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Professor Dr A. J. P. Oort, his research work and scientific interests

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Arend Joan Petrus Oort was born in 1903 at Oegstgeest (near Leyden) where his father practised medicine. After his final examination at the Leyden grammar school (gymnasium) he received his training in biology at the University of Utrecht. As a young student he paid a visit to his parents, who then (1924–1925) resided at Bogor (Buitenzorg), Indonesia, where he worked at the famous Visitor's Laboratory ("Treub-Laboratorium") of the Botanic Gardens, on the formation and disappearance of amylum in leaves in connection with evaporation. His stay gave him also the opportunity to study some tropical diseases caused by *Gloeosporium* species in the Institute for Plant Diseases, under the guidance of Miss Dr M. B. Schwarz. Back in The Netherlands Oort published a list of about 60 species of the genus *Mycena* comprising four new ones occurring in The Netherlands (1928). The taxonomy was based on macroscopical as well as on microscopical characters. As a student his interest in mycology and phytopathology was already outstanding, but his critical remarks on the Surinam species of the genus *Securidaca* (Polygalaceae) published later (1939c), and the part he took in the description of the Polygalaceae in Pulle's Flora of Surinam (1939d), showed that he was also an able worker in other fields of botany. In 1928 he obtained his Master's degree with the highest qualification (cum laude).

After a preliminary report (1929) Oort's doctoral thesis on the sexuality of *Coprinus fimetarius* appeared in 1930. If a great number of *Coprinus* spores were sown on sterilized horse dung a primary haploid multinuclear mycelium developed that within a week changed into a secondary mycelium with clamps and two nuclei per cell. In the young basidia that developed, karyogamy occurred followed by meiosis and the formation of haploid spores. In monospore cultures the mycelia remained haploid; in cultures originating from two spores the dikaryotic phase might develop. By pairing each strain of the 24 that were isolated, with all others respectively, it turned out that four sex groups could be distinguished. Spores and haploid mycelium contained the factors AB, Ab, aB or ab; dikaryotic mycelium was heterozygous for two factors. Copulation could only result in clamp connections and fruiting bodies when the components had no factor in common and the diploid had the factors AaBb. Sometimes slow-growing haploid fruiting bodies developed with a reduced number of spores.

As early as 1929 Oort went to Wageningen as assistant to Professor Dr A. H. Blaauw, Head of the Laboratory of Plant Physiological Research of the Wageningen Agricultural University. Most of the work in this laboratory was concerned with the influence of light on processes of growth and development. It is therefore not surprising that Oort combined his interest in mycology with this subject. Globular sporangia of

Phycomyces blakesleeanus showed a small one-sided excrescence. When observed, it seemed to grow gradually larger, then decreased in size and became invisible. After some time it reappeared at the other side of the sporangium. It became clear that a small zone of the sporangiophore just below the sporangium was the site where rotation and lengthwise growth occurred simultaneously after exposure to light (1931). This spiral growth appeared to be correlated with the direction of protoplasmatic streams which declined from the vertical and with the spiral structure of layers of the birefringent cell wall of the sporangiophore (Oort and Roelofsen, 1932). Several years later the use of an electron microscope would have facilitated this type of research which was carried out with the light microscope.

Still another publication on the influence of light on the growth reactions of these sporangiophores appeared (1932), before Oort was appointed as assistant to Professor Dr H. M. Quanjer, Head of the Laboratory for Mycology and Potato Research (the present Laboratory for Phytopathology), Agricultural University, Wageningen. In 1949 he succeeded Quanjer in the chair of plant pathology and head of the laboratory.

It is no simple task to summarize in a few pages the results of all investigations Oort has carried out in the 35 years he was an active plant pathologist. He published more than 60 papers, some together with members of his staff. We therefore had to make a choice.

For many years Oort's main interest was the study of fungus diseases of cereals. He gave a clear description of various footrot diseases of cereals (1933) and was the first to use the name "oogvlekkenziekte" (eyespot) for a footrot caused by *Cercosporella herpotrichoides* (1936b). Before his publication this disease had frequently been confused with take-all (*Ophiobolus graminis*) but Oort's careful studies made it clear that eyespot is a distinct disease of cereals, inducing lodging and thus causing considerable damage and losses in yield, especially on heavier soils. However, Oort also studied take-all, and much later (1965) he gave a communication on its occurrence in newly reclaimed polders where *Ophiobolus* appears to be a "pioneer parasite", damaging wheat, particularly in the 2nd, sometimes also the 3rd year of continuous wheat growing. Thereafter the disease is not important because natural antagonists are then well established in the soil.

His main interest in the years before the war concerned, however, the loose smuts, *Ustilago tritici* of wheat and *U. nuda* of barley. First he tried to improve the hot-water treatment in use for the control of seed infection (1934). Temperature and time of treatment were varied in order to obtain disinfection without impairing viability. Later (1936a) he came to the conclusion that a broad safety zone is needed in order to keep the "dosis curativa" below the "dosis tolerata", since the physiological condition of the seed is not the same in different years. He closely cooperated with the General Netherlands Inspection Service for Seeds of Field Crops and for Seed Potatoes (NAK) concerning the regulations for field inspection of sowing seed, as another important means of reducing the loose smut infection rate of wheat seeds. The number of fields that had to be rejected after inspection was extremely high when varieties which were susceptible to loose smut were grown. It was questionable whether removal of smutted heads before flowering would be helpful in reducing seed infection. Another problem concerned the spread of spores from contaminated heads to neighbouring fields. To solve this last question an experiment was carried out by growing wheat from carefully disinfected seed (1940a). In the centre of the field a small plot of 100 m^2, grown from heavily infected seed of the same variety, produced 1350 smutted heads. Seed samples were harvested all over the field in eight directions from the infected centre and sown the following year. In all directions dissemination of loose smut had occurred, sometimes up to 90 m from the infection source. Since none of the control measures seemed to be adequate, the final solution of the problem was expected from the breeding of resistant varieties.

In 1938 Oort published a general article on the breeding of disease-resistant varieties, a subject then still greatly neglected in The Netherlands (1938b). Admittedly, breeders could send in their new potato varieties to have them tested on resistance to wart disease and virus diseases, but breeders did not select on their own fields. In his publication Oort not only stressed the point that the breeding of resistant varieties ought to be stimulated and organized by the government, he also gave as his opinion that breeding of resistant varieties by individual breeders must be carried out in close cooperation between the institutions of the government and the individual plant breeder. In later years this procedure was adopted and it proved to be most successful (1942).

Testing of hybrids for resistance was, however, no simple task. Stakman had discovered the existence of physiological races of barley and wheat loose smut fungi. In their life cycle a meiosis followed by a recombination of nuclei may give rise to an endless number of variations, among others in pathogenicity. A resistant wheat or barley variety might select physiological races that are more virulent than the original ones applied to them. For screening hybrids on resistance an inoculation method had to be developed (1939a).

An apparatus originally designed by M. B. Moore but modified, consisted of an inoculation chamber in which a number of culms were inserted just below the heads. By a hand-operated vacuum pump a spore suspension was drawn up into the inoculation chamber until the fluid had risen above the heads and had replaced the air between the glumes. Heads inoculated in that way produced for the greater part smutted kernels if the variety was susceptible. Valuable data were published on the susceptibility of a large number of wheat and barley varieties (1940b, 1947d, 1950a and c).

Though this apparatus appeared to be useful for screening hybrids, differences in degree of susceptibility were obscured especially in the case of barley by the high number of infected heads (1950c). Therefore also other experiments were carried out in the field. Hybrids or varieties to be tested were grown in the neighbourhood of susceptible and heavily contaminated plants. It appeared that neither wheat nor barley could be cross-infected with loose smut. The existence of physiologic specialisation was established. Six races could be distinguished on nine groups of wheat varieties.

First susceptibility was only expressed as the percentage of smutted plants. Later it appeared that wheat seedlings grown from infected seed might die off or become dwarfed without producing a smutted ear. Such hypersensitive plants remained unobserved in the fields and the variety showed "field resistance". On the other hand susceptible plants might not show disease symptoms before the flowering stage (1944, 1947d). In a paper read at the 7th International Botanical Congress at Stockholm (1950a) Oort discussed these reactions from a purely scientific point of view: in each plant two principles might work together. On the one hand the plant may be susceptible to a higher or lesser degree but it is congenial to the parasite and the seedlings are normal in appearance. The second principle, superimposed on the first, determined whether either normal-looking seedlings will develop or seedlings with abnormal symptoms often leading to their death. This reaction first described as hypersensitivity, was later indicated as incompatibility. In a more recent publication he reviewed the earlier observations in the light of Flor's gene-for-gene relationship. Probably two sets of factors for resistance and two sets for incompatibility in the host correspond to four sets of complementary factors for virulence in the pathogen. In this way the interactions of eight variety groups of the host with six physiological races of the pathogen could be explained (1963a). Soon, however, the expectation of controlling plant diseases fully by breeding resistant varieties appeared to be too optimistic. In 1945 it was discovered that the wheat variety 'Staring', which was considered to be resistant to all races known in The Netherlands, became spontaneously attacked by a new smut race to which it was fully susceptible.

The line of Oort's studies on rusts is analogous to those on the smut diseases. Although black rust is well-known in The Netherlands it seldom causes losses of any importance. In 1940, however, due to exceptional weather conditions, black rust was serious on rye (1941) but as a rule yellow rust, especially on wheat and barley is a far greater problem. For his studies of this rust a cooled greenhouse was already built before the last war. A very interesting survey on distribution and interrelationship of physiological races of yellow rust of wheat (*P. striiformis* = *P. glumarum*) in Europe was published (1955b). As early as 1949 he had given a short communication on this subject at an international congress (1949b). He came to the conclusion that the geographical distribution of races is largely connected with the distribution of special wheat varieties, and also with climatic conditions. Groups of interrelated races occur. Oort assumed that races of one group originated from a parent race by mutation. Races belonging to one interrelated group appeared to have the same geographical distribution. In breeding for resistance a small number of representative races of the parasite might suffice but Oort ends his paper as follows: "However, it will be impossible to prevent loss of resistance as a consequence of the occurrence of new races originating by mutation". We now know that *P. striiformis* very rapidly develops new physiological races which may attack resistant varieties. Again the hope of breeding resistant varieties proved unduly optimistic. Questions related to this subject permanently had Oort's attention and he frequently refers to it in his publications. In his inaugural speech as professor (1949c) he explained that breeding for resistance could only come into full development after the base for modern genetics had been laid, and after reliable infection methods were available. He stressed the importance of studying the physiological differentiation of the parasite which necessitates coordination of the work of plant breeder and plant pathologist. He then suggested the establishment of an organisation forming a link between breeder and plant pathologist. Some years later an Advisory Committee for plant disease resistance and a department for disease resistance of the Institute of Phytopathological Research came into being. Recently the task of this Advisory Committee, in which plant breeders and plant pathologists participate, has been broadened to all problems related to breeding for resistance.

Between these elaborate studies minor problems interested him, including the relation between the presence of allylthiocyanate in black mustard and its resistance to clubroot (1945b); fungi that trap nematodes (1949a) and mycorrhiza in tree roots (1951a). Reviews appeared such as that on diseases of barley (1939b), a survey of diseases of grasses and cereals (1951b) and a note on disease problems in the tropics (1959a).

A problem that fascinated him for many years concerned the demand for sclerotia of *Claviceps purpurea*, the ergot of rye, for their alkaloid content. In Western Europe culture methods of rye had improved to such an extent that ergot could hardly be found. Therefore it would probably be worthwhile to cultivate sclerotia in large quantities. First, knowledge was obtained of the physiological specialisation of the fungus (Mastenbroek and Oort, 1941). Rye plants appeared to be susceptible to all races found on grasses. A description of inoculation experiments followed later (1952a). An apparatus was constructed bearing needles which were alternatively dipped into a spore suspension and pricked into rye heads while the machinery was wheeled along the rows in the field.

Though the results of the first experiments were satisfactory, many questions had still to be solved before the method could be applied in practice.

Another topic was the die-back of blackberries caused by the fungus *Septocyta ramealis*. Spores, developed in pycnidia occurring in stem lesions, could be trapped from April until the end of August. During summer no new infections were observed on the young vegetative sprouts but lesions appeared on them after a cold treatment. Hygienic measures and spraying were recommended (1952b).

A short note on a heavy attack of wheat by *Septoria nodorum* drew attention to this disease that seemed to reduce yield. Pycnidia were found in flecks on leaves and in discoloured glumes (Oort and Saaltink, 1949).

Another serious problem was the *Gloeosporium* fruit-rot occurring during cold-storage (1956a, b and c). *G. perennans* and *G. album* were the main fungi isolated from the fruits, which appeared to have been infected in the orchard. Canker-formation and die-back of branches were also found. This was in agreement with Oort's opinion, expressed in 1925, that *Gloeosporium* spp. causing fruit-rot probably originate from stem canker and die-back. Notwithstanding successful inoculation experiments, and the keeping of fruits covered with polythene bags for certain periods on trees, the erratic occurrence of the rot after storage could not fully be explained.

Another noxious disease that permanently drew Oort's attention was potato blight, caused by *Phytophthora infestans*. Shortly after planting a young crop seemed healthy until rather suddenly the disease made its appearance. In The Netherlands the origin of the infection was still an open question: oospores might overwinter in the soil or mycelia might remain alive in weeds, but no facts were available as proof. Diseased tubers when planted did not develop sprouts or they produced healthy ones. By the careful observations of van der Zaag it became clear that the first symptoms of the disease appeared in cull-piles, where infected tubers which had developed short, thin, infected sprouts were found. From them, sporangia spread to healthy sprouts and leaves which readily became infected in a moist atmosphere. Moreover, slightly diseased tubers which had escaped inspection and which were planted in the field could act as such a primary infection source (1953b, 1953c and 1960).

In a number of lectures (1949c, 1955a, 1964 and 1966) Oort stated his views on various aspects of phytopathology which should be studied in future. In his inaugural speech in 1949 he emphasized next to the importance of breeding for resistance, the study of epiphytotics and that of the complicated problems concerning soil pathogens (1949c). He also laid stress on the possibility of making use of antagonists or antibiotics in controlling diseases. The possibility of control by internal therapy was also mentioned. Under Oort's supervision all these aspects were gradually studied in his laboratory.

He was in the chair during the preliminary discussions leading to the final establishment of the new TNO Coordination Committee for the prevention and control of soil-borne diseases and pests.

He also became chairman of a "Research Unit for Internal Therapy of Plants" founded in 1950 in which the Laboratory of Phytopathology of the Agricultural University at Wageningen and the Institute for Organic Chemistry of the University of Utrecht participated. As a result, for many years phytopathologists and biochemists have been able to cooperate under the supervision of the leaders of these laboratories, Dr A. J. P. Oort and Dr G. J. M. van der Kerk, respectively. Funds were provided by the Organization for applied scientific Research in The Netherlands (TNO) and in the beginning also by the Netherlands Organization for the Advancement of Pure Research (ZWO). The aim of the Research Unit was to develop compounds with systemic chemotherapeutic activity, so-called "systemics", which would protect a host plant before it was invaded by a pathogen, or which would have a curative effect (Oort and van Andel, 1960a and b). In this review only that part of the research will be mentioned, which was carried out in Oort's laboratory at Wageningen; for a general review of the activities of the Research Unit for Internal Therapy of Plants the reader is referred to the contribution of Professor Dr G. J. M. van der Kerk in this issue.

Research was for the greater part carried out with derivatives of carbamic acid, which were prepared at the Institute for Organic Chemistry at Utrecht. A "systemic" had to fulfil the following conditions: it had to be transported in the plant, it should exert fungicidal action or it had to increase the resistance of the plant, and it should not be phytotoxic. Fungicidal action in vitro was not essential. For testing a host-parasite combination was chosen. Nearly all experiments were carried out with cucumber seedlings and *Cladosporium cucumerinum*, the cause of "cucumber scab".

Van Raalte observed that tetramethylthiurammonosulfide (TMTM) was translocated through the parenchyma of a potato petiole. A derivative, S-carboxymethyl-N, N-dimethyldithiocarbamate was active against *C. cucumerinum* in low non-toxic concentrations. It showed, however, activity as a growth hormone. The action of a related compound, sodiumdimethyldithiocarbamate, NaDDC, was studied in cucumber seedlings by Dekhuyzen. The plant converted this compound into several other fungicides among which was L-DDC-alanine.

Another line of research was followed when it appeared that amino acids which are not active against fungi in vitro, affected cucumber seedlings that were inoculated with *C. cucumerinum*. It were mainly the unnaturel D-form or the DL-mixture, which decreased symptom-expression and which were phytotoxic at high concentrations. There were no indications that these amino acids were transformed into fungicidal compounds in the host plant and it was assumed that they influenced the metabolism of the plant, rendering it more resistant (Oort and van Andel, 1960a and b.) Internal seed disinfection was carried out by Dekker (Oort and Dekker, 1955 and 1960). Pea seeds internally infected with *Ascochyta pisi* were soaked in culture filtrates of *Streptomyces rimosus* containing the antibiotic rimocidine or in pimaricine originating from *S. natalensis*. The active principle penetrated into the cotyledons and the plumule. Only in a low percentage of infected seeds was the fungus still present after treatment. Rimocidine also proved to be effective against *Colletotrichum lindemuthianum* in French beans and against *Phoma betae* in beet seeds.

Dekker also investigated the systemic action of 6-azauracil and related compounds against *Sphaerotheca fuliginea*, the powdery mildew of cucumber (Oort and Dekker, 1963; Dekker and Oort, 1964; Oort and Dekker, 1964). These chemicals were applied to the roots of seedlings or to leaf discs infected with mildew conidia and floating on nutrient solutions containing the chemical to be tested. As soon as a haustorium had entered an epidermal cell its growth was inhibited. The effect of 6-azauracil was reversed by uracil or precursors such as orotic acid. The compounds active against mildew probably act on living cells in a phase of rapid growth, as in the case of penetrating hyphae, which are more strongly inhibited than the cells of the host plant. Practical application seemed promising.

These studies lead not only to a better insight into the character of resistance but they also improved understanding of the physiology of the healthy plant. In a lecture given in 1966 Oort mentioned in this context another aspect of modern fundamental research that should be carried out in the future. It concerned the phytoalexins, substances produced by plants when attacked by non-parasitic microorganisms to which they are resistant. A defence mechanism is naturally built up. In the framework of the Unit for Internal Therapy, research on these fungitoxic and probably more or less specific substances, started in 1965.

Oort's keen interest in recent developments in research on the biochemical background of pathogenesis is demonstrated by his initiative in organizing the symposium on "Physiological and biochemical aspects of host-pathogen interactions" on the occasion of the opening of the new excellently equipped Laboratory of Plant Pathology of the Agricultural University at Wageningen in 1967. This laboratory may be seen as the crowning achievement of a professional life devoted to the service of plant pathology.

In addition to his research and teaching we should also mention the active role he played in both the Netherlands Mycological Society and the Netherlands Phytopathological Society. His keen intellect, scientific knowledge and critical mind were of great importance for his students and also for his colleagues when he wrote his much appreciated reviews of new books and articles. The same qualities gave him authority in numerous meetings of Councils and Committees, in which he always was an amiable and appreciated member, frequently acting as chairman.

For his scientific achievements Oort was rewarded with a Membership of the Royal Netherlands Academy of Sciences (1958) and an Honorary Doctorate of the State Faculty of Agricultural Sciences at Ghent, Belgium (1963).

Samenvatting

Prof. Dr. A. J. P. Oort, zijn onderzoek en wetenschappelijke belangstelling

Arend Joan Petrus Oort werd in 1903 te Oegstgeest geboren. Hij studeerde biologie te Utrecht en slaagde in 1928 cum laude voor zijn doctoraal examen. Twee jaar later promoveerde hij op een proefschrift over de geslachtelijke voortplanting van *Coprinus fimetarius*. In 1929 kwam hij naar Wageningen, waar hij eerst assistent was van Prof. Blaauw op het Laboratorium voor Plantenfysiologisch Onderzoek, en vervolgens van Prof. Quanjer op het Laboratorium voor Mycologie en Aardappelonderzoek. Hier deed hij baanbrekend werk op het gebied van de schimmelziekten bij granen, voornamelijk stuifbrand. In 1949 volgde hij Quanjer op als hoogleraar. Oort nam het initiatief tot de oprichting van de "Werkgroep Interne Therapie bij Planten", waarvan hij de

voorzitter werd. In nauwe samenwerking met het Organisch Chemisch Instituut TNO te Utrecht wordt in deze werkgroep belangwekkend onderzoek verricht over systemische fungiciden en over de fysiologisch-biochemische achtergrond van planteziekten. Diverse andere onderwerpen hadden zijn belangstelling, waaronder de epidemiologie van door schimmels veroorzaakte ziekten, de fysiologische specialisatie van pathogenen en de kweek van sclerotia van *Claviceps purpurea*, de veroorzaker van moederkoren. In samenwerking met studenten bracht hij het probleem van de overwintering van *Phytophthora infestans* tot een oplossing en bestudeerde hij het *Gloeosporium* vruchtrot bij appels, de taksterfte bij bramen en vele andere schimmelziekten. Hij had de leiding bij de voorbereidende besprekingen tot de oprichting van een TNO coördinatiecommissie "Bestrijding van ziekten en plagen in de bodem".
Zijn scherpe intelligentie, zijn grote wetenschappelijke kennis en zijn kritische instelling waren niet alleen van grote betekenis voor zijn studenten en medewerkers, maar gaven hem ook grote invloed in de vergaderingen van talrijke comité's, werkgroepen, besturen, e.d. Hij was een actief lid van de Nederlandse Mycologische Vereniging en de Nederlandse Planteziektenkundige Vereniging, waarin hij bestuursfuncties bekleedde, en hij gaf gedurende vele jaren zijn krachten aan het Tijdschrift over Planteziekten, eerst als lid daarna als voorzitter van de redactie.
Zijn grote wetenschappelijke verdiensten vonden erkenning in zijn benoeming tot lid van de Koninklijke Nederlandse Akademie van Wetenschappen (1958) en in de toekenning van een eredoctoraat aan de Rijkslandbouwhogeschool te Gent in België (1963).

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