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YIELD LOSS DUE TO CEREAL APHIDS AND POWDERY MILDEW IN WINTER WHEAT

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SUMMARY

Wheat cultivation has changed considerably during the last decades, and as a result pests and diseases have gained importance. Powdery mildew and cereal aphids are becoming major yield-depressing factors, due to the effect of intensive wheat cultivation on their population growth, and their considerable influence on yield loss. It is shown that yield loss due to cereal aphids depends on production level and that a shift in the different components of yield loss occurs at high yield levels. Direct assimilate consumption is of minor importance at high yield levels. Indirect effects due to honeydew are decrease of photosynthesis (both light use efficiency and maximum photosynthesis) and stimulation of leaf senescence. These effects increase in importance at higher yield levels.
Powdery mildew has a considerable influence only on maximum photosynthesis. This effect is more than proportional to infestation level and is due probably to an effect on carboxylation resistance. It is pronounced in young leaves and decreases with leaf age.

Introduction

Cereal yields in Western Europe have increased considerably during recent decades. Some thirty years ago yields were, on average, 3000-4000 kg of grain ha^{-1}. Nowadays yield levels of 7000-8000 kg of grain ha^{-1} are frequently average yields in the Netherlands reaching 6500 ('79), 6900 ('80), 7400 ('81) and 7400 kg ha^{-1} ('82). The major reasons for this increase in yield levels were, during the early fifties, the considerable advances in agronomic practices such as water management, soil improvement and, later, the better use of nitrogen fertilizers and new cultivars. In the sixties and seventies growth regulators, together with an increased use and better timing of nitrogen fertilizers, pest and disease control became widespread in modern wheat cultivation, so formerly inconceivable yields of 10.000-12.000 kg ha^{-1} are becoming common for some farmers in the Netherlands. New compounds for chemical control, and an increased knowledge of the epidemiology of pests and diseases, have significantly contributed to the increase in winter wheat yields in most countries in Western Europe. The combination of efficient nitrogen use and control of pests and diseases has enabled farmers to exploit fully the modern high yielding winter wheat varieties. This is illustrated by reference to the increasing yield levels over the period 1950-1982, Fig. 1. In the late sixties and early seventies the increase in average yield levels (de Vos & Sinke, 1980; de Wit, 1968; Spiertz, 1979) started with the introduction of better pest and disease control. The importance of pests and diseases at high yield levels may stem from their epidemiology and the nature of the damage. In this paper these

Figure 1

Productivity of winter wheat in the Netherlands

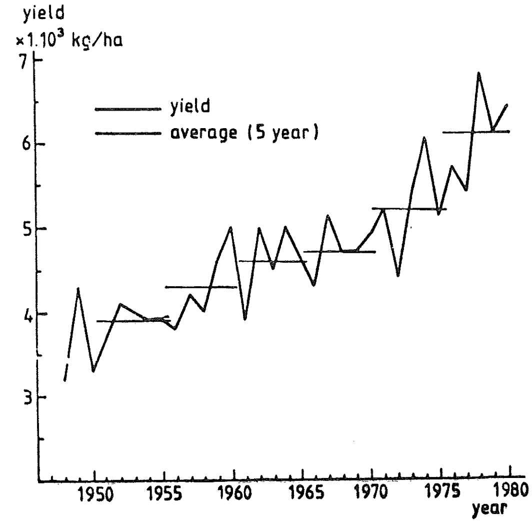

Figure 1. Productivity of winter wheat in the Netherlands during the last decades.

factors are discussed and illustrated for a pest and a disease which are typical for high yield levels: cereal aphids and powdery mildew.

Shifts in importance of pests and diseases

Diseases and pests have been common in winter wheat since it became a domestic crop. The presence of wheat diseases is discussed in the Bible and it seems that wheat cultivation frequently suffered from diseases and pests. Praying and preventive measures were for ages the only defence. Resistance breeding has become common practice only this century; this has led to wheat varieties with reasonable resistance against diseases. However, resistance is very often overcome, so the breeding and introduction of new cultivars has become a continuous process during the last decades. In the Netherlands winter wheat suffers most from yellow rust (*Puccinia striiformis*), brown rust (*Puccinia recondita*), powdery mildew (*Erysiphe graminis*), *Fusarium* spp., *Septoria* spp. and cereal aphids (*Sitobion avenae*, *Metopolophium dirhodum*, *Rhopalosiphum padi*). Until some decades ago preventive measures, resistance breeding and sanitary measures were the only effective controls. Chemical control measures were introduced into wheat cultivation in the late sixties and, since 1970, there has been a tremendous increase in pesticide usage in winter wheat in the Netherlands (Zadoks, 1980). Stripe rust and leaf rust were thought to be the most important diseases in the past, as they often appeared as heavy epidemics. Nevertheless, most control measures during the late seventies and early eighties were directed at powdery mildew, glume blotch (foot rot diseases) and cereal aphids (Daamen, 1981). Apparently, while breeders have been able to produce varieties with adequate resistance against rust, many of the modern varieties lack a sufficient resistance against powdery mildew and leaf blotch, in spite of breeding efforts over the past twenty years or so. Resistance against cereal aphids is poorly studied, partly due to the apparent lack of genetic variation but perhaps also because cereal aphid damage has been recognized as a serious problem only during the past ten years.

Yield determining and yield reducing factors

Potential yield in winter wheat is determined by crop physiological characteristics and incoming radiation. For different locations potential yield is computed using simplified crop growth models (Sibma, 1977; de Wit, 1965). It appears that there are differences in total amount of dry matter attainable at different sites. In the sixties predicted potential yields varied between 10.000 kg ha^{-1} to 14.000 kg of kernels ha^{-1}, depending on site and harvest index. It took some time for actual yields to reach the potential yield, but now more and more farmers are becoming able to produce more than 8000 kg of winter wheat ha^{-1}. Plant breeding led to the introduction of very lodging-resistant, highly nitrogen-responsive varieties with an excellent harvest index (.50-.55). Agronomy practices here improved, with appropriate soil treatment, sowing bed preparation, nitrogen fertilization and use of growth regulators all leading to a form of wheat cultivation that produces very high yields (de Vos & Sinke, 1980). This combination of agronomic measures determines the attainable yield level. When water is abundantly available and weather conditions are moderate, yield variation is large only if yield-reducing factors are active and important. It has become clear during the last decades that pests and diseases are the major yield- reducing factors, and a trend towards preventive overspraying started in the early eighties in parts of Western Europe. However, in fields with low yield expectation due to inappropriate agronomic measures, spraying activity should be limited. A poor crop can't become a rich crop by increasing spraying activity. A pesticide will not increase kernel number or number of tillers but can only protect a crop against pests and diseases. EPIPRE (Rabbinge and Rijsdijk, 1983) is based on the assumption that spraying should be executed only when it is financially attractive.

Epidemiology of cereal aphids and powdery mildew

Population growth of cereal aphids has been studied in several countries of Western Europe, because of the considerable increase in the importance of cereal aphids as yield-reducing factors (Carter et al., 1980). Several simulation models of cereal aphid populations have been developed and evaluated (Carter et al., 1982; Rabbinge et al., 1979), and have been used to explain the population upsurge and collapse. The major reasons for rapid increase lie with the condition of the crop: high nitrogen availability (nitrogen levels of more than 2.5% of dry mass) stimulates reproduction and reduces development time and mortality (Vereijken, 1979). The collapse of the population is due mainly to the shift in condition of the crop at the late milky ripe stage. Emigrants, winged aphids, appear and leave the fields. The resulting population decrease is amplified by natural enemies, parasites, predators and fungal pathogens (Rabbinge et al., 1979). Detailed sensitivity analyses of simulation models of cereal aphids (mainly S. avenae), have shown the importance of different external factors on population development (Carter et al., 1982). Crop development and the initial number of aphids (at flowering) are the major factors determining rate of population growth and time of collapse (Fig. 2). Thus, predictive models and methods have been developed based on visual observations or sampling of the aphid density at flowering. These models appear reliable in predicting the population peak in crop development stage Decimal Code 77 (Rabbinge & Rijsdijk, 1983). Although all detailed model studies and experimental work concerns S. avenae, the great correspondance between the cereal aphid species, as far as population growth is concerned, is such that the same predictive rules can be used for all cereal aphids (Ankersmit & Carter, 1981).
The epidemiology of powdery mildew has not been studied in as much detail as that of cereal aphids. Nevertheless, information is available on the increase of the fungal epidemic in relation to crop condition. It appears that when nitrogen in the leaves increases, the latent period of the fungus decreases,

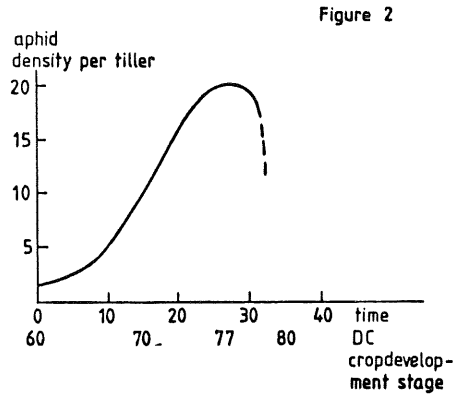

Figure 2. Standardized curve of population upsurge and collapse of cereal aphids.

and the infectious period, and spore production per infectious lesion, increase (Last, 1962). Thus the epidemic has a more rapid development in nitrogen rich crops than in crops which are poor in nitrogen (< 2%) (Rabbinge et al., in prep.). In modern wheat culture nitrogen levels in the crops are so high that conditions are favourable for a rapid population growth of the fungus.

Yield decrease due to cereal aphids

Yield decrease due to cereal aphids depends on number and residence time of cereal aphids on the crop (Rautapää, 1966). Analyses of a long series of experimental data have shown that both aphid index (the integrated number of cereal aphids in time) and peak density (the number of aphids per tiller at crop development stage 77) have a high correlation with yield loss (Rabbinge & Mantel, 1981). Detailed analysis has shown the different components of yield loss. Primary suction damage, due to assimilate consumption, and secondary damage due to honeydew covering the leaves, can be quantified. It has been demonstrated experimentally, with a good theoretical basis, that honeydew has a direct effect on leaf photosynthesis and transpiration (Rabbinge et al., 1981) and that it promotes senescence (Table 1). The importance of the effect on photosynthesis and crop growth rate has been analyzed, with simulation studies, and appears to be considerable (Table 2). Simula-

Number of aphids	CO_2-assimilation Only suction	Only ageing	Suction and honeydew	Assimilates consumed
0	182.4	182.4	182.4	0
5	182.5	178.9	167.6	4
10	182.6	175.3	157.2	8
20	182.9	167.0	131.0	16
40	183.3	145.4	74.0	32

Table 1. Computed effect of cereal aphids on photosynthesis in kg CO_2 ha^{-1} day^{-1} when different damage effects are introduced.

Yield level	Yield reduction	Primary damage	Secondary damage
6570	820	220	600
8360	1130	230	900
11050	1900	380	1520

Table 2. Simulated effect of cereal aphids on yield in winter wheat, due to 25 aphids per tiller at the peak density.

tion results (Rabbinge, in prep.) and analysis of field data (Mantel et al., 1982) demonstrate the contribution of each of the damage components to total yield loss at different yield levels. Table 3 shows the yield loss in kg ha^{-1} caused by one aphid per tiller, computed from field experiments for different yield levels. The yield loss in kg ha^{-1} is divided by the aphid density per tiller at the peak. It is clear from this Table that there is an increase in yield loss due to cereal aphids at higher yield levels. This increase is progressive with increasing yield levels.

Yield level (kg/ha)	Yield loss (kg/ha/aphid)		
	$\overline{X}$	Sx	n
< 5500	17.6	6.2	8
5500-6500	20.2	4.6	6
6500-7000	30.6	5.9	5
7000-7500	46.8	5.3	7
> 7500	66.3	5.8	3

Table 3. Yield loss due to cereal aphids at different production levels, yield loss in kg ha^{-1} is divided by the number of aphids per tiller at the peak.

The yield loss due to assimilate consumption in these conditions is computed as:

$$Y = \overline{X}.a.b.c.10^{-2},$$

in which
$\overline{X}$ = weighted average weight of the cereal aphids based on an analysis of age and weight composition of the aphids (in crop development stage 77),
a = number of tillers per m^2, this is assumed to be 500.,
b = peak number of cereal aphids,
c = assimilates consumed per mg aphids,
10^{-2} = factor of scale ($mg\ cm^{-2} \rightarrow kg\ ha^{-1}$).

Vereijken (1979), Rabbinge et al. (1981) and Rabbinge et al. (in prep.) have shown that the production of 1 mg of cereal aphid biomass requires, at reasonable nitrogen levels, about 5 mg of phloemsap when feeding on the ear, and about 10 mg of phloemsap when feeding on the leaf. More detailed information on suction rate and exact effect on crop physiology is presented elsewhere (Rabbinge et al., in prep.). At a yield level of circa 5500 kg ha^{-1}, assimilate consumption accounts for 59% of the total yield loss due to aphid damage, while at circa 7500 kg ha^{-1} level only 16% can be ascribed to this factor (Table 4). Thus, secondary damage effects are more important at high yield levels. In Table 5 an estimate is made of damage due to different components. It is demonstrated that, especially at high yield levels, stimulation of leaf senescence is the major factor that determines yield loss. This is confirmed by the results of a computer simulation model, see Table 2 (Rabbinge et al., in prep.). High yield levels are mainly due to an extended kernel filling period (Spiertz, 1979; de Vos & Sinke, 1980) and a

Yield in kg ha^{-1} x 100 kg	Acceptable peak of aphid density	Yield loss in kg ha^{-1} due to assimilate consumption	Percentage of total yield loss due to assimilate consumption
< 55	14.2	147	59
55-65	12.4	129	52
65-70	8.2	85	34
70-75	5.3	55	22
> 75	3.8	39	16

Table 4. Contribution of assimilate consumption in yield loss due to cereal aphids at a damage threshold of 250 kg wheat ha^{-1}, related to production level.

Yield in kg ha^{-1} x 100	Yield loss in kg ha^{-1}	Suction damage due to cereal aphids in kg ha^{-1}	Honeydew effect in kg ha^{-1}	Ageing of the plant	Shortening kernel filling period (days)
< 55	264	∿ 157	∿ 100	∿ 20	0
55-65	303	∿ 157	∿ 110	∿ 40	0
65-70	459	∿ 157	∿ 120	∿ 180	∿ 1
70-75	702	∿ 157	∿ 130	∿ 420	∿ 2
> 75	995	∿ 157	∿ 140	∿ 700	∿ 3

Table 5. Composition of yield loss in kg ha^{-1} due to cereal aphids in winter wheat at different production levels and a peak density of 15 aphids per tiller.

reduction of this period will result in a yield loss of up to 200 kg ha^{-1} day^{-1}. Normally the effect on length of kernel filling period is not discrete but promotion of senescence does influence the net growth rate during an extended period.

Yield decrease due to powdery mildew

Yield loss in cereals due to powdery mildew has been studied for many years (Last, 1953). Some authors indicate that at relatively low infestation levels a considerable effect on yield can be demonstrated (Darwinkel, 1980; Daamen, 1981). This is greatest when the epidemic appears early in the growing season, due perhaps to the nature of the host-parasite relationship. A considerable effect of powdery mildew on the maximum photosynthesis has been demonstrated in detailed laboratory experiments (Rabbinge et al, in prep.; Fig. 3). This effect is curvilinearly related to the percentage of leaf area covered with powdery mildew. At low covering percentages there is already a considerable decrease in maximum photosynthesis. At 3-4% coverage, photosynthesis at light saturation (300 W m^{-2}) is reduced by 35% (Fig. 4). Analysis of leaf conductivity in relation to the decrease in photosynthesis and transpiration has shown that physical resistances (boundary layer resistance, stomatal resistance and mesophyl resistance) are not affected. The considerable influence of powdery mildew on maximum photosynthesis is thus probably due to a physiological effect resulting in an increase of carboxylation resistance (Rabbinge et al., in prep.). The size of this effect depends very much on the physiological age of the leaf; this may explain the absence of a progressive relation between yield loss and production level at a certain disease level. Powdery mildew reduces net growth rate, and may

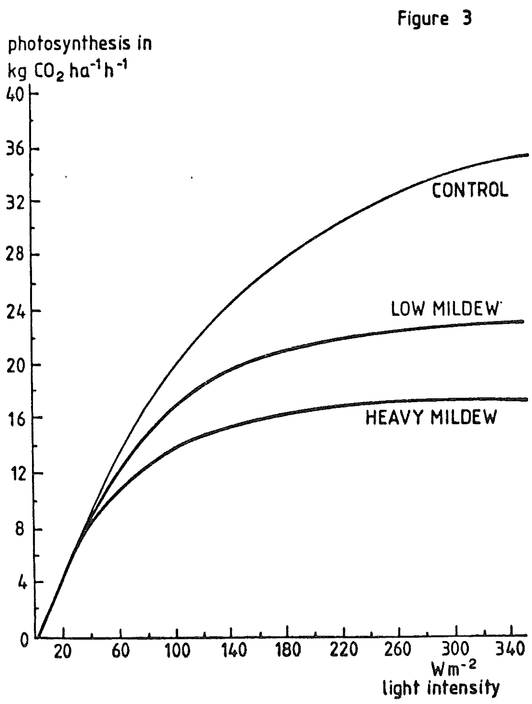

Figure 3. Light response curves of individual leaves of winter wheat at different levels of powdery mildew infestation.

thus affect final yield considerably. In a preliminary study an effect, similar to that measured in the field (Daamen, 1981) could be demonstrated using a crop growth simulator which uses the photosynthesis curves measured in the laboratory as input data. This simulation study also demonstrated that the damage relation is proportional to yield level.

Discussion

Cereal aphids and powdery mildew have increased in importance for fairly similar reasons. Both cereal aphids and powdery mildew show a rapid population increase in crops rich in nitrogen. Modern wheat cultivation is such that a wheat crop stays an attractive host until the late milky ripe stage. Thus, the epidemiological reasons for the increased importance of the pests are similar. The reasons for the increased loss per unit of disease or pest are different. In cereal aphids a secondary effect, honeydew covering the leaves and thus increasing stomatal resistance, affects both light use efficiency and the rate of photosynthesis at light satiation. In addition, leaf senescence is stimulated, and black moulds are promoted. These secondary effects are progressive with production level. Higher yields are mainly due to extended kernel filling periods; the effect of cereal aphids on the length of this period is probably the major reason for this progressive damage relationship. Powdery mildew has a considerable effect on leaf photosynthesis at light satiation, probably by affecting the carboxylation re-

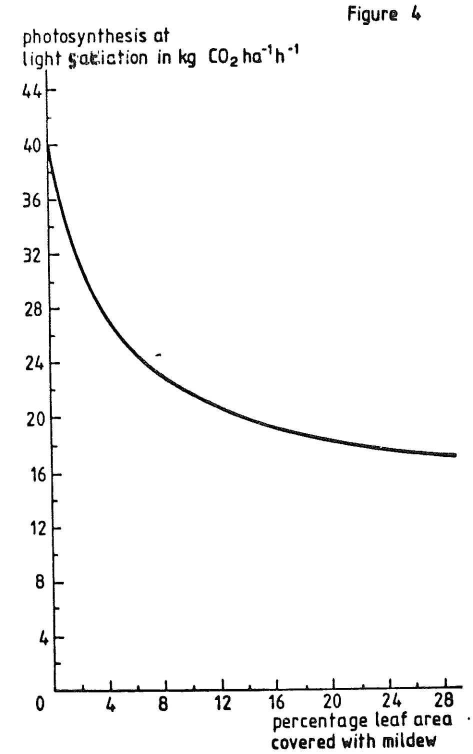

Figure 4. Photosynthesis of winter wheat leaves in kg $CO_2\ ha^{-1}\ h^{-1}$ as a function of leaf area covered with powdery mildew.

sistance. This effect is clear in young leaves and decreases in old leaves. As a result powdery mildew results in leaves with the photosynthetic characteristics of old leaves early in the season. Complete killing of the leaves is exceptional so the effect of powdery mildew is a decrease in growth rate rather than growing period. The effect of powdery mildew is therefore probably proportional to yield level, rather than progressive as in cereal aphids. More detailed analysis of crop behaviour with crop enclosures, and integration of field data with detailed observations in the laboratory, are currently in progress. This integration, using simulation models as a tool, may lay the basis for more accurate, physiologically based, damage relationships, which are urgently needed in modern wheat cultivation.

REFERENCES

Ankersmit, G.W. and N. Carter, 1981. Comparison of the epidemiology of Metopolophium dirhodum and Sitobion avenae on winter wheat. Neth. J. Pl. Path. 87: 71-81.

Carter, N., A.F.G. Dixon and R. Rabbinge, 1982. Cereal aphid populations; biology, simulation and prediction. Simulation Monographs, Pudoc, Wageningen, 91 pp.

Carter, N., I.F.G. McLean, A.D. Watt and A.F.G. Dixon, 1980. Cereal aphids - a case study and review. Appl. Biol. 5: 271-348.

Daamen, R.A., 1981. Surveys of diseases and pests of winter wheat in the Netherlands, 1979-80. Med. Fac. Landbouww. Rijksuniv. Gent, 46/3: 933-937.

Darwinkel, A., 1980. Grain production of winter wheat in relation to Nitrogen and diseases. II Relationship between nitrogen dressing and mildew infection. Z. Acker- und Pflanzenbau 149: 309-317.

Last, F.T., 1953. Some effects of temperature and nitrogen supply on wheat powdery mildew. Ann. appl. Biol. 40: 312-322.

Last, F.T., 1962. Effects of nutrition on the incidence of barley powdery mildew. Plant Path. 11: 133-135.

Mantel, W.P., R. Rabbinge en J. Sinke, 1982. Effecten van bladluizen op de opbrengst van wintertarwe. Gewasbescherming 13: 115-124.

Rabbinge, R., G.W. Ankersmit and G.A. Pak, 1979. Epidemiology and simulation of population development of Sitobion avenae in winter wheat. Neth. J. Pl. Path. 85: 197-220.

Rabbinge, R., E.M. Drees, M. van der Graaf, F.C.M. Verberne and A. Wesselo, 1981. Damage effects of cereal aphids in wheat. Neth. J. Pl. Path. 87: 217-232.

Rabbinge, R. and W.P. Mantel, 1981. Monitoring for cereal aphids in winter wheat. Neth. J. Pl. Path. 87: 25-29.

Rabbinge, R. and W.P. Mantel, 1982. Monitoring and warning systems for cereal aphids in winter wheat. In: J. Bernard, Utilisation du piège à succion en vue de prévoir les invasions aphidiennes. Euraphid, Gembloux. Comm. des Comm. Européennes. Réunion du groupe d'experts, pp. 51-53.

Rabbinge, R. and F.H. Rijsdijk, 1983. EPIPRE: A disease and pest management system for winter wheat taking account of micrometeorological factors. EPPO bull. 13(2): 297-305.

Rautapää, J., 1966. The effect of the English grain aphid Macrosiphum avenae (F.) (Hom., Aphididae) on the yield and quality of wheat. Ann. Agric. Fenn. 5: 334-341.

Sibma, L., 1977. Maximization of arable crop yields in the Netherlands. Neth. J. agric. Sci. 25: 278-287.

Spiertz, J.H.J., 1979. Weather and nitrogen effects on rate and duration of grain growth and on grain yield of wheat cultivars. In: J.H.J. Spiertz and Th. Kramer (Eds.). Crop physiology and cereal breeding. Pudoc, Wageningen, pp. 60-64.

Vereijken, P.H., 1979. Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat. Agric. Res. Rep. No. 888, Pudoc, Wageningen, 58 pp.

Vos, N.M. de en J. Sinke, 1980. Enkele resultaten van onderzoek over het produktievermogen van tarwe op dalgrond. Onderzoek 1979, Stichting voor de Akkerbouwproefboerderijen op zand- en dalgrond in Middenoost- en Noordoost Nederland. Emmen, p. 110-115.

Wit, C.T. de, 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. No. 663, Pudoc, Wageningen, 88 pp.

Wit, C.T. de, 1968. Plant production. Misc. papers Landbouwhogeschool, Wageningen, no. 3, 25-50.

Zadoks, J.C., 1980. Economische aspecten van de gewasbescherming; een verkenning. Landbouwk. Tijdschr. 92: 313-323.