants, insects or fungi.

For all the importance of the biotic factors in the domain of ecology, it is biometeorology that quantifies the abiotic atmospheric environmental factors determining the matrix or basic pattern within which the organism can accomplish its life cycle. In this pattern it determines the (bio- or phenological) time scale or calendar by being decisive for the starting dates and duration of the life stages of many species. Their phenology is tightly linked up with (bio)meteorological threshold values or climatic thresholds (day-length effect, plant geography).

The *degree* to which phases are successfully accomplished, finding expression in, for instance, the numbers of insects and the quantities of crop yield, is not determined by abiotic factors only, let alone by atmospheric quantities only. Here, the variation on the ground pattern between 0 and 100% successful accomplishment of a life cycle for attainment of a production level results to a very high extent from biotic factors or factors like soil fertility, living space and food competition.

We shall investigate how this biomet theory can be made subservient to our epidemiological aim.

2.2 The approach to downy mildew epidemiology

In previous publications (44, 47, 48) the author paid due attention to empirical/statistical and fundamental procedures that can be applied in order to develop a warning scheme. For reasons there discussed he opted for a fundamental approach, starting in the laboratory and continued in field trials conducted with lab-like precision (De Weille, 48). In the course of the years his working methods became a fixed procedure for evolving predictive warning schemes (49). Step by step, this procedure will be followed in this treatise (Ch. III-IV-V), at the end of which we hope to have arrived at a biometeorological model fit for the purpose of being handled by or in conjunction with the Weather Service.

2.3 Biometeorological model building

In 2.1 it was already enunciated that the phasic development of a good many organisms is conditioned by ecoclimatic threshold values and it was stated that these effects may be quantified.

Examples of plain bioclimatic indices and more advanced bioclimatological rules can be readily adduced from literature in the domain of plant geography and climatological crop ecology (Euverte, 16, Nuttonson, 32, 33, and many others). In the epidemiological field the global rules by Van Doorn (10, 12, 13) and Post (12, 13) were already instanced, whereas quite a variety of that kind of criteria were given in the author's previous work on potato blight (47).

2.3.1 Phases

The author is an advocate of the build-up of phase-to-phase development models in which consecutive environmental criteria are summed up for each consecutive developmental stage. This implies that the models in question are constructed on a phenological basis whereas the term 'environmental' should be understood to have reference to the real atmospheric environment of the organism, consequently in our case the *microclimate* in the onion crop.

The stages to which the subsequent conditions together constituting the (bio)-*climatological* model refer are in this case:
sporophore (conidiophore) formation,
sporulation,
maturation of conidia,
survival of conidia before their detachment,
survival after their detachment from the conidiophores,
germination,
survival of germ tubes,
infection stage, penetration into host.

The development within the host is not in the first place weather-dependent, although the duration of the incubation period is conditioned by temperature.

Corresponding stages in models relating to insects are oviposition, the oval period, hatching, larval stages, pupation, pupal stage, adult stage etc., whereas in crop plant models the criteria refer to sowing-to-emergence, emergence, emergence to flowering and so forth.

2.3.2 Two categories of models

2.3.2.1 Bioclimatological models, structures specifying the weather dependence of insect abundance, potential crop yield or days of crop infection by fungal parasites, can be utilized in their primordial form (list of successive conditions) or in the form of a computer simulator (programme of successive conditions) (example: Waggoner & Horsfall, 39; Alternaria solani). The difference is of course a practical, not a basic one. In the case of epidemiology, where forecasting the fulfilment of the model conditions is a so desirable aim, the determination of synoptic model situations on which such forecasts can be based is bound to provide more relief than slight gains in time or savings in labour ensuing from computerizing the bioclimatic complex. Nevertheless, the latter procedure merits a welcome since it does constitute an important step forward in that its application in connexion with the more intricate environmental responses of higher organisms is promising.

2.3.2.2 Synoptic model situations depicted in weather maps showing certain well-defined characteristics can be truly named *biometeorological* models.

If synoptic situations can be sorted out that match disease-inducing conditions in the crop the latter become predictable and, to all intents and purposes, that is what is really needed.

2.4 Materials

The constructal elements readily at hand are provided by the existing body of meteobiological knowledge. A survey will here be given of what is known about the environmental responses of Peronospora destructor. Missing building-bricks tempt to additional research for completing the model under construction (Chapter III).

2.4.1 Formation of conidiophores

In general, the research workers who studied the ecology of the fructification process have not discriminated between its two substages, viz. the formation of aerial hyphae, the conidiophores, and that of spores, the conidia. Only recently De Weille (50) did so, stating that conidiophores are formed in a saturated or nearly saturated atmosphere, just like the conidia themselves, but that formation of the latter requires more than just saturation (see 2.4.2.1).

2.4.2 Formation of conidia

2.4.2.1 From tests by Yarwood (52, 54) it appeared that *light* exerts a marked effect on sporulation in at least a number of downy mildews, among which figures that of onions.

In natural darkness sporulation occurred consistently; under otherwise favourable conditions sporulation could already be prevented by incandescent-lamp light applied at night at intensities as low as 170 ft.-candles shed on the leaves at a distance of about 6 cm.

Neither continuous light nor continuous darkness appeared to allow sporulation, but its inhibition by continuous darkness was remedied by temporary exposure to light. Exposure to daylight for about 12 hours was most favourable to the recuperation of sporulability (52).

From his experimental results Yarwood (52, 54) concluded that sporulability is induced by exposing infected plants to light and that this exposure of mildewed plants to light brings about subsequent sporulation in darkness. The inhibitive effect of light during sporulation shows that the normal alternation of light and darkness is a prerequisite for the diurnal cycle of sporulability which, under favourable T and humidity conditions, implicitly entails a diurnal cycle of sporulation (54).

In exemplification of the daily rhythm of conidial formation Yarwood (52, 54) quoted the following series of observations: at T = 18 °C an abundance of conidiophore initials were observed at midnight. The conidiophores were fully developed at 3 a.m.; conidia were being formed, having attained about $\frac{1}{3}$ their natural size. At 6 h. they appeared fully mature. At 7 they were readily released by shaking the leaves (54), at 9 many had been liberated (52). In an endeavour to find an explanation for the sporal material's delay in take-off, Yarwood (54) considered the lapse of time between 6 and 9 o'clock as a priod of maturation, without however connecting the latter concept with the level of the inoculum's germinating capacity. It appears from the adduced monography that in his train of thought maturation is primarily a morphological matter.

The observation that sporulation occurs chiefly at night was corroborated by Van Doorn (10) and De Weille (50).

2.4.2.2 In the above paragraphs light proved to be a regulating factor; the most critical and decisive factor in the fructification process is, however, *humidity*.

According to Yarwood (54) the minimum r.h. allowing fructification at an appreciable level is 90%. The optimum r.h. is 100%. Van Doorn (10) however found that below 96% no sporulation occurs and that even in the range of 96% to 100% r.h. sporulation may quite often fail to occur. It did occur however if, in a saturated atmosphere, the plants were covered by small droplets of water, in experiments applied with the help of an atomizer (10), in nature probably most often eventuating from condensation (Yarwood, 53). Van Doorn (10) communicated that more sporophores and spores are produced according as the drop size is smaller, since the spores form in the boundary layer around the droplets. A complete film of water does not favour fructification, whereas complete saturation of the atmosphere does allow for sporulation though not as abundantly as do droplets.

It can be concluded that sporulation necessitates a 100% r.h., the presence of liquid water strongly stimulating this process (10). Dr. Van Doorn's conclusions fall very well into line with statements by McKay (27) that, although downy mildew spreads to some extent during rain periods, its greatest development takes place during bright warm weather when *dew* occurs at night, and by Yarwood (54) that the ultimate infection of the crop actually requires 2 humid nights, one for spore production and one for infection.

2.4.2.3 Sporulation of any significance takes place at temperatures between 3° and 22 °C. Few conidia are formed at lower or higher (up to 25°) temperatures (Van Doorn, 10; Yarwood 54).

2.4.3 *Viability of attached conidia*

Yarwood (54) stated that, depending on environmental conditions, the longevity of conidia attached to their sporophores on plants kept outdoors may last 3, sometimes even 5 days, detached spores remaining viable for a lesser period.

2.4.3.1 The above view, passed on for the sake of fairness, that conidia on sporophores are less short-lived than free spores is not in harmony with experimental results published by other workers. Both Jones (23) and Whetzel (51) stressed the extreme susceptibility of attached inoculum to relatively low atmospheric humidity to the effect that, owing to drying out, the germinating power K is frequently not retained for more than 1 hour, according to Whetzel even under the most favourable conditions (51).

The quantity K is usually expressed as the percentage of germination in a sporal sample germinated under standardized favourable conditions like those discussed under 3.3.1.3, dealing with the author's method.

Data produced by Van Doorn (10: p. 25) show that desiccation is indeed fatal to the conidia, nullifying K within 5 hours, but that at 100% r.h. K is not reduced within 7 or more hours.

2.4.3.2 The same set of data also shows that light does not affect spore viability.

2.4.3.3 From communications by Yarwood (54) and Van Doorn (10) concerning temperture limits for germination, infection and spread we can postulate an influence of *temperature* per se (not through r.h.). Spore viability is apparently weakened by $T > 22°$, sublethal tempertures in the range 25-28 °C. bringing about an inactivating effect and $T > 30°$ tending to be lethal.

2.4.4 *Detachment*

Conidial dispersal caused by changes in moisture content in the air has been described for a number of Peronospora species other than P. destructor. Pinckard (35; Peronospora tabacina) describes how the process of abcission of conidia begins with incipient drying and is concluded by hygroscopic distortion of the aerial mycelium. Cylindrical in the moist and turgescent state, the sporophores collapse when dry, thus taking a flat ribbon-like form, especially when the spores are ripe. Changes in humidity of the air surrounding the hygroscopic hypha give rise to a twirling motion to their extremity, whereby the ripe spores are thrown off in every direction. Owing to the erratic clock-wise and counterclockwise rotation of the conidiophores and their branchlets the dislodgement of conidia can even be effected by mechanical entanglement of these sterigmata.

Hill (18, 19; Peronospora tabacina) made observations supporting the view that the turgidity of conidiophores depends on the water supply from the leaf rather than on the ambient humidity.

This would lead to a daily cycle of sporal discharge due to the collapse of conidiophores as a consequence of water withdrawal, through the mycelium in the leaf, brought about by atmospheric daytime conditions.

At any event distorted ribbon-like conidiophores were frequently observed in the author's collodion leaf prints (cf. 44, 47) of onion leaves, so that the publications of Pinckard and/or Hill may help to explain the epidemiology of the onion downy mildew.

2.4.5 Spore flights

If the liberation of conidia takes place according to a daily cycle (Hill, 18, 19; P. tabacina) such will entail a corresponding daily cycle of dissemination. Indeed, Hill (18, 19), operating a Hirst spore trap (Hirst, 20), trapped the greatest numbers at approximately the same time each day, viz. between 10 and 11 hrs. From 16.30 until next morning 5.45 almost no spores could be trapped.

Yarwood (52) observed a similar daily dispersal period for Peronospora destructor conidia. Many spores are liberated before 9 a.m. .Numerous spores are caught between 9 a.m. and 3 p.m., only few at other times.

On being disengaged from their sterigmata the conidia are blown about by the slightest breeze (Whetzel, 51). In so far as they are actually wafted above the fields they make up a spore flight (De Weille, 47).

2.4.6 Viability of detached conidia

2.4.6.1 With the exception of Yarwood (54; see 2.4.3), who stated detached conidia to remain viable for only about 1 day, workers on Peronospora usually observed fairly durable longevity in free conidia as compared to data given by scientists who studied the behaviour of attached ones. They hardly ever examined both categories of asexual inoculum as separate phenological entities.

Newhall (31) caught conidia in the air at different elevations and on testing their endurance they were found to survive freezing, exposure of up to 7 hours to bright sunshine in drops of water and several days' exposure to air in the dark at $T = 9$ °C and r.h. $> 70\%$. The data he presented are in disproof of the idea that the thin-walled conidia are delicate and easily desiccated and so are the data given by Katterfeld (25) and Shipley (36). The former stated that in summer, under conditions of sunshine in dry air, the spores may lose their viability in $1\frac{1}{2}$ or 2 hours, but may live for 10 days in humid air. The latter author wrote that under favourable weather conditions conidia may germinate after several weeks, but retain their germinative power for only a day or two when dried up.

2.4.6.2 The lack of precise meteobiological data concerning the environmental responses of free conidial material, besides a number of interesting data produced by Newhall (31), and the intriguingly conflicting verdicts on the two phenological categories prompted the author to a thorough investigation into the matter.

In the discussion of the author's laboratory research (Ch. III) Newhall's data (31), giving evidence of a detrimental influence of relatively high *temperature* and low r.h., will be paid particular attention.

2.4.7 *Germination*

2.4.7.1 As stated under 1.2.1.6 germination necessitates the presence of liquid *water* in which the germ tube can develop.

2.4.7.2 Germination can take place at *temperatures* from 1 to 28 °C; the percentage germination attained is high in the range 7-16 °C (Yarwood, 54).

2.4.7.3 Katterfeld (25) stated that at 10-12 °C 2½ hours were needed to obtain 87% and 5 hours to attain 100% germination. Under conditions favouring germination Van Doorn (10) found incipient germination after a *time* of 4 hours and concluded that, in general, conidial germination starts about 4 to 6 hrs. after favourable environmental conditions start to prevail.

2.4.7.4 Although De Bary (4) stated *light* to inhibit germination of spores in the Oomycetes this communication was not verified by later observations (Doran, 14; Van Doorn, 10).

2.4.8 *Infection*

2.4.8.1 Successful penetration of the infecting hypha growing from the germinated conidium to a stoma where its apex enters host tissue requires prolonged *wetness* of the foliage, so a continuation of the conditions conducive to germination.

2.4.8.2 The optimum temperature for infection is 13 °C, the maximum (T_x) is about 25 °C (Yarwood, 54; Van Doorn: 10).

2.4.8.3 According to Katterfeld (25) the period of *time* needed to convey the disease from a diseased plant to a healthy one through conidia amounts to 11-16 hours, Van Doorn (10) mentioned a period of 12 to 21 hours between incipient germination and penetration, which in his experiments amounted to 16 to 27 hours after inoculation. This is in agreement with Yarwood's communication that two humid nights are involved in the whole train of events from sporulation to and including ingress into the host plant (54).

2.4.8.4 Van Doorn (10) found *light* not to interfere with the infection process.

2.4.9 Incubation period

Van Doorn had the impression that high *temperature* after inoculation (25-30 °C) lengthens the incubation period (10), which may then last 18 to 20 days instead of 10 to 17 days. McKay (28) wrote that newly affected spots may fructify within 12 days.

2.4.10 Survey

The main meteobiological materials borrowed from literature for the build-up of a bioclimatological model are the following:

a. fructification is a nocturnal process requiring saturation or near-saturation of the ambient atmosphere at $T < 22$ °C with preference for the presence of free water;
b. the attached inoculum's viability is best maintained under prolonged conditions of high atmospheric humidity;
c. spore flights constitute a daytime phenomenon with a maximum density during the last hours before noon;
d. the longevity of free spores tends to exceed that of attached inoculum and is enhanced by humid conditions;
e. germination and infection require free water on the plants and fairly low T ($T_x = 25°$, $T_{opt} = 13$ °C);
f. total duration of processes (a) through (e) can be assessed at scantly 24 hours.

CHAPTER III

LABORATORY RESEARCH

3.1 Introductory notes

In Chapter II (1.3.1.1) the author argued that, in order to be in time, an epidemiological warning has to indicate, in a predictive sense, the infection date, so that spray application can take place prior to that date.

In order to develop a workable forecast scheme it would be advantageous if not imperative to identify the infection dates or at least a number of them. To that end we must know when the following requirements are and were met that characterize infection days, viz.

a. the climatic conditions facilitating crop infection are fulfilled,
b. a significant amount of viable inoculum is present to profit by these environmental conditions.

It was felt that in this connexion our knowledge concerning the viability of spore masses was not yet adequate to judge the potential danger of spore flights finding expression in the average germinative capacity K of the constituent conidia.

The questions to be answered were:

1. how is a significant value of K attained?
2. once a significant level has been attained, how is it maintained (or lost) previous to conidial dislodgement?
3. how is it maintained (or lost) after disengagement?

Considered phenologically, this meant that research had to be conducted with regard to

1. maturation (of attached conidia),
2. viability and survival of attached conidia,
3. viability and survival of detached conidia.

In 1956/'57 the author had conducted research on the influence of light and ultraviolet radiation on the longevity of spores of Exobasidium vexans (40, 41, 42), finding u.v. radiation to exert a fungicidal effect. Since similar experiments did not appear to have been conducted by potato blight and downy mildew epidemiologists it was decided that this item was to be examined.

For honesty's sake it should be confessed that at the beginning of the author's research the total epidemiological problem had not been posed in the systematical form in which it is chronicled in this treatise and set down in this introductory description, in which the items have been rearranged so as to get the quests in the (pheno)logically correct order. Instead, the complete picture of meteobiological interactions came out bit by bit under constraint of the necessity to interpret the viability of K in longevity tests (De Weille, 45).

The unintentional methodic errors to which the author owes an essential part of the knowledge to be conveyed in this chapter are by no means withheld (see 3.4).

3.2 Appliances in laboratory research

The instruments used in the author's laboratory experiments were identical to those utilized in the preceding and simultaneous investigations concerning potato blight. An extensive description can therefore be considered superfluous. For more information than is provided by the following brief discussion see De Weille (47: 2.3.1, 2.3.3).

3.2.1 Environmental control

3.2.1.1 For the purpose of culturing fresh sporal material of the onion mildew fungus diseased pot plants were put in closed *exsiccators* in which the space under the perforated platform upon which the pot was placed had been filled with water.

3.2.1.2 For the purpose of exposing free conidia to various combinations of T, r.h. and visible and u.v. radiation the environmental control unit called *mycotron* (47: fig. 8) was used. In 4 climatic cells four different levels of r.h. could be created simultaneously at each programmed level of T, which was identical for all cells. In an additional fifth cell 100% r.h. was maintained at that temperature.

3.2.1.3 For the purpose of exposing the conidia to different levels of light and u.v. energy use was made of a battery of *discharge tubes* of the usual type and/or of a special experimental type originally made by Messrs. Philips Ltd. for internal experimental purposes but kindly put at the disposal of the KNMI at the author's request. These special tubes emit long-wave u.v. energy ($\lambda > 300$ nm; λ_x (max. energy) at ca. 350 nm) (fig. 4). The intensity i was varied by varying the height at which the battery was suspended above the mycotron.

3.2.2 Measurement of environmental factors

Measurement of T was practised with a mercury thermometer, that of r.h. with Negretti & Zambra resistance hygrometers and that of u.v. with a Pressler cell whose UG 11 filter was topped by a hemi-spherical solid quartz diffusor (47: fig. 11) (Vassy, 38).

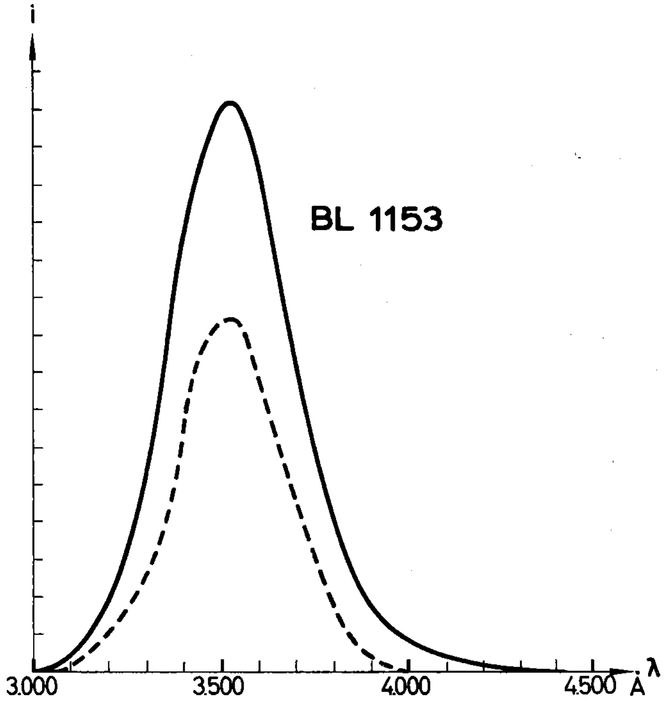

Fig. 4 Solid line: wave-length distribution of irradiation source. Dash line: energy measured after transmission.

3.3 Procedures in laboratory research

3.3.1 Biological procedures

Part of the laboratory procedures were, again, identical to those applied in the corresponding research on Phytophthora infestans (47), so that those aspects of the present study are dealt with very concisely.

3.3.1.1 *Culturing* the fungus on living onion plants was practised in exsiccators or vivaria in which the air was kept saturated. If the plant material placed therein is already mildewed in some form or other, conidiophores bearing conidia will readily be formed after a sojourn of one night in this medium. If the plant material is wetted with the help of a plant sprinkler when entered into the humid environment, considerably greater quantities of conidia can be cropped than are otherwise harvested without nebulizing the foliage.

If not yet mildewed, the plant material to be placed in the saturated atmosphere must be wetted, whereafter fresh sporal material can be applied to the moist leaves. In the author's research most artificial transfer of inoculum was performed in this way with the help of a soft paint brush. After the incubation time corresponding with the temperature at which the vivarium was kept, conidiophores and conidia appeared. A comparatively quick and abundant result proved to be obtained if a sporing diseased leaf surface was linked up with a healthy one by means of a thin film of water at and around the contact plane.

3.3.1.2 *Harvesting* conidial material was performed by means of a soft paint brush moistened by breath. The spores cohere to the humid brush hairs as they do, some seconds later, to the object slides, dimmed in the same simple way, to which they were applied. After spore application the dimmed surface cleared.

3.3.1.3 After exposure to the environment studied, the storage period in, for instance, the mycotron, the slides were brought to the *germination* medium. Covered with artificial dew obtained by breathing or atomizing distilled water, they were placed in closed Petri dishes at a r.h. of 100%, maintained with the help of wet filter paper and subsequently conveyed to a space where T was between 12 and 16 °C. The test samples remained there for a period of at least 16 hours.

3.3.1.4 On removal from the Petri dishes the spores were killed by flambation and stained with methylene blue. The *germinative capacity* K, here defined as the percentage of spores germinating under the conditions described in 3.3.1.3, was determined by microscopical examination.

3.3.2 Statistical procedures

The laboratory practice of counting spores in the samples revealed that the empirical variability exceeds what we should expect mathematically.

Experience has shown that only samples of about 500 spores or more ensure some accuracy, which means that the results (K′ and K″) of replicate samples resemble the value of K originally found (De Weille, 43).

But even then the number of cases in which the limits of + and $-2s$ are surpassed (empirical values $K' > K + 2s$ or $K'' < K - 2s$) as counted over 1000 germinated samples, appears to amount to 9% instead of 5% as expected theoretically. This phenomenon is due to a fairly great number of outliers, untypical observations that cannot be taken into account when drawing K-curves and their confidence belts.

This problem was dealt with in an earlier publication on the variability of K (45). It was shown that this variability, including the frequent occurrence of outliers (necessarily disregarded when plotting K-curves) is due to unequal dispersal of germinated conidia in the preparation, in which they are found in more or less distinct spheres of germination. This persistence or contagion phenomenon makes n seem smaller than observed.

To diminish rigorously the influence of less significant samples strongly discriminating weights were allotted to all results based on counts of $n < 500$. Fig. 5 visualizes the applied scale according to which $g = 10$ is allotted to $n = 500$.

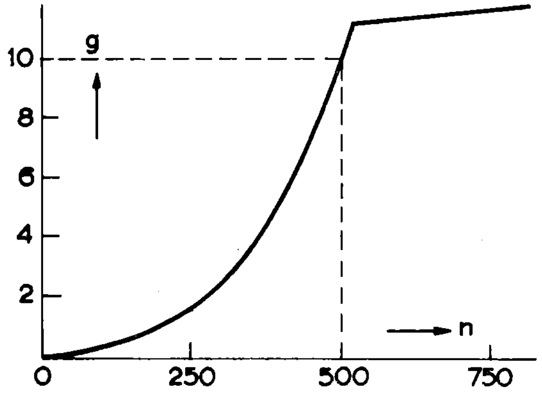

Fig. 5 Evaluation of g according to n.

In addition, corresponding data were combined for the sake of enhanced reliability. In that case the tables to which the text refers state Σg as an additional measure of significance.

In short, the statistical procedures, normally consisting in computing standard deviation data, now also imply (a) disregard of untypical observations, (b) discriminative weighting and (c) summation of corresponding counts for computing supervalues of K.

3.4 Maturation and environment

Irradiation experiments conducted in 1960 with detached conidia of Peronospora destructor yielded a set of curves not readily explicable. Yet the body of data on which they had been based was very reliable. The curves were of one and the same type. One is given in fig. 6.

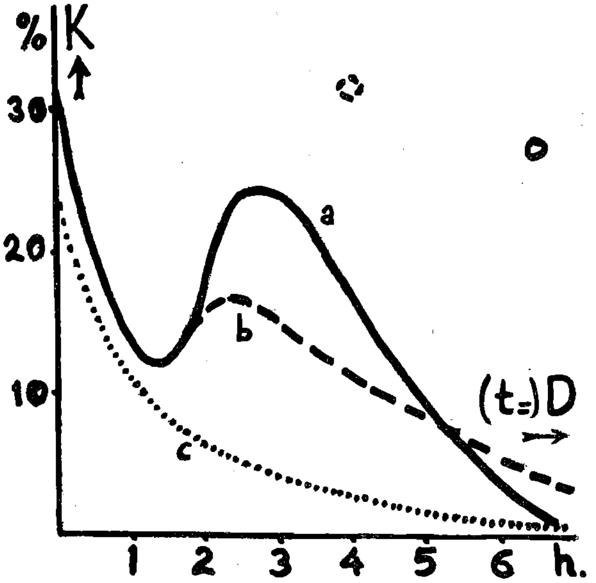

Fig. 6 Early irradiation results.
Solid line a: irradiated samples.
Dash line b: controls.
Dotted line c: illustrates sytematic error.
Note typical outliers.

Continued research elicited the cause of the seemingly illogical results: an untoward harvesting practice underlay them. The samples exposed to u.v. irradiation or control storage during the longest period D had been harvested first. The shorter the sporal material's exposure to the experimental environment the later it had been harvested.

Additional research (45) elicited the maturation process leading to the results illustrated by the curves a and b in fig. 6: during the morning in which the experiment was conducted K had increased with time, presumably according to curve c (from right to left).

This did not substantiate Yarwood's initial statement (52) that conidia are mature at 6 a.m., about 3 hours after their formation. However, in a later publication (54) the same author used the term morphologically mature, indicating the attainment of the definitive shape and size of the spores, a statement that can be endorsed.

In this post-doctoral dissertation (10: pp. 23-25) Van Doorn demonstrated how rapidly attached inoculum loses viability. Nevertheless his table 7 contains two cases of increasing instead of decreasing viability, the only cases in which the spores had

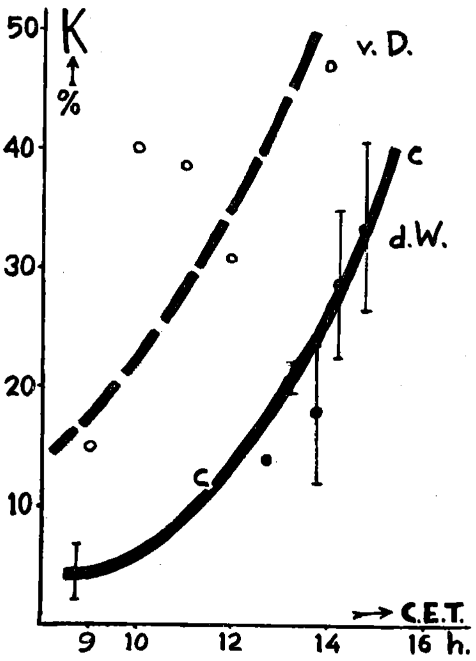

Fig. 7 Maturation of attached inoculum according to data by Van Doorn (10) and the author. Vertical bars: + and — 2s.

been surrounded by saturated air. The relevant data were averaged by the author and plotted in fig. 7.

Periodic harvesting experiments at De Bilt give rise to similar results, also visualized in fig. 7. The experimental data are given in table 1.

t	N	n	Σ g	K	s
8.45	3	1513	26	4.3	1.1
12.45	1	744	12	12.0	
13.15	2	1015	15	21.1	0.3
13.45	2	407	3	18	3.0
14.15	3	1447	22	28.6	3.3
14.45	2	841	12	33.5	3.5

Table 1
Progression (in attached inoculum) of germinative capacity K with time t (CET) at 100% r.h.
N = number of samples.
n = total number of spores counted.
Σ g = totalized weights of corresponding samples.
s = standard deviation of weighted mean K.

When plotted inversely along the abscissa, i.e. with t progressing from right to left in order to match the situation depicted in fig. 6 the curve c of fig. 7 is in agreement with c in fig. 6.

The data show that, whereas a saturation deficit of the ambient air is disastrous to the viability of attached inoculum, K will increase under conditions of water vapour saturation until its subsequent decrease owing to senescence or a fall in atmospheric humidity.

3.5 Viability and survival of detached inoculum

After, in preceding mycotron experiments, – in contrast with the behaviour of attached inoculum and in agreement with Newhall's findings (31) –, up to 8 hours' exposure of loose conidia to a wide range of temperatures and atmospheric humidities had failed to elicit any spectacular response, a series of irradiation experiments was started.

In these experiments conidia were exposed for up to 7 hours to u.v. irradiation regimes ranging from 100 000 to 300 000 erg/mm^2. hr., in later experiments usually 200 000 erg/mm^2. hr. at T varying from 15 to 25 °C, most often 20 °C, and r.h. from 70 to 100%.

Again, no influence of T and r.h. could be shown. A modifying effect of T may not have shown because of the great variability of the experimental data finding expression in high standard deviations.

After the irradiation research had been terminated the resultant corresponding values of K stemming from all experiments were averaged and studied as a function of Q, the quantity or dose of u.v. radiant energy received.

As biological radiation effects solely depend on the amount of energy received regardless of the mutual proportion of its components D (duration) and i (intensity) ($Q = Di$) (cf. De Weille, 45) the energetic quantity Q can be replaced by the duration in hours t of exposure to constant u.v. radiant energy of 200 000 erg/mm^2. hr. as is done in the table. This is not affected by the integration in the averaged data of the results of an experiment conducted with half that hourly amount of radiation.

The averaged results are given in both table 2 and fig. 8.

The data show that, as compared with non-irradiated control series, u.v. radiation, if not applied in too great a dose, evokes a stimulating effect. In the open, quantities

irradiated						not irradiated					
u.v. 200 000 erg/mm^2. h						T and r.h. as in left hand table					
D	N	n	Σ g	K	s	D	N	n	Σ g	K	s
0	2	841	14	13½	3½	0	2	841	14	13½	3½
¼	7	4402	60	13½	1¾	¼	4	2288	34	14½	2¾
⅔	6	4067	56	13	1½	½	3	1447	22	16	3¼
¾	9	4315	64	14	1¼	¾	3	1574	23	20	3¾
1	6	2596	41	14½	¾						
1¼	6	2294	33	15½	1	1¼	2	407	3	16	3
1½	5	2504	46	14	2½	1½	3	1295	17	17½	¼
1¾	3	1705	33	17	3½						
2	4	2238	43	18	2½	2	3	1759	27	17	1
2½	4	2118	39	25	3	2¼	1	744	12	12	–
2¾	2	1098	20	30	8½						
3	3	2094	32	26	5	3	3	1275	20	10½	1¾
3¾	1	996	12	20	–						
4	3	1250	16	15	5¼						
4¼	4	1683	24	12	3½						
4½	3	1280	20	12	1¾						
5¾	1	572	11	2	–	6¼	3	1513	26	4½	1

Table 2 Average result of a number of irradiation test series.
D = duration of exposure to test medium in hrs.
N = number of samples processed.
n = total nr. of spores counted.
Σ g = sum of allotted weights g.
K = germination capacity in % (experimental result).
s = standard deviation of weighted mean K.

of u.v. energy corresponding with the left half of fig. 8 are readily attained even on days very deficient in sunshine. Meanwhile the data justify the assumption that in the open field the inactivating power of bright sunshine will constitute a significant fungistatic factor, for data computed by De Boer (7) show that at de Bilt hourly values of Q attain values up to a maximum exceeding 1 500 000 erg/mm^2. h.at midday in June. Biologically however, solar radiation, having its maximum emission alongside of the visible violet, is less active than the experimentally applied artificial u.v. with its maximum at 350 nm.

This implies that, as a follow-up to the laboratory experiments, the evaluation of the fungicidal effect of solar radiation necessitates *field tests.*

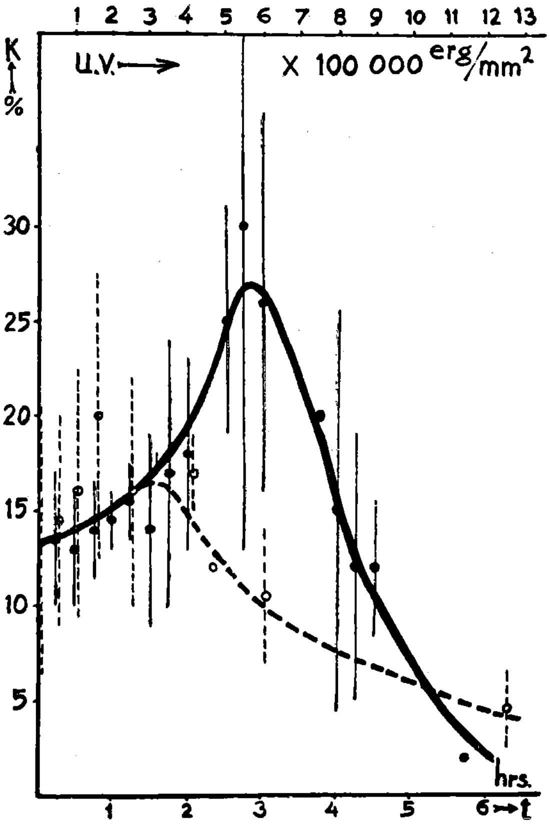

Fig. 8 Graphical representation of results summarized in table 2.
Q = total quantity of u.v. supplied.
t = duration D of exposure in hours. Solid line: irradiated; dash line: controls. Vertical bars indicate + and — 2s.

3.6 A tentative bioclimatological model

Conformably to the method discussed in Ch. II: 2.3, the knowledge contained in 2.4.10 and the experimental results treated in III: 3.4 and 3.5 can be utilized in order to formulate a tentative bioclimatological model serving as a working hypothesis for the field tests.

In the following model an effort has been made to quantify the different environmental influences (cf. 43). Without engagement and making use of previous experiences (47) the provisional model rules to be tested are:

1. conidiophore formation requires r.h. $\geqslant 97\%$;
2. formation of conidia requires nocturnal r.h. $\geqslant 97\%$, preferably coupled with condensation;
3. maturation and survival of the newly formed, still attached, inoculum require prolonged high r.h. $\geqslant 97\%$, at least until noon;
4. for survival of the detached inoculum the duration of bright morning sunshine must be less than $2\frac{1}{2}$ hours;
5. germination and infection requiring prolonged leaf wetness following the humid conditions stated under 1, 2 and 3, day-time rainfall is a prerequisite for the successful accomplishment of crop infection.

For easing the processing of meteorological data the above conditions can be rewritten as follows:

1. for sporulation a saturation deficit (s.d.) $\leqslant 0.4$ mm prevails in the crop at 0, 3 or 6 h. CET;
2. for maturation
   and survival: a.m. sunshine < 3 hours;
3. for germination
   and penetration: precipitation between 9 and 21 h. CET.

It goes without saying that for the ultimate infection of the crop all three criteria, or alternative criteria ensuing from the tests, must be met consecutively.

CHAPTER IV

FIELD RESEARCH

4.1 Introductory notes

The questions posed in 3.1 are only partly answered by the results described in the preceding chapter. It is essential to study also, preferably in the same degree of detail, the behaviour of the downy mildew agent in the open field, where environmental conditions are, at any event, more freaky than in controlled environment. Therefore, test fields were established in which the fungus was introduced by planting within the healthy crop a systemically diseased pot plant made available by the IPO.

In order to ascertain maximum accuracy and comparability with the results of pure lab research, laboratory tests of daily collected field samples were conducted throughout the growing season. Thus, field and laboratory findings readily fell into line with one another.

4.2 The test fields; location and features

4.2.1 In 1960 the downy mildew field research was conducted on test fields quite different from those laid out in the following years.

At *Ouddorp*, for instance, where the author had assumed the responsibility for processing the observational data obtained in the IPO/SNUiF downy mildew experiment, the test field, formerly designed by Dr. Post, was circular with a diameter of 16 m. It was divided into quadrants in order to facilitate the study of wind direction as a factor affecting the spread of the disease. The primary inoculum source was placed in the centre.

Meteorological equipment located near the fringe of the test field had been made available by the KNMI. It included a Campbell-Stokes sunshine autograph and a Stevenson screen containing the customary thermometer sets and a hygrograph. Rainfall data were derived from a nearby precipitation station. Within the crop a thermo- and a hygrograph belonging to the IPO recorded microclimatic conditions.

Measurements started on the first of June, 1960, immediately after insertion of the primary inoculum source.

Biological observation differed from the standard procedure adopted by the author (see under 4.3.2). It consisted of daily counts (in each of the quadrants separately) of newly invaded leaves but these were picked off on observation.

At *de Bilt* the author had meanwhile set up a general downy mildew field for orientation with reference to the two species attacking onions and peas, respectively. It contained 6 plots planted with onions, shallots, marrowfat and green peas as illustrated in fig. 9. Primary infection sources had to be introduced repeatedly before the first plant contracted the disease. Only the fourth diseased onion pot plant managed to be instrumental as a primary focus. It was planted on the 22nd of June, 1960.

Meteorological information was derived from the equipment in the nearby potato blight experimental field and from a thermograph, a hygrograph and thermometer sets located in plot 4 for the purpose of recording crop microclimate.

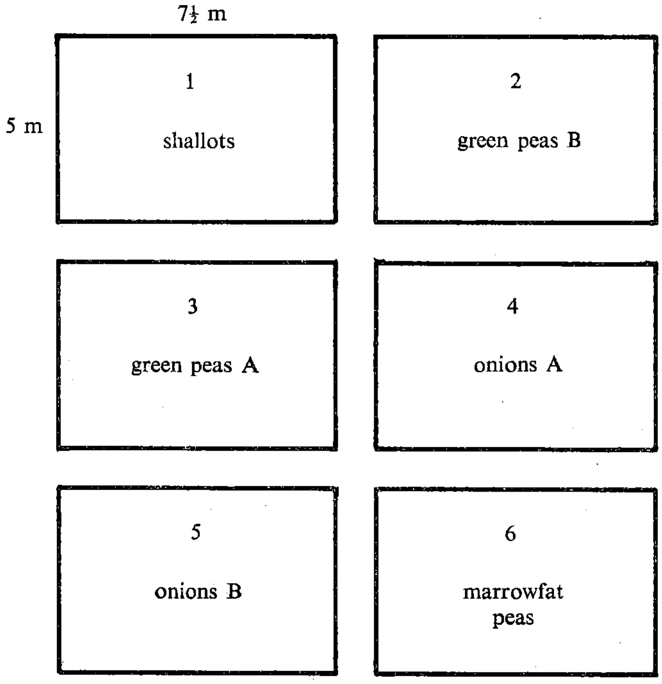

Fig. 9 The 1960 test field at de Bilt.

4.2.2 In 1961 and '62 there was a 26 × 8 m KNMI/SNUiF test field at *Middelharnis*. In 1961 there was an additional KNMI plot measuring 16 × 6 m at *Bennekom*.

These fields were provided with a rather complete meteorological equipment comprising a screen with complete outfit, recording rain gauges and sunshine autographs as well as thermo- and hygrographs, dry- and wet bulb, maximum and minimum thermometers under special screens located between the plant rows.

4.2.3 At *de Bilt* the field tests were continued until the end of the 1965 growing season.

In the odd years the onions were grown in a 30 × 20 m test field, whereas in the even years a 30 × 16 m field was at the author's disposal.

Full use could of course be made of all meteorological data collected at the Institute. In addition, the same micrometeorological observation programme as described under 4.2.1. was also carried out here.

4.2.4 The experimental fields stated under 4.2.2 and 4.2.3 had not been subdivided into object plots like those utilized in the first experimental year 1960.

4.3 Observation

4.3.1 Meteorological observations

4.3.1.1 At de Bilt and on the isle of Goeree-Overflakkee (Ouddorp and Middelharnis) daily readings of all instruments were performed at ca. 8.15 CET, at Bennekom at ca. 9.15 CET. The thermographs and hygrographs in the screen as well as in the crop were checked every day. These instruments had a clockwork with weekly rotation. For method of reading: see De Weille, 46.

4.3.1.2 Non-standard instruments used in the crop were the de Wit leaf wetness recorder and the *pluvioscope* (for both instruments see 47: pp. 67-70). Where necessary the pluvioscope, recording rainfall duration, and the standard rain gauge together made up for the sometimes lacking pluviograph, so that both the time of incidence and the duration of showers and the quantity of precipitation could always be recorded. The intensity of precipitation was not studied.

4.3.2 Biological observations

4.3.2.1 The biological observations were made daily, and in some cases even more frequently so as to match the also daily made physical measurements.

4.3.2.2 From 1961 onward, each morning *sporal samples* were taken according to the procedure described in 3.3.1.2. The spores were harvested from a number of apparently freshly sporulating lesions, or from somewhat older lesions in case young ones could not be found. The harvested conidia, on object slides, were germinated under the conditions described in 3.3.1.3. Finally, K was determined according to the directives given in 3.3.1.4. If possible, per sample at least 500 spores were counted.

On some days sporal samples were taken at different hours in order to check the progression of K. On some occasions replicate samples were taken so as to be informed about the internal variability inherent in the samples.

During some sunny periods when apparently no sporulation occurred and, of course, as long as the crop remained healthy (in some field tests the crop did not contract the disease at all) no sporal samples could be taken.

4.3.2.3 Microphenological events upon the leaf surface were followed daily by applying the *leaf print* technique (47: pp. 75-77). This procedure shows the state of affairs in the microflora upon the foliar surface in the form of a collodion film. To that end a 6% solution of collodion in alcohol and ether is plastered thinly onto a part of the leaf where the liquid is allowed to dry up. No sooner is it dry, or almost so, than the film is torn off.

With the leaf side uppermost, the print is stuck upon an object slide with the help of the same mixture as was used for the preparation of the 6% collodion solution. It takes some exercise to plaster the film along the slide without spoiling the leaf surface structure imprinted upon the upper side of the preparation. This happens when too much of the film has been dissolved by applying too much of the solvent. On the other hand the application of too little of the dissolvent will cause the film to remain lumpy and thus less suited to microscopic examination.

The replicas can be stored until microscopical examination starts. Then they are studied, either in water or in glycerol, under a cover glass. Too lumpy films are first made supple by means of alcohol 60%, so that they can be straightened with some success prior to being wetted with the fluid medium in which they are to be examined.

Microscopical scrutiny of good prints will reveal a striking picture of the leaf surface. The outlines of epidermal cells including the stomata are clearly visible. But even if this is not he case the film will not fail to show the small objects present on the leaf surface when the replica was made. Among these are probably dead and probably healthy downy-mildew conidia. Germination can sometimes be noticed. In rarer cases even penetration of the germ tube into host tissue is made visible by this technique.

4.3.2.4 It is essential that all observations are considered in conjunction with one another. The presence of germ tubes indicates germination, the absence, at least if not very many spores have been caught, does not however exclude it. In the same way, the presence of many probably viable conidia indicates a spore flight while their absence does not exclude it.

Moreover, the infection noticed may well have taken place the day before the print was made, but the possibility that it happened one day earlier cannot always be excluded. Recorded extreme weather conditions may sometimes exclude one of the dates.

The presence, in the replica, of apparently dead, shrivelled spores does not guarantee that exactly the day preceding sampling had been so sunny as to kill them.

4.3.2.5 The biological observations discussed under 4.3.2.2 produce numerical results, the leaf print technique leads to +, 0 and −, or yes/no/no-answer results.

Both kinds of experimental results can be used for the composition of a list of (micro)phenological data.

4.3.2.6 Microscopical observation for the purpose of examining the *spread* of the disease over the fields consisted of daily observation of marked plants. These plants were in the first place those surrounding the primary infection source (and, initially, that pot plant itself) and, in the second place, a number of plants, marked with rings, selected according to the *grid system* (44, 47).

This implied that the plants at the angular points of each square metre of the field or, in other words, the plants standing at the intersections of an imaginary squared trellis with a 1 m mesh width were the *observation plants.*

4.3.2.7 For the purpose of making *symptom observations*, the test plants, evenly distributed over the area according to the 1 × 1 m grid, were inspected every day with reference to their state of health. The date on which each plant showed its first downy mildew symptoms was recorded on a map.

4.3.2.8 Plants standing at the intersections of a 4 × 4 m grid, consequently forming part of the population of plants coming under 4.3.2.7, had been selected for recording the *intensity* of attack by counting the number of lesions per leaf. Contrary to the kind of observations mentioned in 4.3.2.7 that lead to categorical results only, this type produced numerical results.

4.3.2.9 The macroscopical symptom observations treated in the foregoing paragraphs could not always be successfully made. At de Bilt no epidemic occurred in 1961 and 1964. At Middelharnis such was the case in 1962.

4.4 Results

Daily made visual observation of newly-produced levies of conidia enabled the author to list the *formation nights*, in which considerable amounts of fresh inoculum are produced, whereas the value of K found as a result of the incubation of sporal samples taken later in the morning or sometimes also in the afternoon evidenced the increase of K characterizing *maturation days* or the failure of K to attain a worthwhile value (5% or more).

Studying collodion leaf prints revealed *germination days*: on such days the detached inoculum constituting a spore flight is found germinated upon the leaves.

In a limited number of cases a germ tube penetrating into host tissue is observed in the print, thus indicating an *infection day* (cf. fig. 11).

The symptom observations discussed under 4.3.2.7 and 4.3.2.8 supply information concerning the spread of the disease so as to identify the typical *epidemics* characterized by accelerated increase of the intensity of attack.

4.4.1 Spore formation nights

Over the entire period of investigation 99 cases of sporulation were recorded in the different fields. There were 25 cases of no sporulation, an observation which is less easily made than the positive one, especially in collodion prints, in which the absence of fresh conidial material may depend on chance. In all other cases the prints did not allow any conclusion to be made, for instance by not containing the vegetable material wanted or for lack of tranparency.

Scrutiny of the 124 cases revealed an apparent interrelationship between sporulation and the saturation deficit (s.d.) in the crop (rather than in the screen) during the late night and the early morning, particularly with the s.d. at 3 o'clock. Sporulation usually occurred at s.d. $\leqslant$ 0.4 mm.

The following rules were compared:

sporulation occurs when the s.d. prevalent at 0 a.m. $\leqslant$ 0.4 mm
sporulation occurs when the s.d. prevalent at 3 a.m. $\leqslant$ 0.4 mm

sporulation occurs when the s.d. prevalent at 6 a.m. $\leqslant$ 0.4 mm
sporulation occurs when the s.d. at 0 or 3 a.m. $\leqslant$ 0.4 mm
sporulation occurs when the s.d. at 3 or 6 a.m. $\leqslant$ 0.4 mm
sporulation occurs when the s.d. at 0, 3 or 6 a.m. $\leqslant$ 0.4 mm
sporulation occurs when the s.d. at 0 and 3 a.m $\leqslant$ 0.4 mm
sporulation occurs when the s.d. at 3 and 6 a.m. $\leqslant$ 0.4 mm
sporulation occurs when the s.d. at 0, 3 and 6 a.m. $\leqslant$ 0.4 mm

The treshold values of 0.3 and 0.5 mm s.d. were dealt with in the same way, so that, in all, 27 different criteria were available for testing.

The statistical testing system of which more detailed examples are given elsewhere (De Weille, 47) is illustrated by fig. 10.

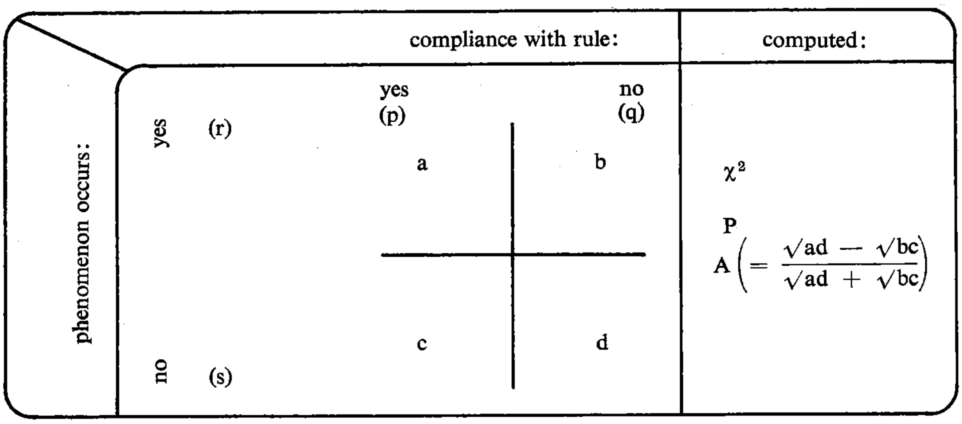

Fig. 10 Two-by-two contingency table and its aim. A = colligation coefficient.

In principle, each criterion is subjected to a twofold test by computing χ^2 values and subsequently, where these values are significant, those of the coefficient of colligation A.

The significance of values of χ^2 finds expression in very low pertinent values of P, the measure for the probability of later values exceeding the now computed χ^2 by $\geqslant 5\%$. By the author P was previously referred to as exceedance probability (47).

Statistical significance of χ^2 shows that r (in this case sporulation) and s (here no sporulation) are indeed related to p and q representing the tested criterion. Insignificant χ^2 data, characterized by higher values of P, indicate a lack of relationship with the tested rule.

As in quite a number of cases P attained values of $\leqslant 0.001$, so that a correspondingly high number of rules are valid, testing was continued so as to determine the relative strength of each individual criterion.

This relative strength is expressed by the coefficient of colligation A (Fig. 10) (cf. Pearson, 34).

If there is strong association between the criterion and the phenomenon studied two (diagonally) opposite fields will contain most of the cases and the other diagonal pair only very few. In the case of weak association numbers will be evenly distributed over the four fields or crowd in a pair of contiguous fields.

The value of A will lie between $+1$ and -1 (maximum colligation). $|A| \simeq 0$ indicates the absence of colligation.

As appears from the last two paragraphs a rough pre-selection within the present 27 rules is certainly possible, so that the tedious computation work can be reduced. In this case apparently chanceless criteria could be rejected either at a first glance or on the basis of the first (χ^2-)test only.

The 4 most significant criteria inferred for the sporulation phenomenon are given in Table 3.

Criteria tested	A	P
s.d. at 3h CET $\leqslant$ 0.4 mm	0.46	< 0.001
s.d. at 0 or 3h CET $\leqslant$ 0.4 mm	0.49	< 0.001
s.d. at 3 or 6h CET $\leqslant$ 0.4 mm	0.57	< 0.001
s.d. at 0, 3 or 6h CET $\leqslant$ 0.4 mm	0.69	< 0.001

Table 3 Comparative test of 4 sporulation rules, from among which the lowermost criterion was ultimately selected.

Other types of rules gave rise to substantially lower values of A and to higher values of P.

There is no doubt that all 4 criteria contained in Table 3 are relevant to the sporulation phenomenon. Within the statistical material we have at hand the lowermost criterion occupies the strongest position.

Some readers may argue that the 'runners-up' are also valid criteria and that with fresh and/or more statistical material another criterion might outdo the fourth one. Yet the ultimate selection of the fourth rule is justified by the fact that the other ones are contained in it, so that a higher new value for any one of them is likely to increase also A_4.

It can be concluded that

sporulation of appreciable importance occurs if at 0 or 3 or 6h CET the saturation deficit in the crop microclimate does not surpass 0.4 mm Hg (0.53 mbar).

The remark can here be made that the potato blight criterion inferred in 1963 (47) differs from the present one inferred for onion downy mildew by stipulating the prevalence of the same high atmospheric humidity as defined here, but at 0 *and* 3 *and* 6h CET instead of or/or, without for that matter leading to different meteorological conclusions (47: Ch. IV; this publ.: Ch. V).

4.4.2 Maturation days

We see that the above findings (4.4.1) entirely verify rule (1) of the rewritten biomet model treated in 3.6 on p. 44.

Testing rule (2) however showed that, although the criterion for maturation of inoculum and its survival defined as a.m. sunshine < 3 hrs certainly covers the majority of the cases, criteria based on total daily sunshine duration gave rise to higher values of A at even lower levels of P in χ^2 tests.

With the help of the results obtained with sporal test samples and some of the leaf prints 70 cases of significant maturation ($K \geqslant 10\%$) and 30 cases of no maturation or no survival could be identified. These 100 cases, containing a few sporal samples taken in 1965 after the other observations including sporulation assessment had already been terminated, were subjected to the combined χ^2/A-test. A few samples refer to non-germination days when laboratory plants were exposed to outdoor conditions.

The following sunshine (ss) rules were compared:

the attainment and preservation of a significant level of K requires a.m. ss $\leqslant 2$ h
the attainment and preservation of a significant level of K requires a.m. ss $\leqslant 2\frac{1}{2}$ h
the attainment and preservation of a significant level of K requires a.m. ss $\leqslant 3$ h
the attainment and preservation of a significant level of K requires a.m. ss $\leqslant 3\frac{1}{2}$ h
the attainment and preservation of a significant level of K requires total ss $\leqslant 4\frac{1}{2}$ h
the attainment and preservation of a significant level of K requires total ss $\leqslant 5$ h

the attainment and preservation of a significant level of K requires total ss $\leqslant 5\frac{1}{2}$ h
the attainment and preservation of a significant level of K requires total ss $\leqslant 6$ h
the attainment and preservation of a significant level of K requires total ss $\leqslant 6\frac{1}{2}$ h
the attainment and preservation of a significant level of K requires total ss $\leqslant 7$ h

As is shown in Table 4 there was very little difference between the four strongest criteria.

Criteria tested	A	P
total daily ss duration $\leqslant 5$ hrs	0.74	< 0.001
total daily ss duration $\leqslant 5\frac{1}{2}$ hrs	0.77	< 0.001
total daily ss duration $\leqslant 6$ hrs	0.75	< 0.001
total daily ss duration $\leqslant 6\frac{1}{2}$ hrs	0.70	< 0.001

Table 4 Comparative test of 4 highly significant maturation/survival rules.

Below 5 hrs of ss duration there was a distinct drop-off in values of A; above 5 hrs there was no considerable gain. Therefore, the maturation/survival criterion can be worded as follows:

downy mildew inoculum matures/survives only if the total (daily) duration of bright sunshine does not exceed 5 hours.

4.4.3 Germination days

There were 61 cases of observed germination as against 27 cases of definitely no germination, in some cases probably associated with non-identified non-maturation days, so $n = 88$.

An overall study of the material revealed, as was anticipated, that germination is closely associated with precipitation. The word precipitation is conceived in such a way that it includes cases of quantiatively unmeasurable drizzle recorded under ww code 50-59.

The rules compared were:

for germination to be accomplished there must be rainfall (rf) including drizzle, i.e.

precipitation between 6 and 9 h CET
precipitation between 6 and 12 h CET
precipitation between 6 and 15 h CET

precipitation between 6 and 18 h CET
precipitation between 6 and 21 h CET
precipitation between 9 and 12 h CET
precipitation between 9 and 15 h CET
precipitation betwene 9 and 18 h CET
precipitation between 9 and 21 h CET
precipitation between 9 and 24 h CET
precipitation between 12 and 15 h CET
etc.

In all, 20 criteria were compared, of which, after pre-selection, 7 were tested.

The highest results were obtained for the 9-21 h. criterion:

$$A = 0.70 \qquad \chi^2 = 31.17 \qquad P \ll 0.01$$

It can therefore be concluded that

germination of viable inoculum necessitates precipitation between 9 h and 21 h CET.

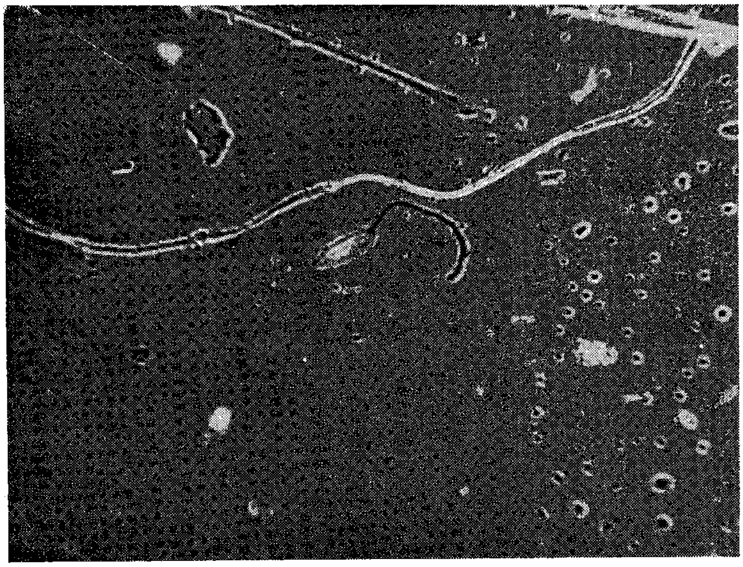

Fig. 11 Infection observed in leaf print.

4.4.4 *Infection days*

There were 11 cases of observed infection in which in the collodion films a germ tube was seen to have penetrated into host tissue (see Fig. 11). As cases of non-infection those of non-germination (21 cases) could be used: consequently $n = 32$.

The application of the A-test revealed that the best criterion would be identical to the germination rule, the χ^2-test resulting in $P \simeq 0.02$.

As soon as the additional assumption was made that two consecutive days should comply with the set rule, the 11 cases were even better covered: $P < 0.01$.

The conclusion will then be that

infection of the crop takes place on typical germination days. Substantial infection can be expected when two or more of such days occur in succession.

When a list of potential crop infection dates was composed based on the now developed bioclimatological model all dates of observed penetration fell on second or later days in runs of dates on which the germination rule was fulfilled. This unsolicited phenomenon strongly substantiated the validity of the criterion.

4.4.5 *The bioclimatological model*

The definitive climatological model typifying onion downy mildew infection days as inferred in 4.4.1-4.4.4 is as follows:

condition for sporulation: s.d. in crop $\leqslant 0.53$ mb at 0, 3 or 6 h. CET

$$\left.\begin{array}{l}\text{condition for maturation:}\\ \text{condition for survival of detached inoculum:}\end{array}\right\} \text{ss.} \leqslant 5 \text{ hrs.}$$

$$\left.\begin{array}{l}\text{condition for germination:}\\ \text{condition for potential infection:}\end{array}\right\} \text{rf. between 9 \& 21 h. CET}$$

condition for substantial infection: 2 such days.

4.4.6 *A date list*

With the help of the aforementioned set of rules and the available body of meteorological data it was possible to compose a list of dates on which the consecutive rules were met. The days on which the complete set of conditions have been satisfied can be considered *model infection days.*

The list is not reproduced in extenso. An example is provided by De Weille (47: 79-83).

The result in terms of numbers of model days as compared with the actually observed phenomena are given in Table 5.

	cases observed	cases inferred
sporulation	99	230
maturation	70	115
germination	61	90
infection	11	90
subst. inf.		30

Table 5

Ideally, the dates on which microphenological phenomena were observed must coincide with an equal number of dates occurring on the inferred list. In Table 5 the right hand set of cases should comprise all those belonging to the left hand set. In actual fact this is almost the matter with the sporulation and maturation cases. Due to the drawback of the leaf print technique, viz. that the replicas may reflect phenological developments that took place on a preceding day the inferred data sometimes precede the dates of observation by one or even two days.

The situation is worst with respect to the infection observations. Of the 11 cases, 6 coincide with an inferred date, 2 are preceded by one, 1 by two and 2 even by three days by the nearest inferred infection date. The 2 cases of lateness by 1 day had already been identified prior to the A test (4.4.4).

4.4.7 Extention dates

4.4.7.1 Extension days can be defined as dates on which progression of the disease is clearly visible. In terms of biological observation this was supposed to be the matter when 1 or more new lesions appeared on 4 or more plants in the 4 × 4 m grid (cf. 4.3.2.8) or an increase in numbers of diseased leaves was noticed on 4 or more plants in the 1 × 1 m grid (4.3.2.7).

4.4.7.2 Applying the criteria described under 4.4.7.1 26 extension dates could be singled out. They occurred in 8 groups of 1 to 4 days. In 1960, two cases occurred simultaneously in Ouddorp and de Bilt and thus belonged to identical groups.

Consulting the date list (4.4.6), the eight groups of extension days could very easily be related to also 8 groups of in all 35 infection dates occurring 10-16 days earlier (in 24 cases 11-13 days earlier).

Having lumped the different stations together the author finally composed the list given in Table 6.

Group	Important extension periods	Significant infection periods
1	27 - 29/6/1960	15 - 16/6/1960
2	4 - 10/7/1960	24 & 27/6/1960
3	15/7/1960	29 - 30/6 & 5/7/1960
4	22/7/1960	8 - 11/7/1960
5	29/7 - 1/8/1960	19/7/1960
6	12 - 15/8/1960	28 - 31/7 & 3/8/1960
7	25 - 27/7/1961	10 - 17/7/1961
8	31/7 - 3/8/1961	19 - 20/7/1961
(9)	15 - 16/6/1963	(no observation)

Table 6 Periods of substantial increase in disease incidence and pertinent periods of crop infection.

The weather conditions leading to the fulfilment of microclimatic and macroclimatic conditions conducive to infection were analysed with the help of synoptic weather maps, in the first instance for the periods stated in table 6 and later for all cases figuring on the date list. This procedure is discussed in Chapter V.

CHAPTER V

POSSIBILITIES FOR PREDICTING DOWNY MILDEW INFECTION WEATHER

5.1 Meteorological situations associated with crop infection

Once a bioclimatological model such as the one discussed under 4.4.5 has been defined the logical next step is to seek the collaboration of experienced meteorological forecasters who are hoped to be able to predict the occurrence of the conditions contained therein. The forecaster will then focus attention upon humid, sunshine-deficient weather in which there is ample scope for rain. It will however be appreciated that it remains difficult, if at all feasible, to forecast the exact time of the day when precipitation will occur.

As was shown in the weather maps pertinent to the crop infection dates occurring in the author's date list (4.4.6; p. 57), fulfilment of the model rules (4.4.5; p. 57) is conceivable under a number of overall synoptic situations. The synoptic weather maps studied by the author formerly constituted the main basis for predicting forthcoming weather developments. Although these maps are still widely used, the forecaster can now also bring other arms to bear on his professional problems. Satellites provide additional information; computerized atmospheric models facilitate numerical forecasting.

Such new techniques may be adopted to replace the classical extrapolation method using synoptic weather maps but are more often utilized in conjunction with the more classic approach.

The above implies that for the meteorologist there are several opportunities to identify present and forthcoming muggy plant-disease weather approximately satisfying the field conditions as laid down in the bioclimatological model. He will discharge his duties without needing any additional guidance in the form of 'model' weather charts and at any time it is recommendable for the crop protection officer to solicit professional meteorological assistance for his epidemiological problems.

Therefore the following examples of characteristic weather situations under which such field conditions as satisfy the bioclimatological model occur are only given to enhance the epidemiologist's notice of such meteorological matters. They are by no means intended to replace the professional meteorological assistance advocated in the preceding paragraph. It is however recognized that there is a strong case for the plant pathologist to be or to get 'weather-wise'.

When the weather maps recording the meteorological conditions preceding the infection periods identified in table 6 (Ch. IV) and those prevailing during these periods were studied it became clear that all infection periods were associated in some way or other with a situation previously described as model situation type 1 (cf. 47: Ch. II). The occurrence of type 1, a weather situation connected with humid air, cloudiness and precipitation, is usually followed by that of other situations also associated with precipitation and thus likewise conducive to infection, so that wherever this weather type occurs the fulfilment of the conditions of the bioclimatological model during at least two consecutive days is quite probable.

This key weather situation to be described next proved to have preceded and, in addition, partly coincided with the infection dates of group 1 (table 6 refers), group 2 including the first section of group 3, the second section of group 3, group 4, group 6 and group 7.

The already mentioned first section of group 3, group 5 and group 8 were characterized by other weather situations usually ensuing from type 1.

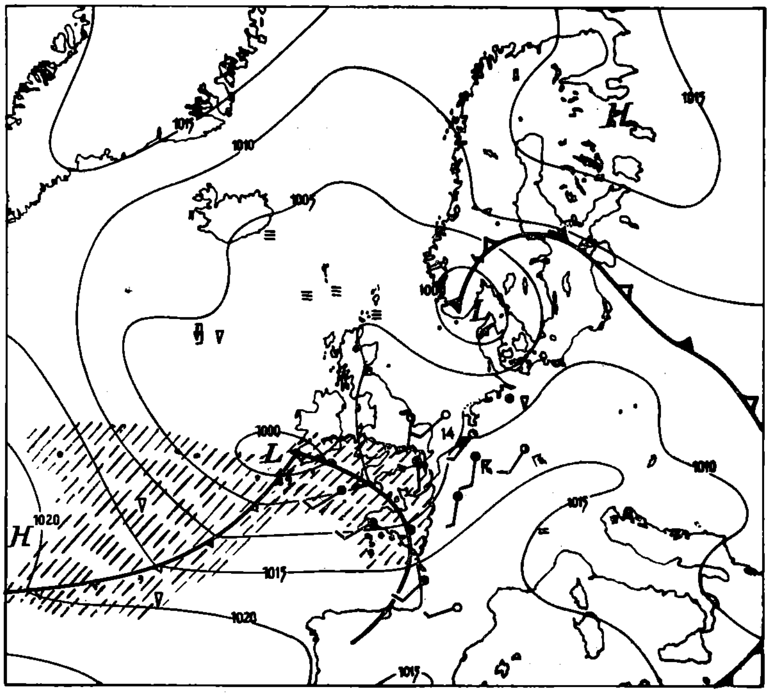

Fig. 12 Weather map of 10-7-1960 at 1 h CET showing model situation 1. Hatched area roughly indicates area of precipitation activity in the atmosphere connected with case of crop infection discussed. Similar situations elsewhere not indicated by hatching.

5.1.1 Key weather situation: type 1

On weather maps this important situation can be recognized as a characteristic case. It can be described best with the help of figures distinctly showing the course of events in the atmosphere.

Fig. 12 shows how a depression (marked L) accompanied by a sector of relatively warm 'subtropical maritime' air moves eastwards over the British Isles towards the European coast, where the passage of the warm front will give rise to precipitation in the low countries.

The warm front just mentioned is the frontal surface between the subtropical maritime air going with the depression and the relatively cold continental air present above Europe. On weather maps the solid line marking the location of a warm front at the surface of the earth is provided with small hemicircles, cold fronts like the one concluding the passage of the sector being indicated by a solid line with small triangles.

Behind the cold front drawn in fig. 12 the warm sector is followed by a mass of polar maritime air.

Fronts are characterized by non-horizontal air movements. In this connection the warm sector shown in fig. 12 can be referred to as 'not yet occluded'. (In meteorological semantics the depression itself is often referred to in that way). Occlusion is the phenomenon that the subtropical air mass accompanying a depression loses contact with the surface.

Those interested in the basic physical processes underlying the meteorological phenomena pointed out are referred to the concise list of recommended textbooks on page 83.

Frontal surfaces between air masses of different temperature and humidity are usually the scene of condensation processes followed by precipitation. In this context subtropical maritime air is called 'unstable'.

For the potato grower one important implication of the humidity of the subtropical air introduced to the low countries by the rainy warm front passage is that it will prevent wet foliage from drying up.

Highly significant in the situation of fig. 12 is the precipitation activity of the warm front preceding the arrival of the cold front concluding the passage of the warm sector.

On weather maps rainfall of any importance is indicated with dots, one dot for each rf-measuring station. Isolated showers are indicated by a sharp-edged triangle, unmeasurable drizzle by a comma, fog being denoted by piled dashes. All these symbols occur in fig. 12, in which the wind arrows attached to the small circles roughly indicating the local degree of cloudiness do not need further explanation than that the wind force is represented by the number of 'feathers' in the tail.

The succession of events ensuing from the situation shown in fig. 12 finds expression in figs. 13, 14 and 15. In fig. 13 the warm front crosses Netherlands territory. In fig. 14 a cold front passage introduces to this region a mass of maritime polar air, which has become unstable by its movement over the relatively warm water of the Atlantic This will lengthen the period of rainfall resulting from the preceding warm front passage. Meanwhile occlusion takes place (fig. 15).

Study of the circulation at higher levels reveals that the occurrence of situation type

1 is invariably connected with a *westerly to southwesterly upper air stream above the temperate zone*. Type 1 is therefore defined by the statement that in connexion with the above circulation pattern **a warm front passes** *with precipitation.*

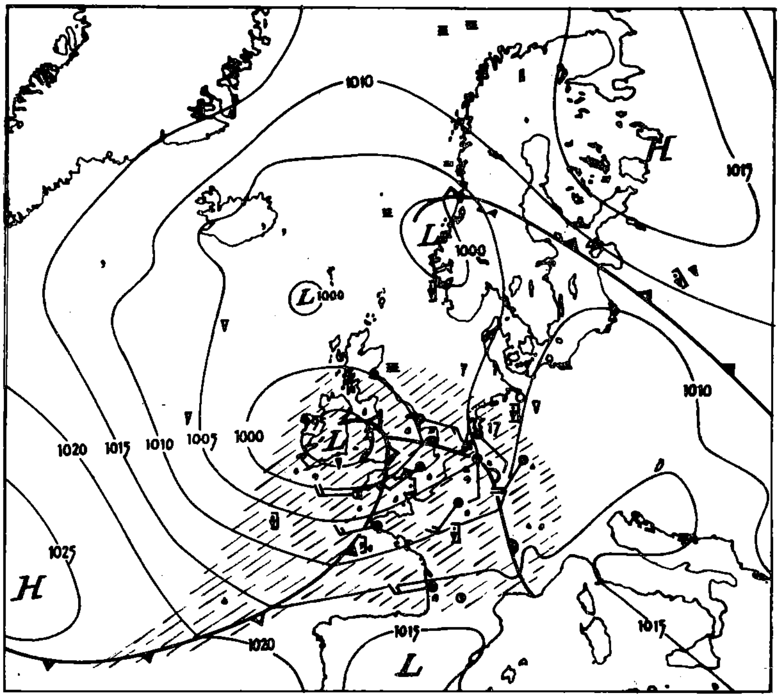

Fig. 13 Weather map of 10-7-1960 at 13 h. CET. Model situation 1. Warm front passage imminent.

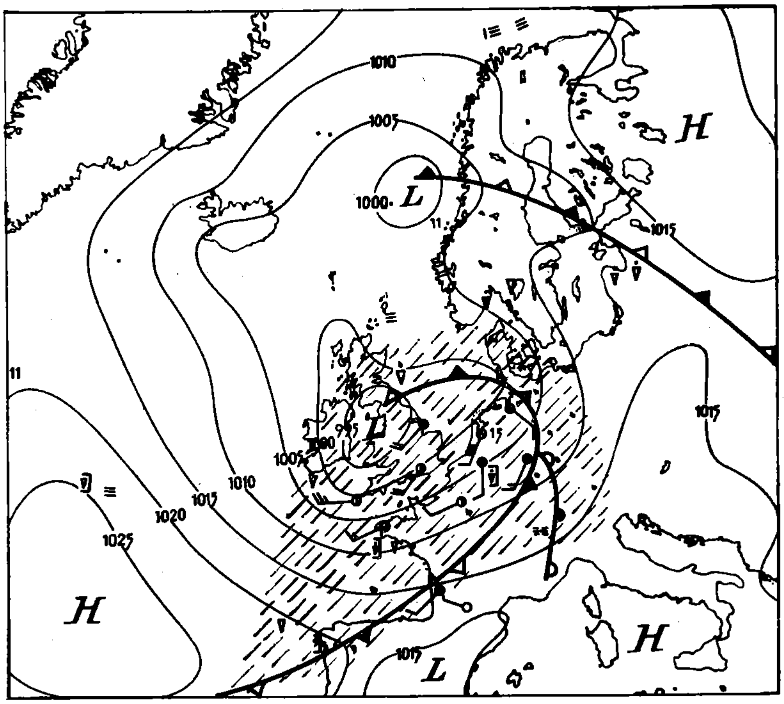

Fig. 14 Weather map of 11-7-1960 at 1 h. CET. Model situation 1. Cold front passage completed. Partial occlusion.

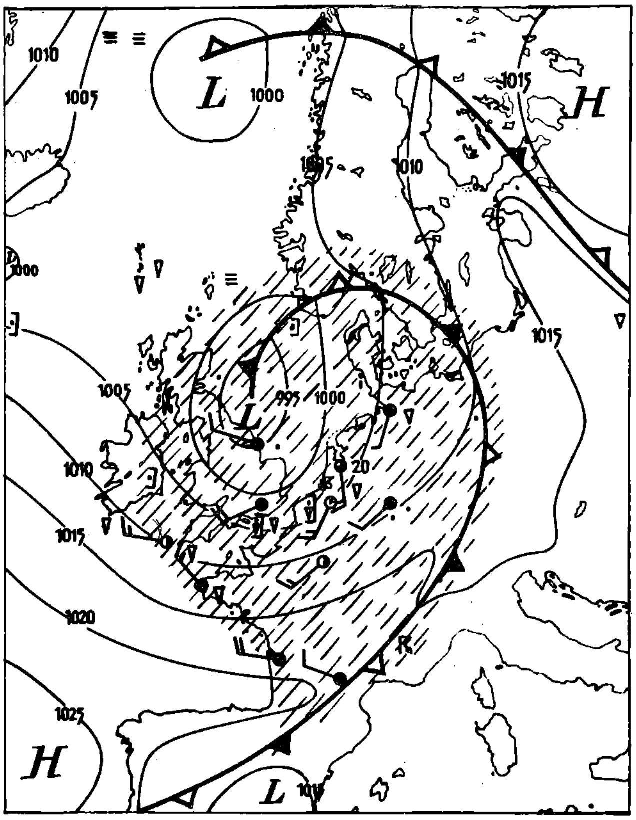

Fig. 15 Weather map of 11-7-1960 at 13 h. CET. Model situation 1 wound up. Occlusion completed.

5.1.2 The secondary weather situation: type 2

5.1.2.1 The figures 12 to 15 show that, concurrent with type 1 in the low countries, a similar but at the earth's surface simpler situation existed in southern, later mid-Norway and -Sweden. At surface level the frontal system, lacking the subtropical sector, consists of a cold front only. Obviously, the relatively warm air mass had been occluded before it had reached the area.

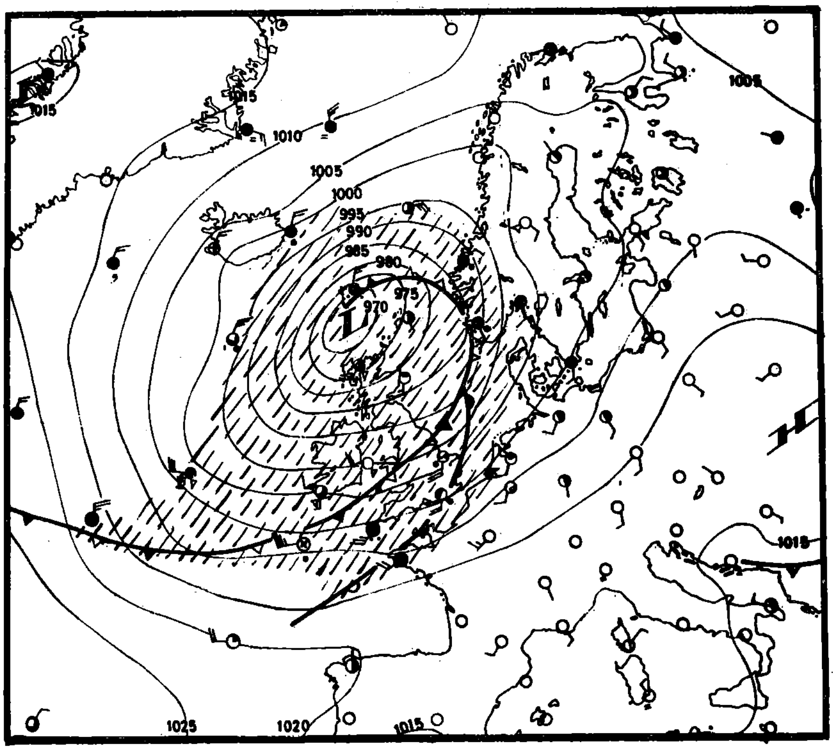

Fig. 16 Weather map of 8-7-1964 at 1 h. CET. Model situation 1. Warm air mass in the process of being occluded.

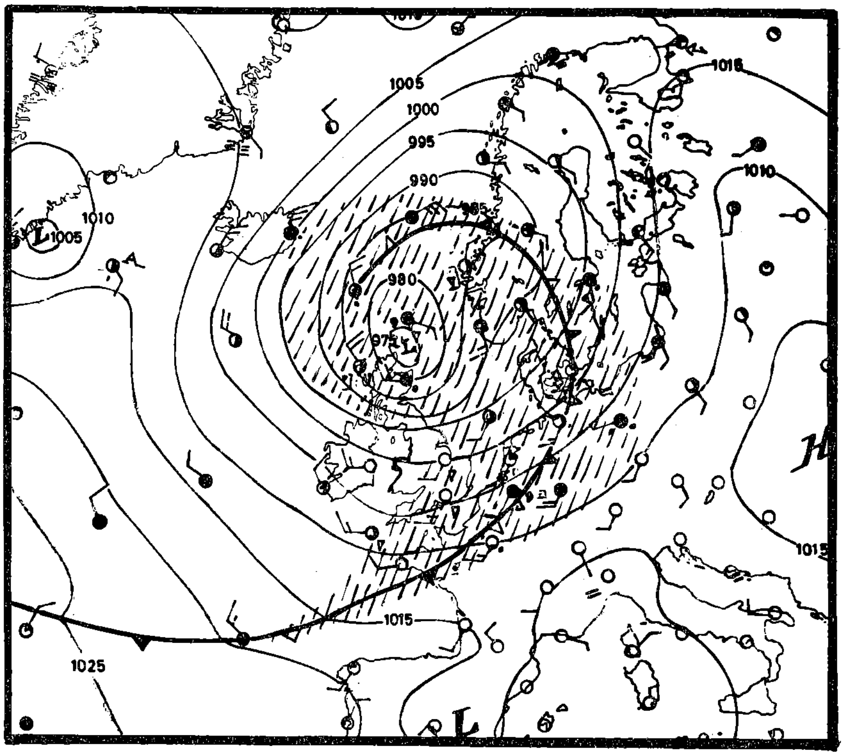

Fig. 17 Weather map of 9-7-1964 at 1 h. CET. Model situation 2a ensuing from early occlusion of subtropical air mass.

Such a course of events can already occur before a depression even reaches the European coast as is demonstrated in figs. 16 and 17 referring to a 1964 infection period occurring in the extended date list. In the case here illustrated occlusion already took place above the Atlantic. At ground level only a cold front reaches the continent. As was explained under 5.1.1 the cool air coming in with wind directions W to SW is unstable, giving rise to showers.

The passage of a cold front with occlusion is here named model situation 2a.

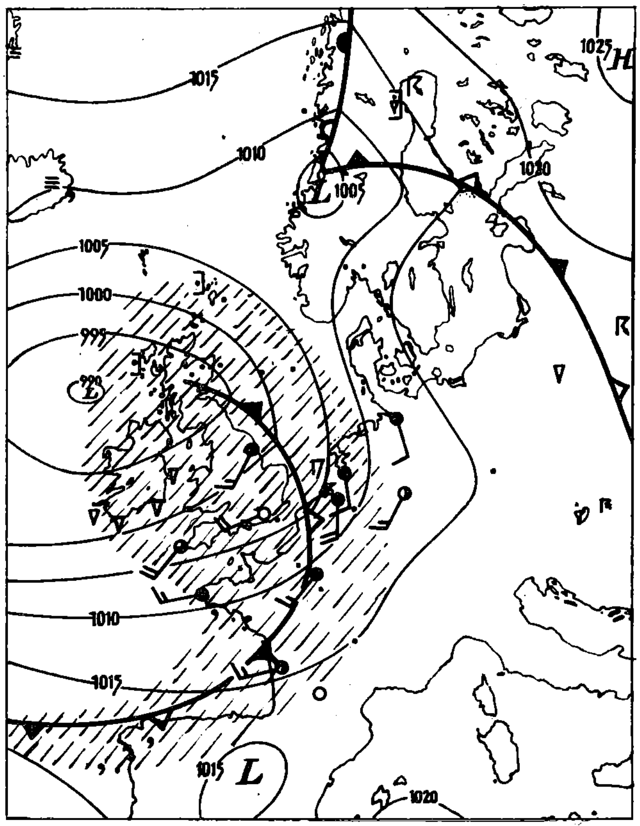

Fig. 18 Weather map of 17-7-1960 at 13 h. CET. Model situation 2a.

In such a situation, when warm air is not directly involved in the overall picture at ground level and does not therefore show up in the usual weather charts, it must be remembered that at a higher level the subtropical air mass does not immediately cease to exist, so that, following condensation at that higher level, a newly occluded depression will readily occasion rainfall. In such situations the rainfall zone will considerably precede the arrival of the cold front.

Weather type 2a occurred in the infection period 5, 6 (following type 1) and 7 (do.) stated in table 6. Fig. 18 refers to infection period 5. A more extensive survey of the weather conditions obtaining in that period was given in a previous publication (47: pp. 109-111).

5.1.2.2 In infection periods 2, 5 and 7 (table 6) type 1 was followed by another variate of type 2. Most often this variate is preceded by type 2a ensuing from type 1. It is also characterized by a movement of humid maritime polar air in an easterly direction. A warm front or an occlusion with cold front may have passed previously, but this is not always clearly the matter.

Sometimes it is merely a *pronounced trough* at the surface and aloft in the humid polar air that moves over the country giving rise to precipitation.

This variate of model situation 2 is referred to as 2b.

The trough situation associated with infection period 5 is shown in fig. 19.

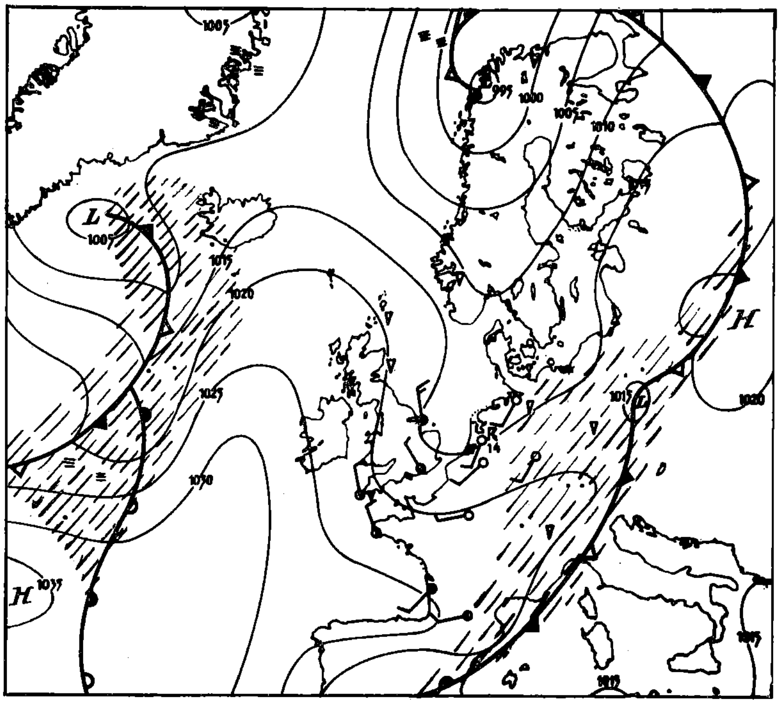

Fig. 19 Weather map of 20-7-1960 at 1 h. CET showing trough situation 2b.

5.1.2.3 When the entire circulation pattern moves, as it were, eastwards the low countries obtain their maritime *polar air from a W*, but more often *NW direction*. The trough is not present, at least not in a pronounced form, above he Netherlands. The incoming polar air is then quite cold, which does not seem very conducive to crop infection, but this low temperature, in combination with the cloudiness inherent in this situation, will anyway prevent wet foliage from drying up.

This not so very frequent variate of weather type 2, referred to as 2c, characterized the synoptic situation during infection period 8 (table 6). Meteorologically, periods 7 and 8 together were typified by the weather sequence 1 → 2a → 2*b* → 2c.

5.1.2.4 Reiterating the preceding sections 5.1.2.1-3 it can be stated that the occurrence of situation type 2, like type 1, is connected with a *westerly to southwesterly* (2a, 2b), less often northwesterly (2c) *upper air stream above the temperate zone.* Type 2 is therefore defined by the statement that in connexion with the above circulation pattern **an occlusion** (a), **cold front** (a) **or trough** (b) **passes** *with precipitation.*

2c should be considered a modified (i.e. moved) version of 2b.

5.1.3 The cyclonic situation: type 4

Five inferred infection models in the extended date list coincided with a weather situation not described in the author's previous work on potato blight (47), in which on the other hand a late-summer weather type 3 was discussed, a fog situation not occurring during the downy-mildew experiments.

The weather types 1 and 2a are characterized by a centre of low pressure, usually in the neighbourhood of Scotland or West or NW of the British Isles. This Low functions as a kind of steering centre for the frontal system involved in plant-disease conducive weather.

Quite different is the situation in which in the upper air a central Low, above or near the low countries, is involved in a *cyclonic vortex* or whirl.

At ground level the situation can be quite stable in such cases, with almost no barometric differences. The weather then depends on minor irregularities in air pressure pattern whereas surface temperatures are quite high. Following intensive daytime evaporation at ground level fog occurs at night. Thunderstorms are not improbable.

Although at first sight not a clear-cut type of weather typically conducive to plant disease, this situation repeatedly coincided with the fulfilment of the conditions of the bioclimatological model.

The circulation pattern outside the cyclonic area at the 5 km level is characterized by an upper air current bending from W to SW, eventually almost S.

5.2 Evaluation of the achievements

Having evolved a bioclimatological model of the crop infection process and having identified weather situations in which, given the indispensable amount of inoculum, downy mildew infection can be expected to occur we are confronted with the question of how to exploit these achievements during the period elapsing from 0-date to closing date (cf. 1.3.4 on p. 25).

5.2.1 Two approaches

The author's approach has so far been in line with what is advocated under 5.1 where, to the crop protection officer, it is recommended 'to solicit professional meteorological assistance' (cf. De Weille, 49). In each individual case an ad hoc decision is then reached by the crop protection officer (or, in the case of the Netherlands Potato Blight Warning Service, by an agricultural officer attached to the KNMI) and the responsible meteorologist-on-duty.

The above collaboration has been operative in the Netherlands ever since 1962 (49). Where applicable, the blight warnings are immediately followed by a similar message concerning downy mildew. In that case the KNMI agricultural officer in question takes action in concert with and under the aegis of the Horticultural News Service (cf. 1.3.4).

An other conceivable approach, more in line with Waggoner & Horsfall's simulator (39), would be a systematic, probably numerical, forecast system based on daily biological and atmospheric data. Such a forecast system does not yet exist but may well be developed in the near future for both potato blight and onion downy mildew.

One of the biological inputs in an automatic or nearly automatic forecast system will have to be the *infection potential*, one of the outputs of the system the probability of a run of at least *2 consecutive model days*. These two requirements represent two roadblocks on the way to ideal epidemiological forecasts.

5.2.2 Two shortcomings

A solution must be found for the two secondary problems identified in the preceding paragraph.

5.2.2.1 In practice one of them, viz. the biological problem, can be overcome quite easily.

Warnings or rather forecasts of crop infection should not be issued if the inoculum population stress constituting the potential infection danger in the field is so flimsy that spraying would seem out of place. In some experimental years the downy mildew disease was not contracted, sometimes even in spite of an observed primary germ tube penetration. The onion plant is neither as easily wetted nor as easily infected as the potato plant (cf. De Weille, 47). At De Bilt the plants did not contract the disease in 1961 and 1964. At Middelharnis this situation occurred in 1962.

This implies i.a. that in one region the disease may occur, whereas during the same period it does not appear in another region.

The obvious solution advocated by the author is that

1. warnings regarding attendant downy-mildew infection be issued on a regional

basis as long as the disease is not generally established;
2. knowledge concerning the local or regional disease incidence be made available to and be taken into account by those responsible for issuing warnings.

Application of the above two practices will undoubtedly result in superfluous warnings being withheld and thus lead to the avoidance of unnecessary spray applications.

5.2.2.2 The second deficiency that must be coped with is more serious and necessitates some further explanation. Reference is therefore made to 4.4.5 on p. 57, where it is stated that substantial crop infection requires *2 model days* (2 consecutive dates when the bioclimatological model conditions are satisfied).

In hitherto unpublished investigations concerning the validity of predictive warnings the author, studying 50 cases over a 6-year period, found that out of those 50 warnings, although valid, not less than 20 preceded a one-day infection period in which, according to 4.4.5, potential but no really substantial infection of the onion crop is accomplished.

At the moment there is no fool-proof system of forecasting *runs* of muggy days meeting model specifications, so that our present conclusion must be that when and where a meteorologist is consulted for an ad hoc decision with reference to a downy-mildew warning it must be borne in mind that the weather expert is not (yet) in a position to evaluate the relative importance of a warning.

5.3 A practical solution

As discussed under 5.2.1 there is at the moment no downy-mildew infection forecast system in the strict modern sense. Instead, warnings are decided upon by ad hoc collaboration of scientists from different disciplines. Yet it can be said that in the Netherlands this collaboration, which obviously does not stand in need of any official status, is practised sys ematically, although *assessment of the potential infection danger* as advocated by the author is hardly taken into account.

Especially with a view to the risk of issuing quite a number of warnings of little avail (4 out of 10 according to 5.2.3.2) it is felt that this infection potential deserves more attention.

In order to yield the best results obtainable as long as the ideal forecast sytem does not (yet) exist, a system of *integrated disease control* which includes all factors appears desirable. Such an integrated approach also provides for regional warnings.

In this context regional telephone warning services (cf. 1.3.3.3) constitute an ideal means of disseminating messages exactly when and where they are needed.

The integrated approach can only profit by day-to-day contact between agricultural and meteorological scientists and their agencies.

5.4 Survey

The fulfilment of the series of rules constituting the bioclimatological model (cf. 4.4.5) finding expression in the model days identified with it was related to the pertinent synoptic situations given in weather maps. By doing so it can be shown to the crop protection officer not familiar with modern meteorological working methods that only a *few synoptic model situations* proved to give rise to infection-conducive weather. In most cases the start of a series of infection days was preceded by weather type 1 or a weather type ensuing from the prevalence of this type 1 (cf. 5.1.1) above the Atlantic.

The synoptic weather types, all connected with precipitation, can be briefly characterized as follows:

type 1: warm front passage; westerly upper air current and movement of relatively warm maritime air at ground level;
type 2: westerly upper air current and movement of relatively cold maritime air at ground level; most often connected with passage of cold front, occlusion or trough;
type 4: cyclonic vortex in upper air around depression associated with unstable situation at ground level. Considerable thunderstorm and fog probability.

In order to reduce the number of unnecessary warnings the author advocates close collaboration of scientists with different disciplinary background in *integrated disease control* based upon both meteorological and biological observation, the latter with a bearing on the inoculum population stress.

SUMMARY

In some years *Peronospora destructor* inflicts considerable damage upon the onion crop. Moreover, it is so obviously weather-dependent that a forecast system would deserve consideration. The action of fungicides only being preventive, so that they should be applied at such dates that infection is prevented by killing the infective inoculum, the desired forecasts would have to precede the infection phenomenon by a period sufficiently long to allow the grower to spray his crop in time.

On the ground of existing biological knowledge and new laboratory results a tentative *bioclimatological model* was developed consisting of a series of consecutive (micro)-climatic conditions to be met (in the crop) for an appreciable degree of infection to be accomplished. (cf. 3.6).

Bioclimatological modelling was continued in field tests where the hypothesis was put on trial. This resulted in a definitive model (4.4.5).

By applying these duly tested criteria to all dates within the research periods in the years 1960-1965 an extensive *date list* could be composed. It contains all potential infection dates according to the model.

A study of the weather-map situations on and preceding the listed dates revealed that only a few specific *synoptic situations*, all connected with a westerly circulation pattern, lead to the fulfilment of the biomet infection criteria (cf. 5.1).

Warnings based upon physical parameters do not take account of the actual inoculum potential. Therefore, the author recommends *integrated disease control* in which the number of warnings is reduced by applying biological threshold values. Where desirable, integrated warnings can be issued regionally.

SAMENVATTING

HOOFDSTUK I. Valse meeldauw in uien, veroorzaakt door de schimmel *Peronospora destructor*, brengt in sommige jaren aanzienlijke schade teweeg. Goede bestrijding is derhalve geboden.

Daar enerzijds die bestrijding alleen voorbehoedend kan gebeuren, d.w.z. voordat de besmetting van het gewas plaatsvindt, en anderzijds de verwekker duidelijk weersafhankelijk is, ligt de gedachte aan een besmetting voorspellend waarschuwingsstelsel voor de hand. De waarschuwing dient zoveel tijd aan de infektie vooraf te gaan, dat de boer tijdig, d.w.z. voor aankomst van de sporenvlucht, het gewas van een sporendodend spuitresidu kan hebben voorzien.

Berekend over het prijspeil van 1970 zou elk procent oogstderving het land bij benadering één milljoen gulden kosten en de boer *f* 150 per ha, zodat een waarschuwingsdienst aldra lonend zal zijn.

HOOFDSTUK II. Een overzicht wordt gegeven van wat er in de literatuur over de *kringloop* van de ziekteverwekker is te vinden. Voor zijn inductie en volvoering stelt elke fenologische fase haar eigen specifieke eisen aan het mikroklimaat. Aan al die eisen moet achtereenvolgens worden voldaan. Voor een overzicht zie 2.4.10.

HOOFDSTUK III. De voorafgaande studie laat enkele vragen onbeantwoord. Er is namelijk onvoldoende klaarheid omtrent de omstandigheden, die regelen

a. de rijping, d.i. het kiemkrachtig worden overdag, van het 's nachts gevormde sporenmateriaal;
b. het behoud ofwel verlies van de kiemkracht van de nog vastzittende conidiën;
c. idem, van de reeds afgestoten conidiën.

Uit laboratoriumonderzoek is gebleken dat a. en b. ten nauwste samenhangen met de *luchtvochtigheid:* rijping en daarna het behoud van kiemkracht vereisen een vrijwel met waterdamp verzadigde atmosfeer totdat de sporen zijn afgestoten.

Het behoud van de kiemkracht c. hangt dan niet langer af van de luchtvochtigheid maar wordt beïnvloed door de ultraviolette (zonne)straling.

Een voorlopig bioklimatologisch model werd opgesteld, dat in zijn voor proefveldgebruik geschikte eenvoudigste vorm als volgt werd samengevat:

1. voor sporevorming: om 0, 3 of 6 uur MET moet in het gewas een verzadigingsdeficit (vd) $\leqslant$ 0,4 mm (0,53 mbar) heersen;
2. voor rijping van het infectans (infectiemateriaal) en behoud van zijn kiemkracht: zonneschijnduur voormiddags < 3 uren;
3. voor kieming en besmetting: regen tussen 9 en 21 uur MET.

HOOFDSTUK IV. In veldproeven werden dagelijks biologische precisiewaarnemingen verricht naast weerkundige waarnemingen in gewas en hut; dit om het voorlopige model te toetsen. Naast de criteria vermeld in Hst. III werden vele alternatieve varianten getoetst. Langs statistische weg werd een keuze gemaakt. Van het voorlopige model werd slechts regel 2. vervangen door een strakker criterium. Het uiteindelijke bioklimatologische model, dat besmettingsdagen kenschetst, werd nu als volgt:

1. voor sporevorming: om 0, 3 of 6 uur MET in het gewas een vd $\leqslant 0{,}53$ mbar;
2. voor rijping en behoud van de kiemkracht van het infectans: zonneschijnduur < 5 uren, gemeten over de gehele dag;
3. voor kieming en potentiële besmetting: neerslag tussen 9 en 21 uur MET; voor belangrijke mate van besmetting: *2 zulke dagen* als hier beschreven.

Mede in verband met de sterke correlaties tussen biologische en fysische gegevens werd het opstellen van een *datumlijst* van belangrijke ($\geqslant$ 2 dagen) en minder gevaarlijke (1 dag) infektieperiodes verantwoord geacht.

HOOFDSTUK V. Over alle tijdvakken van onderzoek van 1960 t/m 1965 werden de weerkaarten bestudeerd. Nagegaan werd in hoeverre bepaalde synoptische situaties stelselmatig voorafgaan aan de besmettingstijdvakken vervat in de datumlijst. Dit leidde tot opmerkelijke resultaten.

Doorgaans werd een infektietijdvak voorafgegaan door een weertype waarbij met westelijke tot zuidwestelijke stroming in de bovenlucht betrekkelijk warme lucht over ons land stroomt (type 1: warmtefront trekt over met neerslag) of een daaruit voortvloeiend weertype waarbij de warmtefront-situatie door occlusie van de sektor subtropische lucht reeds boven de Atlantische Oceaan werd opgeheven. Er stroomt dan koudere maritieme polaire lucht over de lage landen, uiteraard steeds uit westelijke richting (type 2). Er kan dan een koufront of occlusie overtrekken (2a, rechtstreeks voortvloeiend uit 1), ofwel een zgn. trog (2b) of geen van beide (2c).

Bij deze gevallen ligt veelal westelijk of noordwestelijk van de Britse Eilanden een lagedrukgebied, dat als draaipunt van het betrokken frontenstesel fungeert. Soms echter ligt in de bovenlucht, – in het 5 km-vlak –, een laag waaromheen zich een cyclonale beweging voordoet. Aan het aardoppervlak daarbeneden is de lucht onstabiel met kansen op onweer en mist (type 4).

Vaak treedt de valse meeldauw niet of nauwelijks op, hoewel aan de klimatologische voorwaarden wordt voldaan. Dit komt o.a. door regionaal gebrek aan infectans. Daarover nu dient een waarschuwingsdienst te zijn ingelicht. *Geïntegreerde ziektebestrijding, gebaseerd op zowel weerkundige als biologische gegevens, is hier geboden.*

RÉSUMÉ

1er CHAPITRE. Pendant certaines années le (faux) mildiou des oignons, causé par le champignon *Peronospora destructor*, cause des considérables dégâts. Par conséquent il s'impose une lutte efficace.

Comme cette lutte ne peut se pratiquer d'une part que de façon préventive, c'est à dire avant la contagion des plantes, et que d'autre part l'agent dépend manifestement du temps, l'idée d'un système d'avertissements prédisant l'infection est évidente. Il faut que l'avertissement précède la contagion d'une telle période que l'agriculteur arrive à temps, c.à.d. avant l'arrivée de l'inoculum flottant, pour pourvoir les plantes d'un résidu de nébulisation pouvant tuer ce matériel sporal.

Partant du taux des prix en 1970 chaque pour cent de perte de récolte dépriverait le pays d'approximativement 1 million de florins et le fermier de *f* 150 l'ha, de sorte qu'un système d'avertissements se récompensera bientôt.

2e CHAPITRE. Des données sur l'*évolution cyclique* de l'agent empruntées de la littérature sont présentées sous forme d'un aperçu. Pour son induction et son accomplissement chaque stade phénologique pose au microclimat ses propres conditions spécifiques. Ces conditions doivent être satisfaites l'une après l'autre. Pour sommaire voir 2.4.10.

3e CHAPITRE. L étude précédante manque de répondre à quelques questions qui se soulèvent. Il existe encore une lacune dans les connaissances concernant les conditions réglant

a. la maturation, savoir l'acquisition, durant le jour, d'un pouvoir germinatif valable par le matériel sporal formé la nuit;
b. la conservation, ou bien la perte, de la vitalité du matériel conidial encore fixé;
c. de même pour les conidies déjà détachées.

D'expériences de laboratoire il s'ensuit que les règles a. et b. sont rigidement liées à l'*humidité atmosphérique:* la maturation ainsi qu'en suite la conservation, jusqu'au détachement des spores, du pouvoir germinatif exige une atmosphère à peu près saturée de vapeur d'eau.

Après le détachement la conservation de la vitalité c. ne dépend plus de l'humidité de l'air; elle est influencée par le rayonnement (solaire) ultraviolet.

Un modèle bioclimatologique tentatif fut établi. Sous sa forme la plus simple, adaptée à l'usage dans les champs d'expérimentation, il peut être récapitulé ainsi qu'il suit:

1. pour formation de spores: à 0, 3 ou 6 h (HEC) il faut qu'il prévale, dans le microclimat de la plantation, un déficit de saturation (ds) $\leqslant$ 0,4 mm (0,53 mbar);

2. pour maturation de l'inoculum et conservation de sa faculté germinative: < 3 h de clarté directe du soleil avant midi;
3. pour germination et pénétration: précipitations entre 9 en 12 h HEC.

4e CHAPITRE. Dans les expériences de champ des observations biologiques de précision et des observations météorologiques dans le microclimat ainsi que dans l'écran furent prises journellement. Ces travaux étaient destinés à la mise à l'épreuve du modèle provisoire. A côté des critères déployés dans le 3e Ch. de nombreuses variantes alternatives furent également éprouvées. Par rapport au modèle provisoire c'était seulement la règle 2. qui fut remplacée par un critère plus rigide.

Alors le modèle bioclimatologique définitif caractérisant les jours d'infection se constitua ainsi qu'il suit:

1. pour formation de spores: à 0, 3 ou 6 h (HEC), dans le microclimat entre les plantes: un ds $\leqslant 0{,}53$ mbar;
2. pour maturation et conservation de vitalité: clarté d'insolation directe $\leqslant 5$ heures pendant l'entière journée;
3. pour germination et infection potentielle: précipitations entre 9 et 21 h HEC; pour germination considérable: *2 jours* tels qu'esquissés ici.

En partie également en raison des fortes corrélations entre les données biologiques et physiques il fut jugé opportun d'établir un calendrier des périodes de contagion d'une plus ($\geqslant 2$ jours) ou moins (1 jour) grande importance.

5e CHAPITRE. Les cartes météorologiques du KNMI furent étudiées par rapport à toutes périodes de recherche de 1960–1965. Il fut recherché à quel point certaines situations synoptiques précèdent, de manière systematique, les périodes de contagion contenues dans le calendrier. Cette recherche conduisit à des résultats notables.

D'ordinaire, une période d'infection fut précedée d'un type de temps avec lequel dans les hautes couches atmosphériques un courant d'ouest à sud-ouest fait écouler à travers de notre pays de l'air relativement chaud (type 1: front chaud traverse avec précipitation) ou d'un type de temps s'en ensuivant, avec lequel, par l'occlusion du secteur d'air subtropical, la situation de front chaud était déjà terminée au-dessus de l'Atlantique. Les pays bas sont alors traversés par de l'air maritime polaire de température plus basse, par nature toujours d'une direction occidentale (type 2). Il se peut alors qu'il passe un front froid ou une occlusion (2a, résultat directement d'1), ou bien un ainsi-nommé creux barométrique (2b) ou aucun des deux (2c).

Il se trouve souvent, à l'ouest ou sud-ouest des îles britanniques, une région de basse pression qui fonctionne, pour le système frontal en question, comme centre de rotation. Parfois la basse pression se trouvant dans les hautes couches (au niveau de 5 km) se situe au centre d'un mouvement cyclonal. A la surface terrestre là-dessous l'air est instable; il y a des chances d'orage et de brouillard (type 4).

Bien des fois le mildiou ne se produit guère, quoique la situation satisfasse à toutes exigences bioclimatologiques du modéle, e.a. à cause d'une disette régionale d'inoculum. Or, il faut que le service d'avertissements en soit informé.

Il s'impose une *lutte intégrée* se basant sur les données météorologiques aussi bien que biologiques.

LITERATURE

1. ANON. Production Yearbook FAO 14 (1960), 507 pp., *1961.*

2. ANON. Trade Yearbook FAO 14 (1960); 315 pp., *1961.*

3. ANON. Guide to agricultural meteorological practices. WMO no. 134. TP. 61, *1963.*

4. BARY, A. DE: Recherches sur le développement de quelques champignons parasites. Ann. Sci. nat., Sér. IV, Bot., 20: 5-148, Paris, *1863.*

5 BERKELEY, M. J.: Notices of British fungi. Ann. & Mag. nat. Hist. 6: 430-439, Lon., *1841.*

6. BERRY, S. Z. & DAVIS, G. N.: Formation of oospores by Peronospora destructor and their possible relation to epiphytology. Pl. Disease Reporter 41 : 3-6, *1957.*

7. BOER, H. J. DE: De hoeveelheid ultraviolet licht in de globale straling te De Bilt. Kon. Ned. Met. Inst., Wet. Rapp. (59-6), 24 pp., De Bilt, *1959.*

8. BRUINSMA, F.: Warme bewaring van plantsjalotten, Med. Proefst. Gr.teelt Volle Grond (5), 39 pp., Alkmaar *1957.*

9. COOK, H. T.: Studies on the downy mildew of onions and the causal organism, Peronospora destructor. Cornell Univ. Agric. Expt. Sta. Memoir (143), 40 pp., *1932.*

10. DOORN, A. M. VAN: Onderzoekingen over het optreden en de bestrijding van valse meeldauw (Peronospora destructor) bij uien. Diss. Wag., 63 pp., *1959.*

11. DOORN, A. M. VAN & POST, J. J.: Het onderzoek aan valse meeldauw in uien in 1957. KNMI, Versl. (V-25), 12 pp., *1958.*

12. DOORN, A. M. VAN & POST, J. J.: Het onderzoek naar de samenhang tussen het weer en het optreden van valse meeldauw in uien in 1958. KNMI, Versl. (V-49), 15 pp., *1959.*

13. DOORN, A. M. VAN, KOERT, J. L. & VLIET, M. VAN DER: De bestrijding van valse meeldauw in uien en sjalotten. Med. Dir. Tuinb. 17 : 432-436, The Hague, *1954.*

14. DORAN, W. L.: Effect of external and internal factors on the germination of fungous spores. Bull. Torrey Bot. Club 49 (11) : 313-336, *1922.*

15. DUDLEY: The onion mold. Cornell Univ. Exp. Sta. Bull. (15) : 193-195, *1889.*

16. EUVERTE, G.: Les climats et l'agriculture. 2nd ed., Presses Univ. France, Paris, Sér. 'Que sais-je?' (128), 122 pp., *1967.*

17. HEALD, F. D.: Manual of plant diseases, 2nd ed., McGraw Hill, N. York/Lond., 953 pp., *1933.*

18. HILL, A. V.: Dissemination of conidia of Peronospora tabacina. Austral. J. biol. Scs. 4, (2) : 208-22, *1961.*

19. HILL, A. V.: Dissemination of conidia of Peronospora tabacina. CSIRO Div. Pl. Industry, Ann. Rep. 1960/1961, C'berra, *1961.*

20. HIRST, J. M.: An automatic volumetric spore trap, Ann. appl. Biol. 39: 257-265, Lond., *1952.*

21. HIURA, M.: Studies on some downy mildews of agricultural plants. IV: On the downy mildew of Welsh onion. Byohugai Zasshi, as reproduced in abstract by Rev. appl. Mycol. 10 : 7, *1931.*

22. JAMALAINEN, E. A.: On factors hampering onion production and on measures for promoting onion cultivation. (Engl. summary of article in Finnish). Rep. Finnish State Agric. Res. Board (225), 44 pp., *1952.*

23. JONES, L. R.: The onion mildew. Vermont Expt. Sta. Ann. Rep. (10), 1896/1897 : 61-62, *1897.*

24. JONES, H. A. & MANN, L. K.: Onions and their allies. Hill, Lond./N. York, 286 pp., *1963.*

25. KATTERFELD, N. O.: Zur Biologie der Peronospora Schleideni. (Russ. with German summary), Bolezni Rastenij 15, (2) : 71-87, *1926.*

26. LOWRY, W. P.: Weather and life. Acad. Press, N. York/Lond., 305 pp., *1969.*

27. MCKAY, R.: Observations on onion mildew, caused by the fungus Peronospora Schleideniana. J. Roy. Hort. Soc. (Lond.) 64 : 272-285, *1939.*

28. MCKAY, R.: The longevity of the oospores of onion downy mildew. Scientific Proc. Roy. Dublin Soc. 27, (N.S.), (12) : 295-307, *1957.*

29. MURPHY, P. A. & MCKAY, R.: The downy mildew of onions (Peronospora Schleideni) with particular reference to the hibernation of the parasite. Proc. Roy. Dublin Soc. 18 : 237-261, *1926.*

30. MURPHY, P. A. & MCKAY, R.: Further observations and experiments on the origin and control of onion mildews. Irish Free State Dept. Agr. J. 31 : 60-76, *1932.*

31. NEWHALL, A. G.: The spread of onion mildew by wind-borne conidia of Peronospora destructor. Phytopathol. 30 : 385-495, *1940.*

32. NUTTONSON, M. Y.: Wheat — climate relationships and the use of phenology in ascertaining the thermal and photothermal requirements of wheat. Am. Inst. Crop Ecol. 388 pp., *1955.*

33. NUTTONSON, M. Y.: Rice culture and rice-climate relationships with special reference to the U.S. rice areas and their latitudinal and thermal analogues in other countries. Am. Inst. Crop Ecol., 555 pp., *1965.*

34. PEARSON, K.: On the probable error of a coefficient of correlation as found from a fourfold table. Biometrika (Cambr.) 9, 22-28, *1913.*

35. PINCKARD, J. A.: The mechanism of spore dispersal in Peronospora tabacina and certain other downy mildew fungi. Phytopathology 32 : 505-511, *1942.*

36. SHIPLEY, A.: Onion disease at Bermuda. Roy. Kew Gardens, Miscell. Inform. Bull. (19) : 1-23, Lond., *1887*.

37. TRELEASE, W.: The onion mold. Wisconsin. Exp. Sta., 1st Ann. Rep. 38:44, *1884*.

38. VASSY, ARLETTE.: Radiosonde spéciale pour la mesure de la répartition verticale de l'ozone atmosphérique. J. sci. Météorol. 10 : 63-75, *1958*.

39. WAGGONER, P. E. & HORSFALL, J. G.: Epidem, a simluator of plant disease written for a computer, Conn. Agric. Expt. Sta. Bull. (698), 80 pp., N. Haven, *1969*.

40. WEILLE, G. A. DE: De fungicide werking van licht van verschillende golflengten t.a.v. blister blight. Bergcult. 26 : 149-157, *1957*.

41. WEILLE, G. A. DE: Blister blight control in its connexion with climatic and weather conditions. Diss. Bogor, *1957*, and Comm. Res. Inst. Sumatra Planters' Ass. (Medan) Gen. Ser. (70), 116 pp., *1960*, and Arch. Tea Cultiv. (Bogor) 20, (1) : 1-116, *1960*.

42. WEILLE, G. A. DE: Blister blight (Exobasidium vexans) in tea and its relationship with environmental conditions. Neth. J. agric. Sc. 8 : 183-210, *1969*.

43. WEILLE, G. A. DE: L'influence de la radiation ultra-violette proche sur le pouvoir germinatif des conidies de Peronospora arborescens. T. Pl.ziekt. (= Neth. J. Plant Pathol.) 67 : 417-432, *1961*.

44. WEILLE, G. A. DE: Some remarks regarding biological observations in behalf of agrometeorological investigations concerning the epidemiology of plant diseases and pests. Arch. Klimatol. Geofys. Biometeor. (Vienna) B-13 : 114-136, *1963*.

45. 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.ziekt. (= Neth. J. Pl. Pathol.) 69 : 115-131, *1963*.

46. WEILLE, G. A. DE: Some notes on the use of hygrograms for phytopathological purposes with special reference to their reliability. Neth. J. agric. Sc. 12 : 229-234, *1964*.

47. WEILLE, G. A. DE: Forecasting crop infection by the potato blight fungus. KNMI, Med. Verhand. (82), 144 pp., *1964*.

48. WEILLE, G. A. DE: The epidemiology of plant disease as considered within the scope of agrometeorology. Agric. Met. (A'dam) 2 : 1-15, *1965*.

49. WEILLE, G. A. DE: A procedure for evolving predictive plant disease warning schemes as applied to the case of potato blight. Proceed. WMO Reg. Train. Seminar Agrometeorol., Wageningen, 1968 : 69-79. Wag. Agr. Univ. Press, *1969*.

50. WEILLE, G. A. DE: Un modèle climatologigue caractérisant les jours auxquels les plantations d'oignons sont infectées par les conidies du mildiou. Cah. Assoc. Franç. Biométéorol. 3 : 22-30, Paris, *1971*.

51. WHETZEL, H. H.: Onion blight. Cornell Univ. Agr. Exp. Sta. Coll. Agric. Bull (218) : 138-161, *1904*.

52. YARWOOD, C. E.: The relations of light to the diurnal cycle of sporulation of certain downy mildews. J. Agric. Research 54 : 365-373, Washington, *1937.*

53. YARWOOD, C. E.: Relation of moisture to infection with some downy mildews and rusts. Phytopathol. 29 : 933-945, *1939.*

54. YARWOOD, C. E.: Onion downy mildew. Hilgardia 14 : 595-691, *1943.*

RECOMMENDED TEXTBOOKS

(cf. p. 62)

Books containing an introductory description of extra-tropical large-scale frontal weather systems:

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60. C. Kramer, J. J. Post en J. P. M. Woudenberg. Nauwkeurigheid en betrouwbaarheid van temperatuur- en vochtigheidsbepalingen in buitenlucht met behulp van kwikthermometers, 1954. (60 blz. met 11 fig.)	3,60
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