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BASIS OF DETRIMENTAL EFFECTS

OF LEAF AND EAR INFESTATION

WITH SEPTORIA NODORUM

VERREET, J.A., HOFFMANN, G.M.
LEHRSTUHL PHYTOPATHOLOGIE

AMBERGER, A.
LEHRSTUHL PFLANZENERNÄHRUNG

TECHNICAL UNIVERSITY OF MUNICH

FRG - 8050 FREISING-WEIHENSTEPHAN

VERREET, J.A. AND G.M. HOFFMANN
TECHNICAL UNIVERSITY OF MUNICH, LEHRSTUHL FÜR PHYTOPATHOLOGIE,
FRG - 8050 FREISING - WEIHENSTEPHAN

AMBERGER, A.
TECHNICAL UNIVERSITY OF MUNICH, LEHRSTUHL FÜR PFLANZENERNÄHRUNG,
FRG - 8050 FREISING - WEIHENSTEPHAN

BASIS OF DETRIMENTAL EFFECTS OF THE LEAF AND EAR INFESTATION WITH SEPTORIA NODORUM ON WHEAT

1. Introduction

Septoria nodorum a pathogenic agent first described by Berkley (1845) appears to be common all over the world but occurs preferably in cooler and wet climates or rainy summers (Hoffmann and Schmutterer, 1983). While its biology has been elucidated to a large extent, Shipton et al. (1971) suggested on grounds of their literature research to investigate the importance of the Septoria disease with respect to plant development more closely since detrimental effects are dependent on the growth stage of the plant. According to a more recent review by King et al. (1983), this important aspect has not received adequate attention as yet. We therefore wanted to investigate at which stage of development on infestation by Septoria nodorum has to be rated relevant for yield production, or, in other words, from what stage on a crops population must be free of infestation to give the maximum yield. To answer this question exactly, pot trials with defined conditions had to be given preference to field trials where start and course of infection are uncontrolled and additional pathogenic infections can occur. An exact and reproducible determination of quantitative effects of Septoria infection requires an uniform plant population, congruent growth and infection conditions, and elimination of disturbing environmental factors (e.g. precipitation).

2. Materials and methods

2.1 Plant cultivation

Spring wheat (var. Famos) was grown till full ripeness in pots (Mitscherlich) filled with a mixture of soil (loamy sand - sandy loam) and sand of 2:1 with 30 seeds per pot.

To secure uniformity, the number of plants per pot was reduced to 28 after emergence, and tillers removed. Pots were set up in a greenhouse with an automatically removable and thus prevented secondary infections. Watering was done with an automatic balaanace which enabled regulation of water supply according to the plant's development. Initial fertilizing: 1.2 g P_2O_5 (dicalcium phosphate), lateron supply of 1.2 g K_2O (potassium sulfate), and 1.8 g N (ammonium nitrate) per pot as solution. N supply = about 160-180 kg N/ha.

2.2 Inoculation, incubation

The pathogenic material used for infection was taken from infected wheat ears from the field and grown in pure culture on

yeast extract agar. For basic investigations, an inoculum of 10^6 spores/ml was used; to approximate more practical conditions, various degrees of infection were achieved with increasing levels of spore concentrations (10^6, 3×10^5, 10^5, 5×10^4, 10^4 and 10^3 spores/ml). The experiment was designed not only to give uniform conditions up to the plant's maturity, but also to enable separate inoculation of single plant organs like leaf or ear at a certain date. Inoculation of leaves was done with a spray normally used for chromatography, ear inoculation was performed with a badger-airbrush. Its fine jet enabled a controlled application to the ear without contaminating the remaining plant parts.

Incubation of all pots of one series (inclusive controls) was done at 100 % relative humidity and a temperature of 22^6C ($+$ 3^6C), for 62 hours in a specially designed inoculation chamber lined with polyvinylchloride which comprised timer-controlled water defensors.

2.3 Experimental outline

At growth stage GS 13, 32, and 39, the whole plant was inoculated with spores (fig. 1), at GS 59 and GS 69, inoculation was done of the whole plant (el), only of the ear (e), or only of leaves (l). To assess yield and physiological parameters, plants were also cultivated up to full ripeness. They were separated into various parts and prepared for further analysis.

N determinations were done by the Kjeldahl technique, carbohydrates by enzymatic tests acc. to Boehringer (Henninger 1979, 1980, 1984) and chlorophyll analyzed spectrofotometrically after Ziegler and Egle (1965), Schopfer (1976). Soluble amino acids were extracted by a method of Schaller (1971), and detrmined in an aminoacid analyzer with a 3-buffer-system.

3. Results

3.1 Dry matter production and yield parameters

Leaf infections in GS 13 did not have any influence on total dry matter production (fig. 2). The plant can obviously compensate the pathogenic infect of the first three leaves (necrotization = 5 %) by full ripeness (the employed experimental technique prevented formation of secondary inoculum and infection of newly developed organs).

Negative effects, however, were already detectable with infections at stage GS 32 (F-2 = third upper leaf = necrotization = 70 %) which reduced dry matter production by 24 % (the employed experimental technique prevented formation of secondary inoculum and infection of newly developed organs = ear, flag and second upper leaf).

The high infestation at GS 39 (F = flag leaf = necrotization = 80 %) reduced total dry matter production by 43 % (the employed experimental technique prevented formation of secondary inoculum and infection of newly developed organs = ear).

Production is especially reduced with heavy infection of total

2

stages of morphological development	10-13	21, 25	29 30 31 32 37 39 49 51	69-71 71-92
	A-D	E F	G H I J K L M N O	Q-R R-W
infection in	GS 13		GS 32 GS 39 GS 59	GS 69

development at infection	infected parts	sampled parts	sampling date
EC 13 3-leaf-stage.	whole plant	1. whole plant	7.-18.-28. d.a.i.
		2. grains, glumes and spindle, F+F-1, F-2+F-3	full ripeness
EC 32 2-node-stage	whole plant	1. whole plant	7.-18.-28. d.a.i.
		2. grains, glumes and spindle, F+F-1, F-2+F-3	full ripeness
EC 39 ligula stage	whole plant	1. whole plant	7.-18.-28. d.a.i.
		2. grains, glumes and spindle, F+F-1, F-2+F-3	full ripeness
EC 59 end of ear emergence	whole plant (el) ear alone (e) without remaining plant parts remaining plant parts (l) without ear	1. whole ear 2. grains, glumes and spindle, F+F-1, F-2+F-3	7.-18.-28. d.a.i. full ripeness
EC 69 end of flowering	whole plant (el) ear alone (e) without remaining plant parts remaining plant parts (l) without ear	1. whole ear 2. grains, glumes and spindle, F+F-1, F-2+F-3	7.-18.-28. d.a.i. full ripeness

Fig. 1: Experimental outline (inoculation and sampling); d.a.i. = days after infection; F+F-1 = flag leaf and second upper leaf with corresponding culm and leaf sheaths; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm

plants in GS 59 (el) and GS 69 (el), with sole leaf infection (l) having more adverse effects than sole ear infections (e) (GS 59e -23%, GS 59l -36%, GS 59el -48%, GS 69e -21%, GS 69l -30%, GS 69el -39%).

The relevance of infections at various growth stages for yield production is described in the following for an inoculum of 10^6 spores/ml.
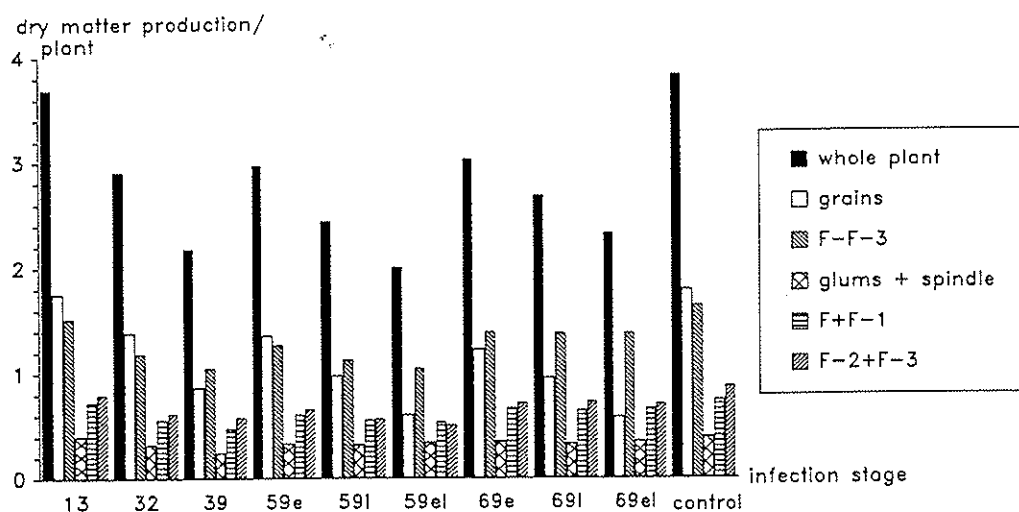
Fig. 2: Effect of Septoria infection at various stages of wheat development on dry matter production of the whole plant and several plant parts; e = sole ear infection,leaves, leaf sheaths and culms are free from infection; 1 = sole leaf infection, ear is free from infection; el = infection of the whole plant; control = uninfected plant; F+F-1 = flag leaf and second upper leaf with corresponding culm and leaf sheaths; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm

Inoculation in GS 13 had no influence on the analysed yield parameters (fig. 3). Infections in GS 32 already reduced single ear yields by 23 %, even though later developing parts like flag leaf (F), second upper leaf (F-1), and ear were not contaminated by the pathogenic agent and remained free of infection up to full ripeness. Great losses (- 52 %) occur following infections in GS 39, as a result of decreased numbers of kernels per ear and thousand corn weight. Sole leaf infections in GS 591 (- 45%) and GS 691 (- 46%) reduced single ear yield more strongly than sole ear infections (GS 59e -24%, GS 69e -32%) with number of kernels/ear and thousand corn weight being likewise affected. Yield depressions were largest after infections of the whole plant in GS 59el (- 66%), and GS 69el (- 67%).

Maximum infestation reveals the yield parameters that can be basically affected with even very early growth stages being sensitive to pathogenic infestation. Biomass and quality of older parts determine the extent of production of younger organs.

By employing various degrees of infection (10^6, $3x10^5$, 10^5, $5x10^4$, 10^4, 10^3 spores/ml) in the growth stages GS 32, 39, 59, and 69, pratical conditions were to be approximated, and their yield relevance characterized. The development of symptoms was evaluated separately for each leaf insertion several times until stage EC 75, and biomass production determined after maturity.

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number of kernels/ear
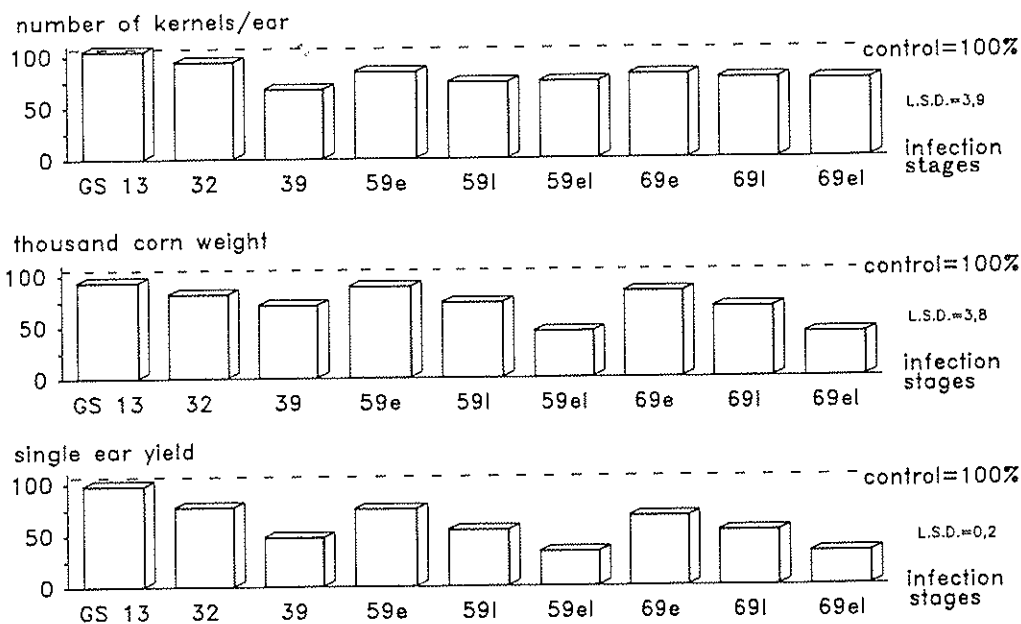

thousand corn weight

single ear yield

Fig. 3: Effect of Septoria infection at growth stages EC 13-EC 69
on single ear yield, number of kernels/ear, and thousand
corn weight of wheat at full ripeness; e = sole ear
infection, leaves, leaf sheaths and culms are free from
infection; l = sole leaf infection, ear is free from
infection; el = infection of the whole plant; control
= non-infected plant = 100%

Differences in single ear yield were significant between all
spore concentrations (fig. 4). Even the lowest concentration
(10^3/ml) leads to a yield decrease of 22% as a result of reduced
number of kernels/ear; with higher concentrations, the thousand
corn weight was also reduced.

Figure 5 shows the manifestation of the disease on the flag leaf
(F) with inoculum concentrations of 10^6, $3x10^5$, 10^5, $5x10^4$, 10^4,
10^3 spores/ml. The rate of infestation (in %) increases up to
growth stage GS 69, with recognizable differences between inocu-
lum concentrations. At onset of milk ripeness, all infections,
especially with high inoculum concentrations, result in an in-
creased necrosis of the flag leaf area. Just before physiological
repiness, the control plant shows symptoms of scenescence in an
order of 28% which is still 14% lower than after inoculation with
the lowest spore concentration of 10^3/ml.

In figure 6, effects of sole ear (e) or leaf infections (l), or
infections of the whole plant (el), with various inoculum concen-
trations (10^6, $3x10^5$, 10^5, $5x10^4$, 10^4, 10^3 spores/ml; control =
uninfected plant = 100) at stage GS 59 are shown.

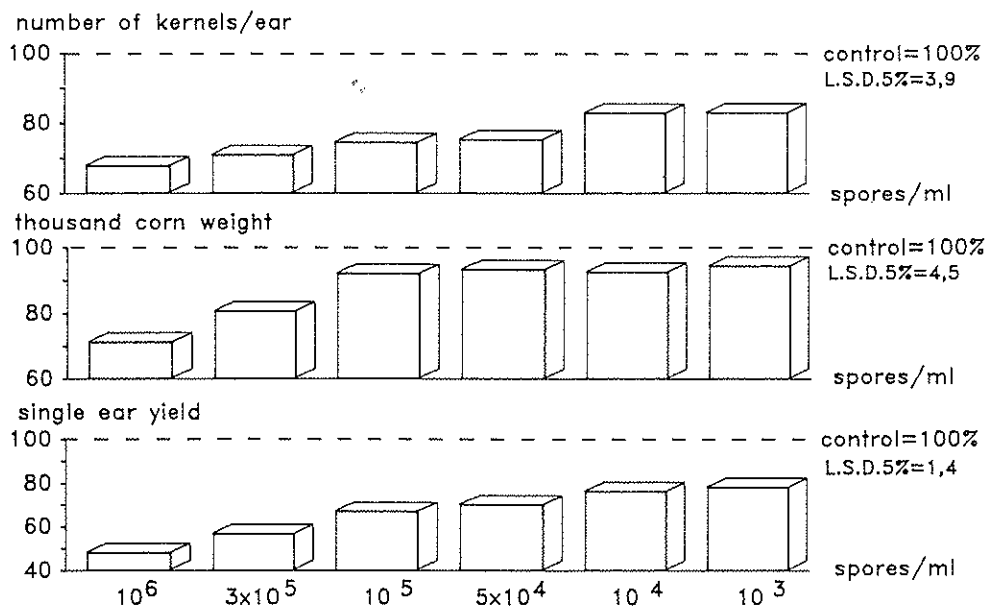Especially with high inoculum concentrations (10^6, $3x10^5$, 10^5

number of kernels/ear

100 — — — — — — — — — — — — — — — — — control=100%
                                                    L.S.D.5%=3,9
80

60   spores/ml

thousand corn weight

100 — — — — — — — — — — — — — — — — — control=100%
                                                    L.S.D.5%=4,5
80

60   spores/ml

single ear yield

100 — — — — — — — — — — — — — — — — — control=100%
                                                    L.S.D.5%=1,4
80

60

40   spores/ml
    10^6 $3x10^5$ 10^5 $5x10^4$ 10^4 10^3

Fig. 4: Effect of leaf infection with various inoculum concen-
         trations (10^6, $3x10^5$, 10^5, $5x10^4$, 10^4, 10^3 spores/ml;
         control = uninfected plant = 100) of Septoria nodorum at
         growth stage GS 39 on single ear yield, thousand corn
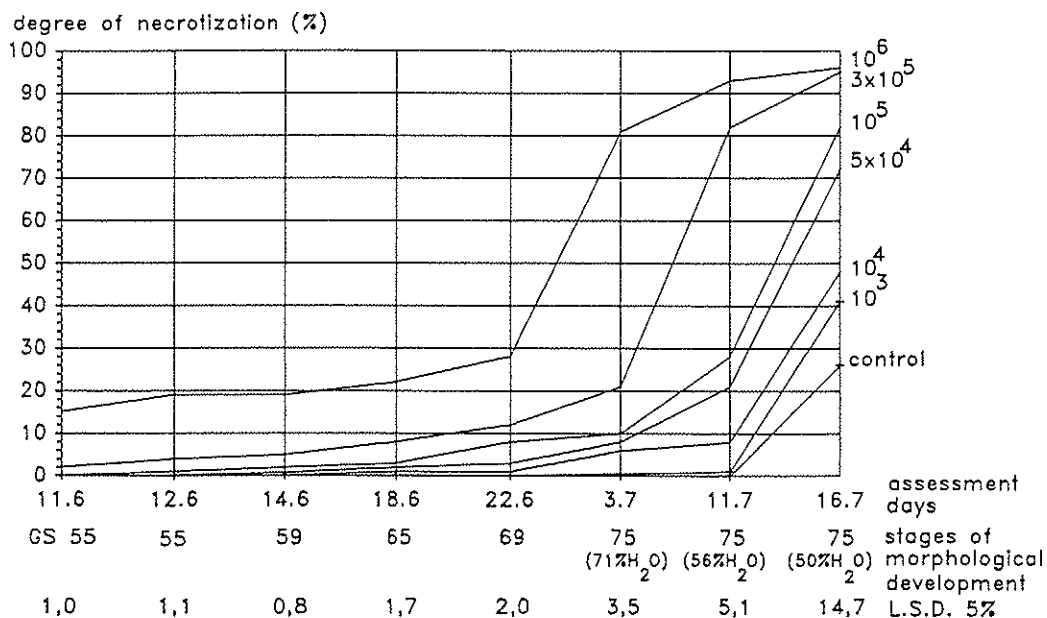   weight, and number of kernels/ear

degree of necrotization (%)

100 10^6
90 $3x10^5$
80 10^5
70 $5x10^4$
60
50 10^4
40 10^3
30   control
20
10
0

11.6	12.6	14.6	18.6	22.6	3.7	11.7	16.7	assessment days
GS 55	55	59	65	69	75 ($71%H_2O$)	75 ($56%H_2O$)	75 ($50%H_2O$)	stages of morphological development
1,0	1,1	0,8	1,7	2,0	3,5	5,1	14,7	L.S.D. 5%

Fig. 5: Effect of leaf infections with various inoculum concen-
         trations (10^6, $3x10^5$, 10^5, $5x10^4$, 10^4, 10^3 spores/ml) of
         Septoria at growth stage GS 39 on disease manifestation
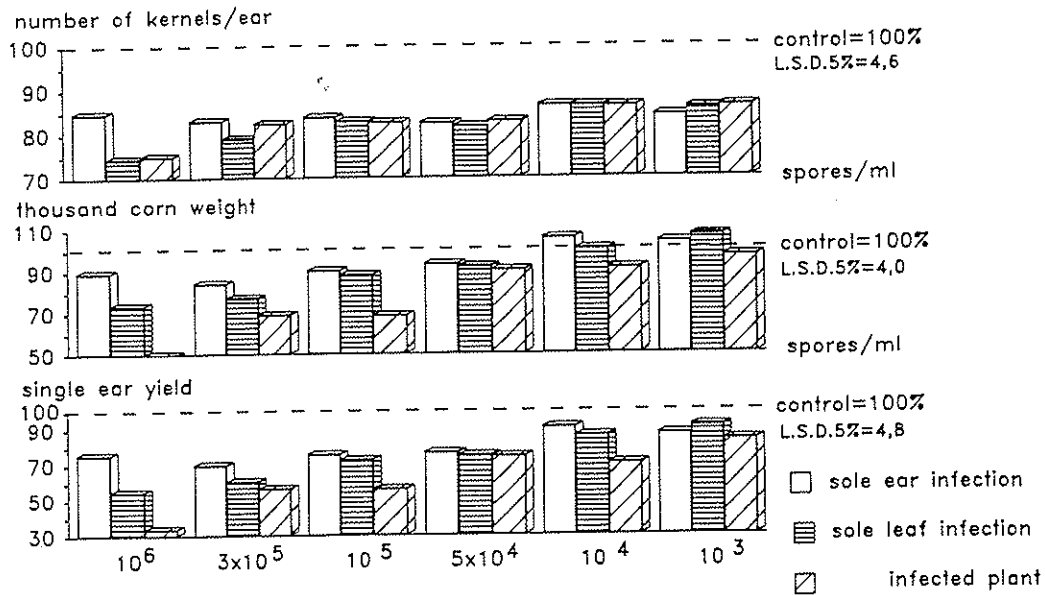   on the flag leaf (F)

6

number of kernels/ear

Fig. 6: Effect of ear (e), leaf (l), or leaf and ear infection (el) with various inoculum concentrations (10^6, 3×10^5, 10^5, 5×10^4, 10^4, 10^3 spores/ml; control = non-infected plant = 100%) at growth stage GS 59 on single ear yield, thousand corn weight, and number of kernels per ear
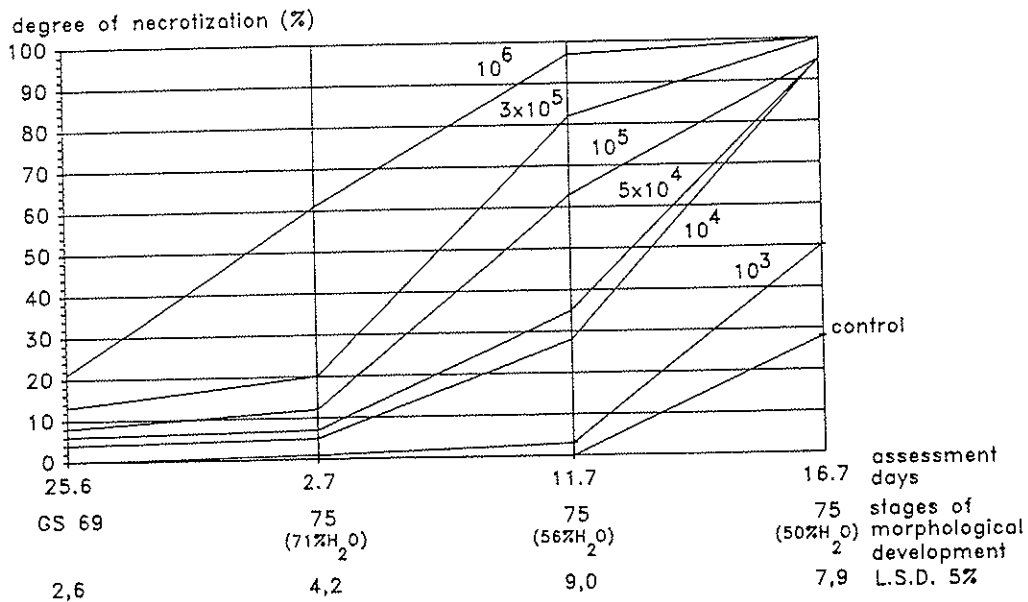

Fig. 7: Effect of sole leaf infections (l) at growth stage GS 59 with various inoculum concentrations (10^6, 3×10^5, 10^5, 5×10^4, 10^4, 10^3 spores/ml) on disease manifestation on the flag leaf (F)

7

number of kernels/ear
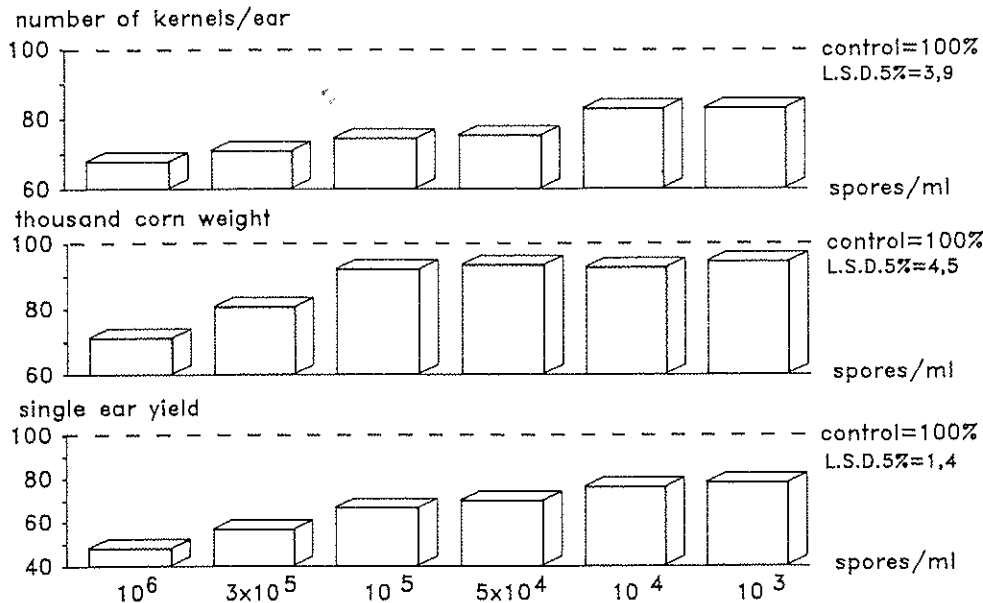
Fig. 4: Effect of leaf infection with various inoculum concen-
trations (10^6, 3×10^5, 10^5, 5×10^4, 10^4, 10^3 spores/ml;
control = uninfected plant = 100) of Septoria nodorum at
growth stage GS 39 on single ear yield, thousand corn
weight, and number of kernels/ear

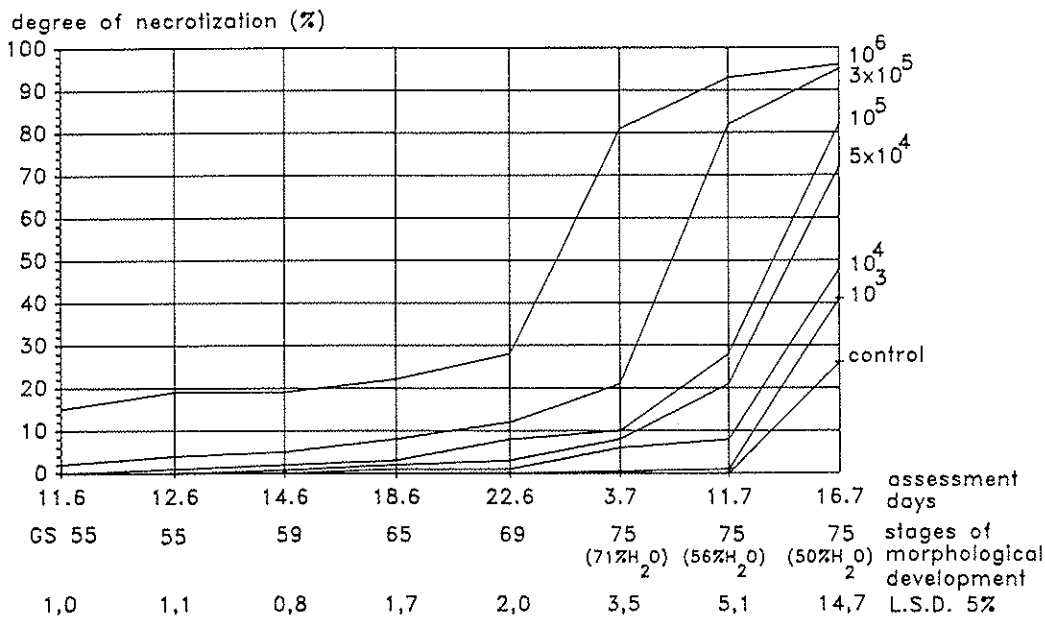
Fig. 5: Effect of leaf infections with various inoculum concen-
trations (10^6, 3×10^5, 10^5, 5×10^4, 10^4, 10^3 spores/ml) of
Septoria at growth stage GS 39 on disease manifestation
on the flag leaf (F)

6

degree of necrotization (%)

90
80
70 10^6
60 3×10^5
50 10^5
40 5×10^4
30
20 10^4
10 10^3
0   control
                                                                      assessment
25.6   2.7   11.7   16.7   days
GS 69   75   75   75   stages of
                  (71%$H_2$0)   (56%$H_2$0)   (50%$H_2$0)   morphological
                                                                     development
2,3   5,0   4,8   6,4   L.S.D. 5%
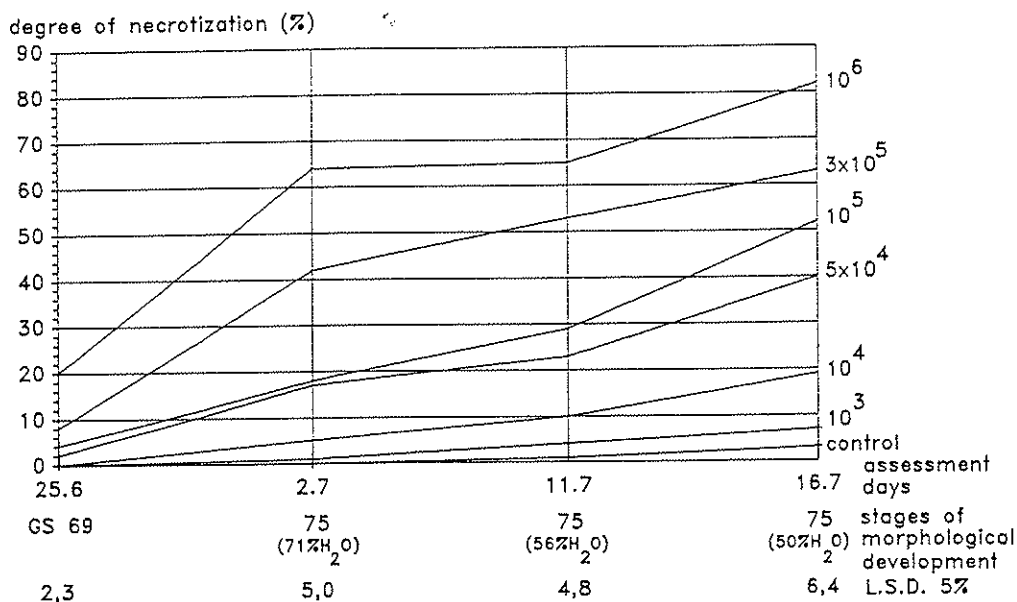
Fig. 8: Effect of sole ear infection (e) at growth stage GS 59
with various inoculum concentrations (10^6, 3×10^5, 10^5,
5×10^4, 10^4, 10^3 spores/ml) on disease manifestation on
the ear (e)

spores/ml), infections of only leaves or of total plants reduce
yield to a larger extent than sole ear infections. With decreas-
ing concentrations, these differences become smaller. Even after
infections with lowest spore concentrations, in all infection
treatments significant yield losses are observed (ear infection -
14%, leaf infection - 9%, infection of whole plant - 16%).

Again, the number of kernels per ear is the yield parameter
affected by all infection levels while the thousand corn weight
is reduced especially with high inoculum concentrations.

Disease manifestation on the flag leaf is characterized by a
great increase in necortization at onset of milk ripeness (GS 75,
71% $H_2$0) which results 31 days after infection (d.a.i.) in com-
plete destruction of leaf tissue of nearly 100% of the assimi-
lating green area whereas normal senescence of a healthy plant at
this point shows tissue losses of 28%. Leaf infections in GS 59
obviously accelerate the dying process of the flag leaf as com-
pared to infections in GS 39, the latter, however, leading to
higher yield depressions because of the longer pathogenesis.

The levels of infestation of the ear (fig. 8) at all inoculum
concentrations reveal a continuously increasing destruction of
those plant parts which are the main assimilating organs expecia-
lly at later stages of milk ripeness. Even the smaller, punctuate
necroses at the lowest infection levels of 10^3 spores/ml, with 8%
infested area and sole ear infection, had negative effects of -
14% on yield (fig. 6).

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These results show that leaf diseases of wheat caused by Septoria nodorum are more severe with respect to yield physiology than has been assumed before. They further reveal that even low spore concentrations also in early stages of plant development (GS 32, 39) have negative effects on grain yield and total dry matter production.

It has to be pointed out here that in the course of plant development each organ is depending on the preceding one. Mass and quality of older parts determine the extent of production of younger organs (Fischbeck et al. 1983). In their literature review, King et al. (1983), discuss yield depressions which result from minor infestations in connection with the formation of toxins by the pathogenic agent.

Devys et al. (1974, 1980), Bousquet et al. (1977, 1980) and Bosquet and Skajennikoff (1974) describe in their investigations the effects of an unspecific phytotoxin which has been isolated from cultures of Septoria nodorum and caused leaf necroses when applied towheat leaves. This phytotoxin Septorin, produced in vitro as an ochracine compound, is supposed to retard diffusion of CO_2 through stomata and consequently reduces net assimilation rate.

This important aspect of toxic effects of the pathogenic agent Septoria nodorum on plant physiology is currently investigated. In contrast to high degrees of infestation where great yield losses are explained by far reaching destructions of assimilating tissue, reductions of yield at only minor disease symptoms cannot be regarded an exclusive consequence of the loss in assimilating tissue.

To obtain further information on the background of pathogenic effects it was not enough to determine yield parameters like number of kernels per ear or thousand corn weight. Quantitative changes in the assimilating potential or in plant constituents had to be also considered.

We like to concentrate on chlorophyll, carbohydrate, total N and amino acid metabolism, and present for reasons of shortness only data of selected treatments.

3.2   Chlorophyll concentrations

Infections in growth stage GS 39 which comprise the whole leaf system reduce chlorophyll concentrations in the whole plant by more than 20% already after 7 days just before visible symptoms occur (fig. 9). 18 and 28 d.a.i. no further decomposition takes place.

Infections in growth stage GS 59 (fig. 10), separately for leaf (l) and ear (e), increase total chlorophyll concentrations 7 days later. 18 and 28 d.a.i., an exclusive infestation of the ear does not change the total chlorophyll concentration which can be explained by the compensating action of the non-infected leaf system; sole leaf infections, however, have strong impact because of necrotization.
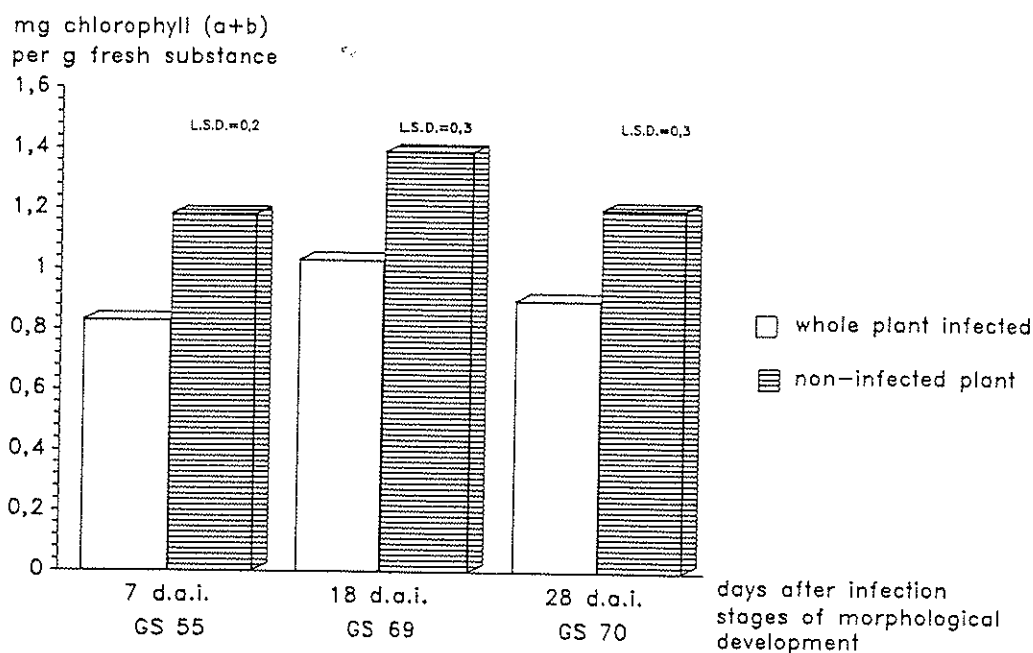
mg chlorophyll (a+b)
per g fresh substance

Fig. 9: Effect of an infection with Septoria nodorum in growth
         stage GS 39 on chlorophyll content in the whole plant

Analysis of separate plant parts 7 d.a.i. in GS 59 (fig. 11)
shows a temporary increase in chlorophyll before appearance of
symptoms in both leaf-culm sections (F+F-1, F-2+F-3). Lateron (18
or 28 d.a.i.), no significant differences to control plants are
induced by ear infestation (e), but leaf infections (l) result in
strong decreases of chlorophyll especially in the upper culm
parts (F+F-1). This effect is also observed in the section F-2+F-
3, but here natural decomposition of chlorophyll because of
increasing senescence has already progressed further.

To sum up:
Sole leaf infections lead to greater losses in chlorophyll than
sole ear infections. The latter situation does not occur under
field conditions because of the characteristics of the epidemic
process, but like the yield results it reveals the greater
importance of leaf infection by Septoria nodorum as compared to
ear infections.

3.3   Carbohydrates

In the following table the effects of a Septoria infection in
stage GS 32 are discussed.

Already 7 d.a.i. (first symptoms are visible), the assimilation
is impaired (e.g. -40% sucrose); this effect is increasing with
time, and differences between sucrose concentrations reach values
of more than 50% (28 d.a.i.) similar to glucose and fructose. At
full ripeness, the yield of starch in grains is 26% less than in
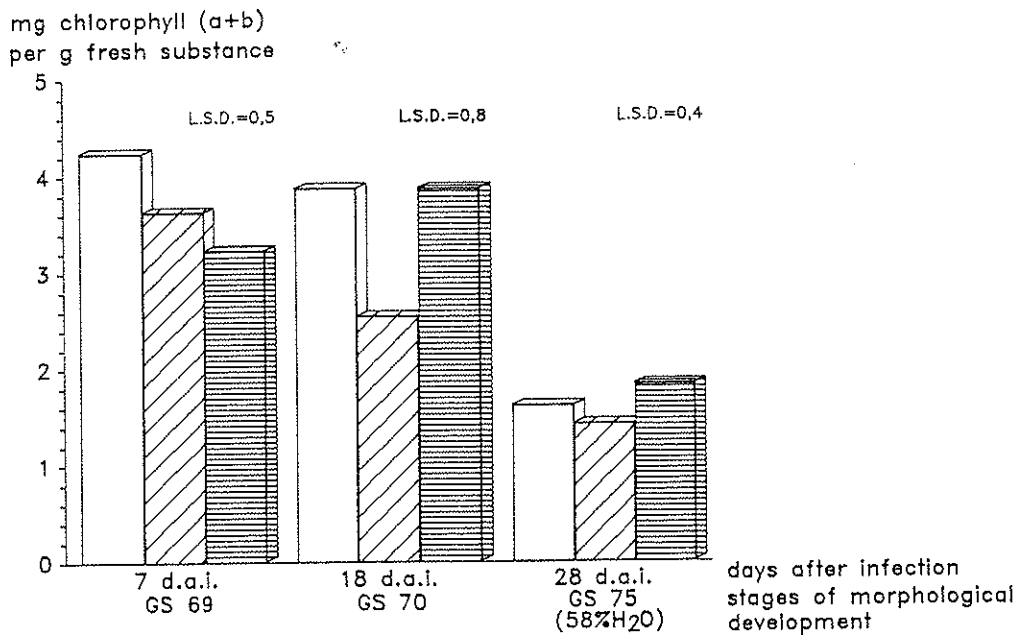control plants.

10

mg chlorophyll (a+b)
per g fresh substance

Fig. 10: Effect of an infection with Septoria nodorum in growth
stage GS 59 on chlorophyll content in the whole plant

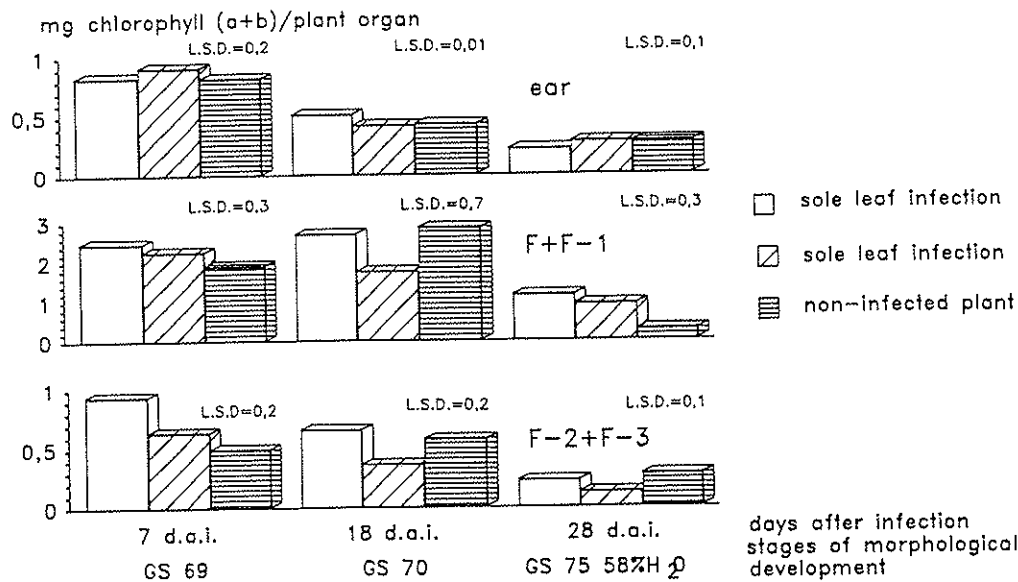Fig. 11: Effect of infection with Septoria nodorum in EC 59 on
chlorophyll content of various plant parts; e = ear,
F+F-1 = flag leaf and second upper leaf with correspon-
ding culm and leaf sheaths, F-2+F-3 = third und fourth
upper leaf with leaf sheaths and remaining culm

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i = infected plant	sampling date						full ripeness	
c = control = non-infected plant	whole plant						grain	
development stage	GS 34		GS 39		GS 61		GS 92 (9% H₂O/grain)	
days after infection	7 d.a.i.		18 d.a.i.		28 d.a.i.		71 d.a.i.	
carbohydrates	i	c	i	c	i	c	i	c
glucose	11,8	15,9	23,0	41,6	57,6	115,1	0,6	0,7
fructose	8,4	7,4	10,1	18,9	40,1	84,5	0,1	0,01
sucrose	14,6	24,0	64,0	146,0	59,4	126,8	22,2	22,7
starch	0	0	0	0	0	0	489,0	662,5
Σ carbohydrates	34,8	47,3	97,1	206,5	157,1	326,4	511,9	685,9

Table 1: Carbohydrate content (mg/plant) after infection in
development stage GS 32   (7-28 d.a.i. or at full ripe-
ness)

i = infected plant	sampling date						full ripeness	
c = control = non-infected plant	whole plant						grain	
development stage	GS 55		GS 69		GS 70		GS 92 (9% H₂O/grain)	
days after infection	7 d.a.i.		18 d.a.i.		28 d.a.i.		54 d.a.i.	
carbohydrates	i	c	i	c	i	c	i	c
glucose	48,9	49,5	35,9	52,6	33,6	49,5	0,3	0,7
fructose	39,4	43,9	26,5	35,3	40,2	45,3	0,04	0,01
sucrose	32,6	22,3	56,0	85,0	127,8	162,4	11,4	22,7
starch	0	1,6	10,0	14,2	83,5	85,3	293,4	662,5
Σ carbohydrates	120,9	117,3	128,4	187,1	285,1	342,5	305,1	685,9

Table 2: Carbohydrate content (mg/plant) after infection in
development stage GS 39 (7-28 d.a.i. or at full ripe-
ness)

Infections in growth stage GS 39 essentially reduce assimilate
production only after manifestation of disease symptoms. Sucrose
concentration 18 or 28 d.a.i. is lower by 35 or 22%, total deter-
mined carbohydrates are 32 or 17% below control plants. At full
ripeness, the starch yield in grains is reduced by over 50%. This
heavy impact of infestation is characterized by the chlorophyll
analyses just described (fig. 9).

As was to be expected, the early negative effects of leaf infec-
tions (1) on primary products of assimilation (glucose,

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	sampling date									full ripeness		
development stage		GS 69			GS 70			GS 75 (58% H₂O/grain)			GS 92 (9% H₂O/grain)		
days after infection		7 d.a.i.			18 d.a.i.			28 d.a.i.			44 d.a.i.		
carbo-hydrates	plant parts	e	i	c	e	i	c	e	i	c	e	i	c
glucose	whole plant	36,0	26,9	33,3	49,0	37,1	35,7	25,5	8,2	24,8			
	whole ear	12,2	8,2	11,5	14,0	9,6	10,9	6,5	3,6	8,6			
	F+F-1	8,3	6,3	6,8	14,5	10,9	8,9	8,0	1,5	8,4			
	F-2+F-3	15,5	12,5	15,0	20,5	16,7	15,9	11,0	3,1	7,9			
	grain										0,4	0,7	0,7
fructose	whole plant	51,5	47,6	51,0	57,8	51,1	53,7	57,0	22,2	34,0			
	whole ear	11,9	11,1	12,9	15,1	11,5	12,7	7,8	7,2	7,1			
	F+F-1	7,8	6,3	6,9	9,5	7,6	9,7	18,0	5,1	10,6			
	F-2+F-3	31,9	30,2	31,2	33,2	32,0	31,3	31,2	9,9	16,3			
	grain										0,07	0,01	0,01
sucrose	whole plant	62,8	50,7	71,9	144,0	96,6	129,2	110,4	52,8	91,1			
	whole ear	15,1	12,8	12,1	40,8	37,9	48,0	52,0	36,2	43,5			
	F+F-1	12,5	8,7	15,2	53,8	28,4	44,4	35,1	9,7	35,9			
	F-2+F-3	35,3	29,3	44,6	49,4	30,3	36,8	23,3	6,9	11,7			
	grain										20,8	38,1	22,7
starch	whole ear	6,7	5,6	8,1	136,4	133,6	141,5	341,6	308,1	374,9			
	grain										533,8	397,9	662,5
Σ carbohydrates		157,0	130,8	164,3	387,2	318,4	360,1	534,5	391,3	524,8	555,1	436,7	685,9

Table 3: Carbohydrate content (mg/plant) after infection in development stage GS 59 (7-28 d.a.i. or at full ripeness); e = sole ear infection, leaves, leaf sheaths and culm are free from infection; i = sole leaf infection, ear is free from infection; control = non-infected plant; F+F-1 = flag leaf and second upper leaf with leaf sheaths and corresponding culm; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm

fructose), and on transport sugars (sucrose) also cause lower starch contents in the grains of the ear (-40%). In contrast, sole ear infection (e) reduce starch contents by 16%. The total values of analyzed carbohydrates of the whole plant confirm these results (ear infections -19%, leaf infection -36%). According to these observations, the formation of assimilates is reduced by infections in GS 32 or later to such an extent that full compensation by non-infected organs (GS 32 = ear + F/F-1; GS 39 = ear) cannot be achieved. Leaf infections in GS 59 reduce carbohydrate contents more than ear infections. By exclusive ear infestation, assimilates are accumulated in non-infected leaves. The negative effects of leaf infections are connected with reduced chlorophyll concentrations and with a great loss of water in the leaves in the course of pathogenesis. According to Amberger (1969), with the occurrence of wilting symptoms oxidizing enzymes are increasing, and catalase activity is reduced in connection with chlorophyll degradation and degeneration of plastids. The lower concentration of glucose, fructose, and sucrose in infested parts is obviously related to the decreasing hydration.

Exclusive ear infestation does not decrease total chlorophyll significantly (up to 4 weeks after infection) (fig. 11), therefore also glucose, fructose, and sucrose contents are not drasti-

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cally changed. Of importance is the beginning accumulation of assimilates especially of sucrose in middle and upper leaf-culm sections. Temporarily, the infestated ear shows higher monosaccharide levels. In this case, insufficient production and supply of assimilates cannot be the decisive factor for yield depression. Judel and Mengel (1983) shaded wheat plants in the grain filling period and observed no reduction of sucrose and glucose contents in the grains but an inhibited formation of starch. Translocation of assimilates and formation of starch is controlled by the growth of grains. This statement is supported by the facto that starch synthesizing enzymes (starch phosphorylase, starch synthetase) do not exhibit any differences in activity between shaded and non-shaded plants. It seems to be essential that during the first 2 weeks after the flowering period activity of starch synthetase 2 (UDP-glucose-glucane-4-glycosyltransferase) is increased 4-fold. This enzyme is of great importance for the production of cell wall substances and consequently for the development of grains. It has to be investigated how far Septoria infections have an impact on the process of grain development and filling. The sink-source-relationship is another important point in this context. According to King et al. (1967), Apel (1972), Apel et al. (1973), Apel and Tschäpe (1973), Apel and Natr (1976) and Solansky (1973) there are correlations between the assimilate demand of specific organs and the photosynthetic rate. The demand of the ear for assimilates is determined mainly by the respiration of the tissue (Damisch 1972, 1973, 1974). With increasing attracting respiration, more carbohydrates (sugars) are translocated to the ear. A reduction in ear size and number of kernels per ear decreases the storage capacity, and consequently the sink, and leads to increased accumulation of carbohydrates in leaves and culm sections. This way, the effects of ear infections by Septoria in stage GS 59 (and also in GS 69 which data are not shown here), on reduction of number of kernels per ear and accumulation of carbohydrates in non-infected leaf-culm sections, and the simultaneous decrease of starch yield can be interpreted.

3.4 N and amino acid metabolism

The remarkable impact of Septoria infection on production and translocation of assimilates is also reflected in the nitrogen and amino acid metabolism. As is known, nitrogen is the most important nutrient because it is the building element in proteins, proteids, chlorophyll, and other important compounds like phytohormones. The extent of plant production is determined only by N fertilizer use. N fertilizing can be done specifically to influence yield determining processes. Yield components like productive tillering, that is number of eared culms/plant, number of spikelets/infructescence, number of flowers/ear, and weight as well as quality of the caryopsis are promoted by an optimal N supply, or in the end by a certain N concentration in plant tissues. The favourable influence of nitrogen is due to diminished reduction processes especially in numbers of eared culms, or after establishment of a maximum number of spikelet and flower primordiae.

Furthermore, a high N supply in small grain crop plants improves conditions for the supply of assimilates by increasing the life

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time, and for their translocation into the caryopsis. Besides, retarded senescence in the caryopsis because of high N concentrations in the grain is possible. Cytokinines have to be mentioned at this point. In the course of development of the caryopsis, nitrogen supply determines initially the number of endosperm cells. It is known today that N deficiency causes low phytohormone concentrations (cytokinines) with the consequence of reduced cell numbers in the endosperm.
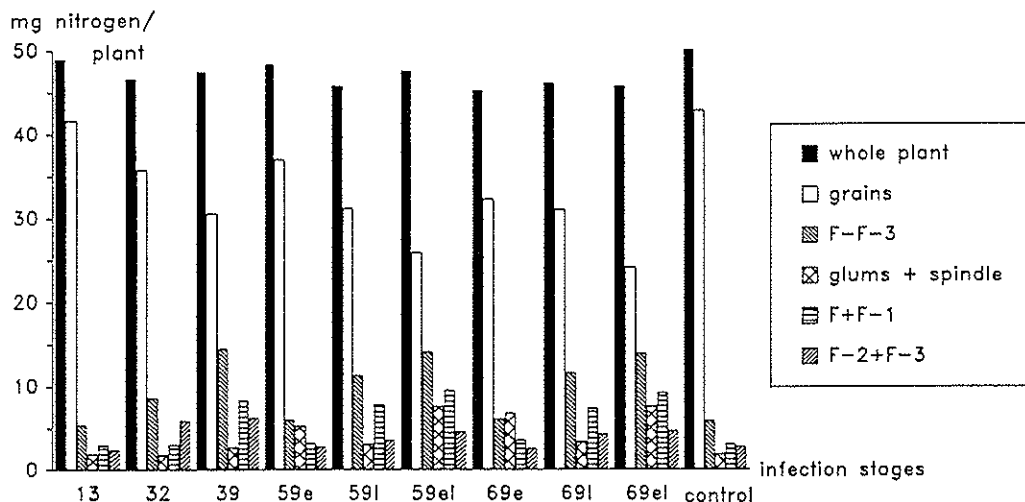

Fig. 12: Effect of infections in various growth stages on N uptake of plant parts; e = sole ear infection, leaves, leaf sheaths and culm are free from infection; l = sole leaf infection, ear is free from infection; el = infection of the whole plant; control= non – infected plant; F+F-1 = flag leaf and second upper leaf with leaf sheaths and corresponding culm; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm

The effect of Septoria infection (10^6 spores/ml) at several stages of plant development on the distribution of nitrogen between various plant parts was determined at full ripeness (GS 91). Fig. 12 shows the N-uptake of the whole plant or the separated plant part grains, glumes and spindles, F+F-1, and F-2+F-3 after infection at 9 growth stages (GS 13, 32, 39, 59e, 59l, 59el, 69e, 69l, 69el, control plants outmost right).

At maturity, the following results were obtained:

1. There are hardly any differences in N uptake of the whole plant between infested and control plants.

2. In contrast, the distribution of N between plant parts varies considerably.

3. The amounts of N in grains of infected plants, with the exception of infections in GS 13, are sometimes considerably below the control values (GS 32 -17, GS 39 -29%, GS 59e -14%, GS 59l -27%, GS 59el -40%, GS 69e -25%, GS 69l -27%, GS 69el -44%).

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4. In glumes and spindles, amounts of N after ear infection are higher than in control organs (GS 59e +183%, GS 59el +303%, GS 69e +259%, GS 69el +304%).

5. In F+F-1, that is the upper leaf-culm section (F+F-1 = flag leaf and second upper leaf with corresponding culm and leaf sheaths), amounts of N are strongly increased especially after leaf infections (GS 39 +168%, GS 59l +151%, GS 59el +206%, GS 69l +138%, GS 69el +198%).

6. The same holds for lower leaf-culm sections (F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm) which show high amounts of N at maturity, not so much after late but after early leaf infections (GS 32 +109%, GS 39 +121%). This is due to the fact that at later stages of development, with the course of natural senescence, the main part of nitrogen has already been transolcated to higher leaf-culm sections. With infection in earlier stages, however, the pathogenic agent can affect physiologically active plant organs and thus retain nitrogen to a larger extent.

According to Koch and Mengel (1977), 88% of the amount of protein present in ripe grains at harvest is normally already contained in the plant before folwering. The accumulation of protein in the caryopsis is mainly a translocation process and does hardly depend on the uptake of nitrogen during growth of this plant part.
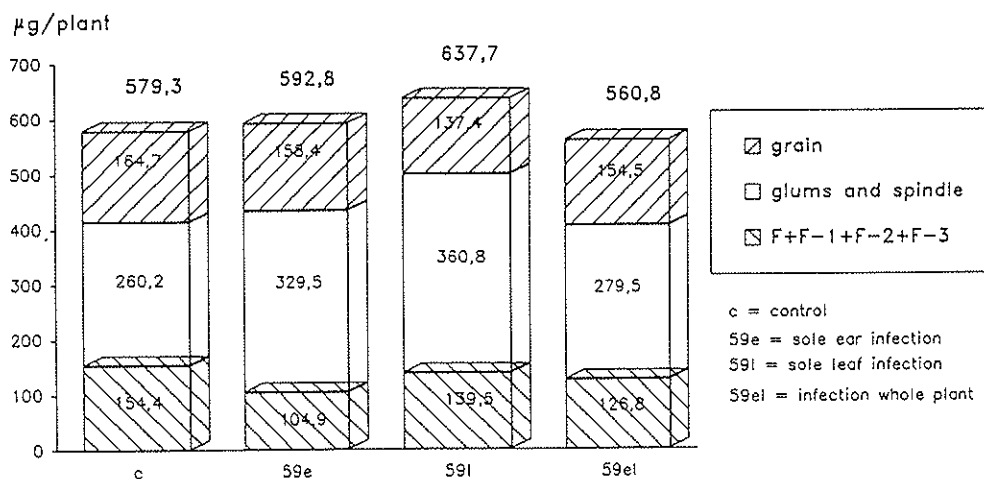
Fig. 13: Effect of Septoria infection in GS 59 on amounts of amino acid - amide nitrogen in the plant at full ripeness; c = control = non - infected plant; e = sole ear infection, leaves, leaf sheaths and culm are free from infection; l = sole leaf infection, ear is free from infection; el = infection of the whole plant; F+F-1 = flag leaf and second upper leaf with leaf sheaths and corresponding culm; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm

Our investigations show an almost equal level of N uptake of the

amino acids in µg N / plant	analyzed organ: glumes and spindles										
	c			e			l			el		
	µg N / plant	% of total	% of c	µg N / plant	% of total	% of c	µg N / plant	% of total	% of c	µg N / plant	% of total	% of c
aspartic acid	10,76	4	100	6,45	2	-40	15,10	4	140	7,38	3	-31
threonine	5,34	2	100	3,57	1	-33	8,58	2	161	2,47	1	-54
serine	17,74	7	100	9,23	3	-48	20,59	6	116	4,93	2	-72
asparagine	13,26	5	100	10,04	3	-24	13,04	4	-2	10,27	4	-24
glutamic acid	15,54	6	100	28,87	9	186	25,52	7	164	35,63	13	230
glutamine	49,04	19	100	72,00	22	147	46,18	13	-6	49,24	18	100
proline	24,24	9	100	10,41	3	-57	51,76	14	214	6,91	3	-72
glycine	8,07	3	100	6,21	2	-23	7,80	2	-3	4,54	2	-44
alanine	30,77	12	100	16,68	5	-46	39,60	11	129	9,38	3	-70
∝-amino-n-butyric acid	----	----	----	----	----	----	----	----	----	----	----	----
citrulline	2,77	1	100	8,77	4	317	1,91	0,5	-31	0,00	000	000
valine	12,16	5	100	7,66	2	-37	20,00	6	165	3,42	1	-72
cystine	1,09	0,4	100	0,85	0,3	-22	1,60	0,4	147	0,31	0,1	-72
methionine	1,28	0,5	100	1,43	0,4	112	11,09	3	866	1,63	0,6	127
isoleucine	5,86	2	100	3,04	0,9	-48	13,75	4	235	2,13	0,8	-64
leucine	6,05	2	100	3,02	0,9	-50	3,16	0,9	-48	0,81	0,3	-87
tyrosine	2,08	0,8	100	1,19	0,4	-43	2,71	0,8	130	0,00	000	000
phenylaline	3,86	2	100	1,83	0,6	-53	8,71	2	226	1,09	0,4	-72
γ-amino-n-butyric acid	15,73	6	100	7,91	2	-50	32,13	9	204	9,62	3	-39
ornithine	5,01	2	100	6,03	2	120	2,71	0,8	-46	4,43	2	-12
lysine	8,84	3	100	17,59	5	199	12,93	4	146	10,74	4	122
histidine	2,04	0,8	100	4,53	1	222	2,12	0,6	104	4,23	2	207
arginine	18,64	7	100	102,20	31	548	26,26	7	141	110,39	40	592
ammonium-N	219,70	46	100	166,20	34	-24	144,81	29	-34	97,13	26	-56
total amino-N	260,19		100	329,51		127	360,81		139	279,54		107

Table 4: Changes in amounts of amino acids (µg/plant) in glumes and spindles at full ripeness (GS 91) after infection of various plant organs at stage GS 59; c = control = non-infected plant; e = ear infection, remaining plant (F+F-1+F-2+F-3) non-infected; l = leaf - culm section (F+F-1+F-2+F-3) infected, ear non-infected; el = infection of the whole plant; F+F-1 = flag leaf and second upper leaf with leaf sheaths and corresponding culm; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm

whole plant in all infected and control plants, and a retention of nitrogen in plant parts infested by the pathogenic agent (that is mainly in glumes and spindles with ear infections, or in leaf-culm sections with leaf infections). This leads to the conclusion that on one hand N uptake has not been inhibited by Septoria nodorum, but that on the other hand translocation of nitrogen from vegetative plant parts to reproductive organs which begins just after flowering and is restricted to the short period of grain filling is inhibited by the pathogenic agent. The formation of large necroses and the corresponding, sometimes extreme dehydration of infested organs, during pathogenesis cannot be without influence on the transport system and is the cause of this reduced translocation. Retention of nitrogen results in deficient nitrogen supply of developing grains. The plant reacts with certain reduction processes, for instance by decreasing number of kernels per ear.

The biggest part of soluble N compounds in the plant are amino acids, amides, and amines with amino acids being the most important for metabolic processes. They are the protein building

amino acids in µg N / plant analyzed organ: F+F-1+F-2+F-3											
	c			e			l			el		
	µg N / plant	% of total	% of c	µg N / plant	% of total	% of c	µg N plant	% of total	% of c	µg N plant	% of total	% of c
aspartic acid	5,68	4	100	4,19	4	-26	4,22	3	-26	2,96	2	-48
threonine	3,99	3	100	2,53	2	-37	2,37	2	-41	1,50	1	-63
serine	11,28	7	100	7,38	7	-35	4,59	3	-59	2,96	2	-74
asparagine	4,37	3	100	1,97	2	-55	5,88	4	135	1,82	1	-58
glutamic acid	11,80	8	100	12,81	12	109	20,39	15	174	17,31	14	147
glutamine	35,38	23	100	17,66	17	-50	33,14	24	-6	38,56	30	109
proline	5,16	3	100	3,34	3	-35	5,50	4	107	1,85	2	-64
glycine	4,61	3	100	4,08	4	-12	2,97	2	-36	2,31	2	-50
alanine	16,63	11	100	7,54	7	-55	4,96	4	-70	3,19	3	-81
⍺-amino-n-butyric acid	----	----	----	----	----	----	----	----	----	----	----	----
citrulline	3,14	2	100	0,90	0,9	-71	0,00	000	000	0,00	000	000
valine	8,06	5	100	0,90	0,9	-71	0,00	000	000	0,26	0,2	-71
cystine	0,90	0,6	100	0,51	0,5	-43	0,45	0,3	-50	----	----	----
methionine	----	----	----	----	----	----	----	----	----	----	----	----
isoleucine	3,33	2	100	1,59	2	-52	1,91	1	-44	1,14	0,9	-66
leucine	4,80	3	100	2,55	2	-47	2,46	2	-49	1,62	1	-66
tyrosine	1,47	1	100	0,96	0,9	-35	0,74	0,5	-50	0,60	0,5	-59
phenylalanine	2,36	2	100	1,43	1	-39	1,60	1	-32	0,89	0,7	-62
y-amino-n-butyric acid	7,04	5	100	5,08	5	-28	1,30	0,9	-82	3,72	3	-47
ornithine	2,86	2	100	3,48	3	122	1,87	1	-35	1,66	3	-42
lysine	5,09	3	100	3,39	3	-33	3,45	3	-32	3.56	3	-30
1-methyl-histidine	----	----	----	----	----	----	----	----	----	----	----	----
histidine	1,09	0,7	100	0,89	0,8	-18	1,16	0,8	106	1,52	1	139
arginine	10,29	7	100	18,94	18	184	37,69	27	366	38,10	30	370
ammonium-N	222,19	59	100	192,03	65	-14	104,13	43	-53	82,93	40	-63
total amino-N	154,51		100	104,86		-32	139,54		-10	126,78		-18

Table 5: Changes in amounts of amino acids (µg/plant) in leaf-culm sections (F+F-1+F-2+F-3) at full ripeness after infection of various plant parts at growth stage GS 59 (rest s. table 4)

elements (Mengel 1984). How far Septoria infections affect amino acid metabolism has not been known so far. Our own results reveal distinct changes in the amino acid composition of wheat plants.

In figure 13, the effects of sole ear (59 e), leaf (59 l), and total plant (59 el) infection at stage GS 59 on amounts of amino acid-, amide-N, of the whole plant as compared to non-infected controls (c) are given at full ripeness.

The sum of amino acid and amide N of infected plants is 13 % higher than of healthy plants (c) after leaf infection; after infection of ear (e) or total plant (el), only minor differences occur. Significantly decreased or increased amounts of specific amino acids are observed after infection of separate plant organs (e, l) or total plant (el) (table, 4, 5, 6).

The increased amounts of agrinine in contaminated glumes and spindles and leaf-culm sections as compared to non-infected controls are very conspicuous (fig. 14).

While non-infected plants at maturity have arginine concentrations of 55 µg/plant, plants with ear infections show very high amounts of arginine especially in glumes and spindles (GS 59e 150µg/plant, GS 59el 169µg/plant). After leaf infection, the amounts of arginine in the leaf-culm section are also increased but not to such an extent. This is due to the lower metabolic

amino acids in	μg N / plant		analyzed organ: grains								
	c			e			l			el		
	μg N / plant	% of total	% of c	μg N / plant	% of total	% of c	μg N / plant	% of total	% of c	μg N / plant	% of total	% of c
aspartic acid	20,12	12	100	20,96	13	104	22,84	17	114	26,23	17	130
threonine	1,58	1	100	1,32	1	-17	1,20	1	-24	1,15	1	-27
serine	3,03	2	100	2,92	2	-4	2,44	2	-20	2,67	2	-12
asparagine	41,36	25	100	43,78	28	106	32,51	24	-21	47,05	30	114
glutamic acid	21,02	13	100	18,37	12	-13	19,89	15	-5	20,31	13	-3
glutamine	1,32	1	100	1,47	1	111	1,54	1	117	2,01	1	152
proline	3,03	2	100	3,14	2	104	1,88	1	-38	1,70	1	-44
glycine	6,48	4	100	5,19	3	-20	4,51	3	-30	4,40	4	-32
alanine	18,11	11	100	14,06	9	-22	13,00	10	-28	12,21	8	-34
α-amino-n-butyric acid	0,73	0,4	100	0,51	0,3	-30	0,57	0,4	-22	0,62	0,4	-15
citrulline	----	----	----	----	----	----	----	----	----	----	----	----
valine	3,95	2	100	3,26	2	-18	4,29	3	109	3,48	2	-12
cystine	0,78	0,5	100	0,70	0,4	-10	0,42	0,3	-46	0,37	0,2	-53
methionine	---	----	----	----	----	----	----	---	----	----	----	----
isoleucine	1,47	1	100	1,32	1	-10	2,19	2	150	1,12	1	-24
leucine	2,06	1	100	1,40	1	-32	2,13	2	103	1,37	1	-34
tyrosine	2,81	2	100	1,09	1	-61	0,87	1	-70	0,71	1	-75
phenylaline	1,28	1	100	0,94	1	-27	1,07	1	-16	0,81	1	-37
γ-amino-n-butyric acid	1,56	1	100	1,23	1	-21	2,24	2	144	1,94	1	124
ornithine	1,61	1	100	1,29	1	-20	1,28	1	-21	1,27	1	-21
lysine	5,28	3	100	4,15	3	-21	3,84	3	-27	3,24	2	-39
1-methyl-histidine	----	----	----	----	----	----	----	----	----	----	----	----
histidine	1,04	1	100	1,99	1	191	0,70	0,5	-33	1,37	1	132
arginine	26,11	16	100	29,29	19	112	17,91	13	-31	20,49	13	-22
ammonium-N	67,34	29	100	74,80	32	111	43,11	24	-36	40,45	21	-40
total amino-N	164,74		100	158,39		-4	137,36		-17	154,50		-6

Table 6: Changes in amounts of amino acids (μg/plant) in grains at full ripeness after infection of various plant parts at growth stage GS 59 (rest s. table 4)
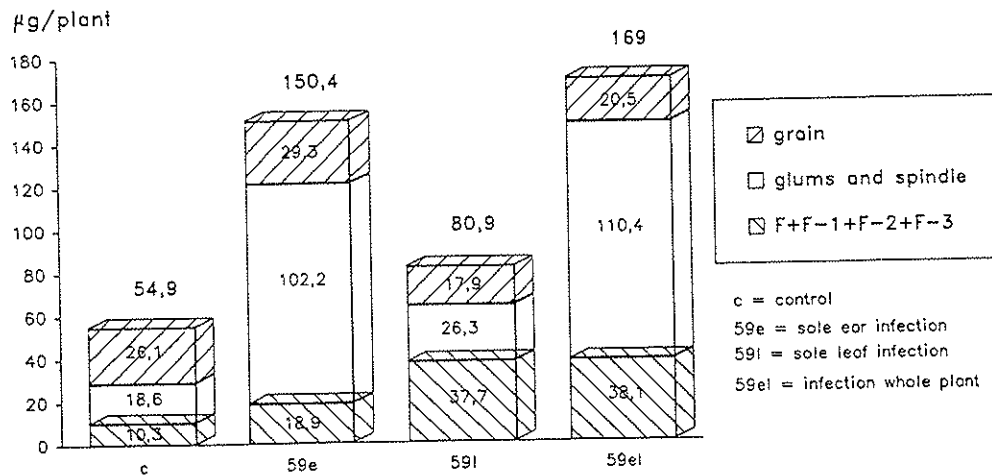

Fig. 14: Effect of Septoria infection at growth stage GS 59 on arginine concentration in wheat plants at full ripeness

activity of these organs at time of infection.

Arginine with 6 C atoms belongs to the basic diamino-monocarbonic acids and, with its 4 N atoms, is an important transport and storage form of nitrogen (Amberger 1983). The high accumulation

of arginine of nearly 300% in these infested plant parts indi-
cates that the diseased plant tries to incorporate the available
nitrogen which is the same in all treatments (fig. 13) as quickly
as possible into a storage pool.

Infection stages GS	spore concentrations ml	classifications of size of particles (g)				total weight (g)
		< 2,8	2,8 - 2,5	2,5 - 2,2	> 2,2	
13	10^6	26	13	3	1	42
32	10^6	15	13	4	3	33
	3×10^5	16	12	4	2	34
	10^5	16	14	4	1	30
	5×10^4	19	13	4	1	36
	10^4	17	14	5	1	37
	10^3	17	14	4	2	37
39	10^6	6	9	6	1	21
	3×10^5	11	8	4	1	26
	10^5	19	8	2	1	29
	5×10^4	20	8	2	0	30
	10^4	22	9	2	0	33
	10^3	24	8	2		34
59e	10^6	18	11	2	1	33
	3×10^5	14	12	4	1	30
	10^5	18	11	3	1	33
	5×10^4	18	12	2	0	33
	10^4	28	10	1	0	39
	10^3	29	7	1		37
59l	10^6	6	10	6	1	24
	3×10^5	9	11	5	1	26
	10^5	16	11	3	0	31
	5×10^4	19	11	3	0	32
	10^4	26	10	1	0	37
	10^3	32	7	1		39
59el	10^6	1	3	6	1	15
	3×10^5	6	11	6	1	25
	10^5	6	10	7	1	24
	5×10^4	19	11	2	1	32
	10^4	21	11	2	0	34
	10^3	25	9	2		36
69e	10^6	13	12	3	1	29
	3×10^5	14	11	3	1	29
	10^5	15	11	3	1	30
	5×10^4	17	10	2	1	30
	10^4	20	11	2	1	34
	10^3	25	7	1		34
69l	10^6	4	9	8	2	23
	3×10^5	4	10	7	2	23
	10^5	8	10	6	1	26
	5×10^4	14	12	3	1	29
	10^4	14	12	4	1	30
	10^3	22	11	1	0	34
69el	10^6	0	1	6	7	14
	3×10^5	1	5	7	4	17
	10^5	4	8	8	2	22
	5×10^4	13	12	3	2	29
	10^4	16	10	1	2	29
	10^3	21	10	2	1	33
control		0	26	12	2	40
L.S.D. 5%		4	2	1	1	4

Table 7: Classification of size of particles after infection with
several spore concentrations (10^6, 3×10^5, 10^5, 5×10^4,
10^4, 10^3 spores/ml; control = non-infected) at various
plant stages (GS 13, 32, 39, 59e, 59l, 59el, 69e, 69l,
69el); e = ear infection, remaining plant (F+F-1+F-2+F-
3) non-infected; l = leaf - culm section (F+F-1+F-2+F-3)
infected, ear non-infected; el = infection of the whole
plant; control = non-infected plant

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It has been known for a long time that Septoria infections lead to a large number of small grains (table 7).

Depending on the sensitivity of the plant's developmental phase to Septoria infections, increasing spore concentrations result in higher numbers of insufficient grains as compared to healthy plants, in other words, the healthier a plant, the higher is the number of high quality grains, and the lower the number of insufficient grains.

This second, important process of reduction in the plant as reaction to the deficient N supply can be interpreted as follows: According to results of Brocklehurst (1977, 1979), and Singh and Jenner (1982), the period of beginning growth of grains just after fertilization is very important because in this phase of cell division the number of endosperm cells is established which determines the final size of the grain and the storage capacity. According to Geißler (1983) the number of endosperm cells is limited or increased by phytohormones, especially cytokinins, in the caryopsis. A deficiency in nitrogen results in low phyto- hormone concentrations which consequently reduces the number of endosperm cells and finally the storage capacity and the grain size. The observed low N supply to grains in our investigations must be seen as the cause of the formation of insufficient grains.

These results show that leaf diseases of wheat caused by Septoria nodorum are more important with regard to yield physiology than has been assumed so far. They further demonstrate that also low spore concentrations even in early stages of plant development, with little expression of symptoms, have negative effects on grain yield and dry matter production.

Septoria infections hardly change the total N content of the plant. The caryopsis of infected plants, however, contains lower amounts of N at full ripeness. This lacking amount of N can be found in plant parts infected by the pathogenic agent; Septoria infections inhibit the translocation of N into reproductive organs. The strong impact of Septoria on chlorophyll, carbohydrate as well as amino acid metabolism of the plant could also be documented.

With our investigations, for the first time deeper informations on the background of the detrimental effects of leaf- and ear diseases by Septoria nodorum, being the cause of sometimes extreme yield losses, could be obtained.

4.   Summary

1. In pot trials with spring wheat (Famos), effects of infection by Septoria nodorum at growth stages GS 13, 32, 39, 59 and 69 on biomass production, yield determining parameters (number of kernels/ear, thousand corn weight, single ear yield), and several plant constituents (chlorophyll, carbohydrate, total N, amino acids) were determined; secondary infections did not occur.

2. With high inoculum concentrations (10^6 spores/ml), 50% to 100

% of leaves and ears (GS 39 to GS 69), and 25% to 70% respectively 5% of leaves (GS 32 respectively GS 13) were infested. The production of biomass was not affected after inoculation in GS 13; otherwise, the greatest decreases were -24% (GS 32), -43% (GS 39), -52% (GS 59), -40% (GS 69).

3. The single ear yield was strongly decreased by infections (GS 32 -23%, GS 39 -52%, GS 59 -66%, GS 69 -66%). In earlier stages, number of kernels per ear were affected, at later stages also the thousand corn weight; leaf infestation had stronger effects than ear infestation.

4. By employing various inoculum cancentrations (10^6, 3×10^5, 10^5, 5×10^4, 10^4, 10^3 spores/ml) at plant stages GS 32 to GS 69, degrees of infestation similar to practical conditions could be obtained; the course of infestation on various plant sections and the ear were determined. Biomass production was decreased even by lowest inoculum concentrations (GS 32 -14%, GS 39 -23%, GS 59 -23%, GS 69 -20%), and single ear yields reduced by 13-22 %. Higher inoculum concentrations resulted in higher losses. The number of kernels per ear was decreased by all spore concentrations, thousand corn weight only with higher inoculum densities.

5. Effects of infection (inoculum concentration 10^6 spores/ml) on chlorophyll concentrations were determined 7 till 28 days after inoculation. Negative effects were significant with infections in GS 39 and later (28 days after inoculation -20 %). Inoculations in GS 59 temporarily increased chlorophyll concentrations in infested and non-infested plant parts (7 d.a.i. +18%), lateron a higher decomposition was observed in the case of leaf infections (28 d.a.i. -34 %); ear infestation did not affect chlorophyll content of the whole plant. After infections in GS 69, the destruction of chlorophyll occurred strongly and suddenly (7 d.a.i.) in infested plant parts; however, after ear infection the content in leaves, and vice versa after leaf infection the content in ears, remained on a higher level.

6. Effects of disease infestation on carbohydrates were significant after inoculation with 10^6 spores/ml. Inoculations in plant stages GS 13, 32, 39 decreased amounts of glucose, fructose, sucrose, and starch during plant growth or at full ripeness. Largest decreases were obtained after inoculations in GS 39, 59, 69 (sum of all determined carbohydrates at full ripeness: GS 39, leaf infestation -56%; GS 59, leaf infestation -36%, ear infestation -19%; GS 69, leaf infestation -60%, ear infestation -63%).

7. Uptake of N of the whole plant was not disturbed by Septoria infection, but the amounts of N in grains of infected plants with the exeption of infections in GS13, are sometimes considerably below the control values. The translocation of nitrogen, from vegetative parts to reproductive organs during the grain filling period is inhibited by Septoria. After all infections, higher amounts of N were found in infected organs (leaves and culms or glumes and spindles) at full ripeness. After leaf infections in growth stages GS 59 or GS 69, leaves

and culms (F+F-1 = flag leaf and second upper leaf with leaf sheaths and corresponding culm; F-2+F-3 = third and fourth upper leaf with leaf sheaths and remaining culm) contained 92% or 97% more in total N, after ear infection glumes and spindles had 183% or 259% more N than non-infected plant parts. These results were confirmed with various inoculum concentrations; with minor disease infestation, for instance (10^4 spores/ml) the following values were obtained: GS 59, leaf infection +21% (leaves and culms, F+F-1, F-2+F-3), GS 59, ear infection +54% (glumes and spindles); GS 69, leaf infection +35% (leaves and culms, F+F-1, F-2+F-3); GS 69, ear infection +133% (glumes and spindles).

8. While the sum of amino acid plus amide nitrogen of the whole plant after infection of various plant parts remaines more or less on the same level as in control plants, considerable differences occur in the amino acid composition of analyzed organs. In infected parts, concentrations of some amino acids are decreased, others increased. Particularly conspicuous is the drastic increase in arginine in contaminated organs.

9. The results are discussed with respect to yield physiology; the consequences of retention of nitrogen in infested plant organs, as well as effects on formation, translocation and incorporation of carbohydrates, chlorophyll, and amino acids are pointed out. The investigations demonstrate the strong influence of Septoria infection on yield of wheat, and indicate causal relationships.

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