Neth. J. Pl. Path. 81 (1975) 1–13

An ecophysiological approach to crop losses exemplified in the system wheat, leaf rust and glume blotch[1]

III. Effects of soil-water potential on development, growth, transpiration, symptoms, and spore production of leaf rust-infected wheat

A. F. VAN DER WAL, HANNEKE SMEITINK and G. C. MAAN

Accepted 8 July 1974

Laboratory of Phytopathology, Agricultural University, Wageningen

Abstract

Uninfected plants of spring wheat 'Kolibri' and plants infected with leaf rust were grown in a climate chamber at three soil-water potentials: -1025 J.kg^{-1} (D, 'dry', near wilting point), -425 J.kg^{-1} (M, 'medium', intermediate), and -250 J. kg^{-1} (W, 'wet', near saturation point). At lower water potentials plant development was faster, growth rate lower, and transpiration less than at higher water potentials. Growth and transpiration of plants at W were approximately twice those at D. Plants at M showed an intermediate response. Growth and yield of rusted plants grown at M were only slightly less than those of the uninfected controls, whereas at D and W considerable losses of plant dry weight and yield were caused by the rust. Infection type, pustule size and spore production were related to soil-water potential; at M, the pustules were smallest and the spore production was minimal. Results show a marked effect of soil-water potential on plant morphogenesis, and indicate that resistance of 'Kolibri' to leaf rust was related to soil-water potential. Optimal resistance was found at M, the intermediate soil-water potential.

Introduction

Water moves from the soil through the plant into the atmosphere along gradients of water potential (Boyer, 1969). Since gradients of water potential may effect plants in health and disease, a climate chamber experiment was carried out to study the effects of soil-water potential on the healthy and the rusted wheat plant (*Triticum aestivum* L.). Only one cultivar, the spring wheat 'Kolibri', was used. Uninfected plants and plants infected with rust were grown at three different water potentials. In the previous paper, the experimental factor was 'disease treatment', represented by four levels: uninfected, leaf rust, glume blotch, and leaf rust + glume blotch. Introduction of a further experimental factor, viz. soil-water potential, necessitated a reduction of

[1] I. A simple and accurate balance for the continuous measuring and recording of (evapo-) transpiration of plants in indoor experiments. P. Tegelaar and A. F. van der Wal, Neth. J. Pl. Path. 80 (1974): 77–84.
II. Development, growth, and transpiration of uninfected plants and plants infected with *Puccinia recondita* f.sp. *triticina* and/or *Septoria nodorum* in a climate chamber experiment. A. F. van der Wal and M. C. Cowan, Neth. J. Pl. Path. 80 (1974): 192–214.

the number of levels of the factor 'disease treatment' in view of the limitations imposed by the available space and manpower. The use of rust in the present experiment was based on the observation that the transpiration rate of the rusted plant increased, at least during a certain period after infection. This increase is of interest since it may affect photosynthesis and other processes under conditions of 'water stress'.

Effects of rust infection on transpiration were reported before (e.g. Weiss, 1924; Johnston and Miller, 1940). In this early work essential elements in the description of environment, plant, or pathogen are missing (Gates, 1968). Here, due attention is payed to the description of environment, plant, and pathogen, with the aim to provide a starting point for analytical studies. Cowan and Zadoks (1973) demonstrated the effect of soil-water potential on transpiration of uninfected and rusted wheat seedlings, and on uredospore production. Van der Wal and Cowan (1974) presumed that the condition of the plant, its 'state', at inoculation time had a decisive effect on subsequent disease development. Differences in morphological development between plants of the same age and cultivar reflect differences in 'state'. By changing soil-water potential in an otherwise identical environment, various water potential differences between soil and air are applied to which plant development and growth can respond. The present experiment was performed to find out whether the 'state' of the plant at infection time affects loss. The wheat plants were observed during the full growth period. No effort was made to relate morphological and physiological differences between plants from various treatments to possible biochemical differences.

Methodology

Terminology in this paper is similar to that used by Van der Wal and Cowan (1974), where the experimental design, variables, responses, statistical methods, materials and techniques (e.g. a detailed description of the conditions in the climate chamber), inoculation techniques, and methods of measuring development, growth, and transpiration as applied in the present experiment are described.

Experimental factors. Disease treatment is applied at two levels, viz. C (uninfected plant) and R (plant infected with rust, *Puccinia recondita* (Rob. ex Desm.) f. sp. *triticina* Eriks. Water potential, a situational factor in the previous experiment, is introduced here as the second experimental factor at three levels: $-1025\ J.kg^{-1}$ (D, 'dry', near wilting point), $-425\ J.kg^{-1}$ (M, 'medium', intermediate), and $250\ J.kg^{-1}$ (W, 'wet', near saturation).

Experimental design and sampling. On each sampling date, all six plants of a sample were taken from one bucket. Consequently, the 'bucket effect' is confounded with the 'sampling time effect'. Successive sampling was done for dry weight and leaf area determination, usually with weekly intervals, but in the second half of the growth period, as it became apparent that the development proceeded more slowly than expected, the sampling intervals had to be extended to save plants for the final sampling.

Responses. The developmental stage of the plants was recorded weekly. Axial development was indicated by the number of stems per plant, a stem considered here as an

axis with at least one node. The number of heads per plant was counted. Dry weight of roots, stems, leaves, and heads was determined and expressed in units of weight per plant. Area of leaves, turgescent enough for a fair measurement, and transpiration were measured as in the previous experiment. Kernel number and kernel weight were determined only in the final samples at each of the three water potential levels. The percentage of infection was determined as the percentage leaf area disrupted by the sporulating surface of the pustules. Figures for percentage of infection are therefore considerably lower than in the previous paper, although identical inoculum densities were used. In addition, pustule size and spore production were measured. Pustule size was measured according to Mehta and Zadoks (1970).

Materials and techniques. After pregermination, the seedlings were planted in soil with a water potential of c. $-400\ J.kg^{-1}$. Between day 15 and day 25, the soil-water potentials were gradually adjusted to the values desired. No wilting was observed during or after the adjustment period.

Inoculation was carried out on day 42, when the plants at D had the development stage 37 (Table 1), with the flag leaves just unfolded. Plants at M and W developed more slowly, but they had a greater leaf area than the plants at D (Fig. 2). Half the number of buckets with plants at each water potential level was inoculated. The spore density was c. 20 spores per mm^2. Unfortunately, the effect of water potential on the development of the plants was greater than expected. The plants at M and W 'outgrew' their infection. The aim was to have almost equally infected plants at all water potential levels. Plants at M were inoculated again in stage 60, on day 66, and plants at W in stage 58, on day 73. Spore density was c. 10 spores per mm^2, half the density used at the first inoculation, to compensate for the spores already on the leaves due to cross inoculation by rusted neighbour plants. In all inoculations c. 90% of the spores germinated.

To collect the spores produced by the inoculated plants, a cuff of smooth cardboard was placed around the six plants of a bucket. Its upper diameter was large enough to intercept all spores falling from the leaves. Its lower diameter fitted close round the stem bases of the plants. At the lower end of the cuff, the cardboard was folded upwards to hold the spores falling from the leaves on the cuff. Before sampling, the rusted leaves were tapped gently, and the ripe spores fell on the cuff. The spores on the cuff were collected by means of a cyclone collector (Mehta and Zadoks, 1970).

Results

Development. The developmental stages of the plants are given in Table 1. On day 35, 20 days after the day on which the soil-water potentials began to diverge, the effect of soil-water potential on developmental stage became visible. The plants at D developed rapidly, those at W were slow in this respect, and plants at M were intermediate. The number of stems per plant was determined from day 42 until harvest. An analysis of variance applied to stem numbers yields a clear water potential effect ($p < 0.01$), but no effect of time. The average number of stems per plant developed at D was 6.6, at M 8.5, and at W 9.5. The number of heads per plant was determined from day 56 onwards to harvest. The effects of time and water potential are both significant ($p < 0.01$). The earliest heading appeared in D; on day 56, 2.4 heads per

Table 1. Development stages of the uninfected plant (C) with time (t) in days after planting at the water potentials -1025 J.kg^{-1} (D), -425 J.kg^{-1} (M), and -250 J.kg^{-1} (W). The development is expressed in the decimal scale by Zadoks et al. (1974). A * means no observation.

t	0	7	14	28	35	42	49	56	63	70	84	98	105	112
D				27	31	37	50	58	64	73	85	92		
M	07	13	22	27	30	32	39	56	60	71	77	*	92	
W				27	30	32	37	43	52	58	73	*	*	92

*Tabel 1. Ontwikkelingsstadia van de niet-geïnfecteerde plant (C) in de loop van de tijd (t) in dagen na het planten, bij de waterpotentialen —1025 J.kg^{-1} (D), —425 J.kg^{-1} (M) en —250 J.kg^{-1} (W). De ontwikkeling is aangeduid met behulp van de decimale schaal van Zadoks et al. (1974). Een * betekent geen waarneming.*

plant were visible, at harvest 6.3. At M 0.8 heads per plant were visible on day 56, but at harvest time there were 8.0 heads. At W the first heads were seen on day 63, whereas at harvest time 8.4 heads per plant were counted. Disease had no significant effect on the number of heads ($p < 0.05$). The number of stems was not tested for disease effect, because of lack of data.

Fig. 1. Mean dry weight per plant (w) [10^{-3}.kg.plant^{-1}] in C and R at D, M and W, versus time (t) [day] from day 28 to day 112. Symbols as in Table 2; ■... = C_W, □.... = R_W, ▲-- = C_M, △--- = R_M, ●— = C_D, ○— = R_D. For the parameters of the regression curves see Table 4.

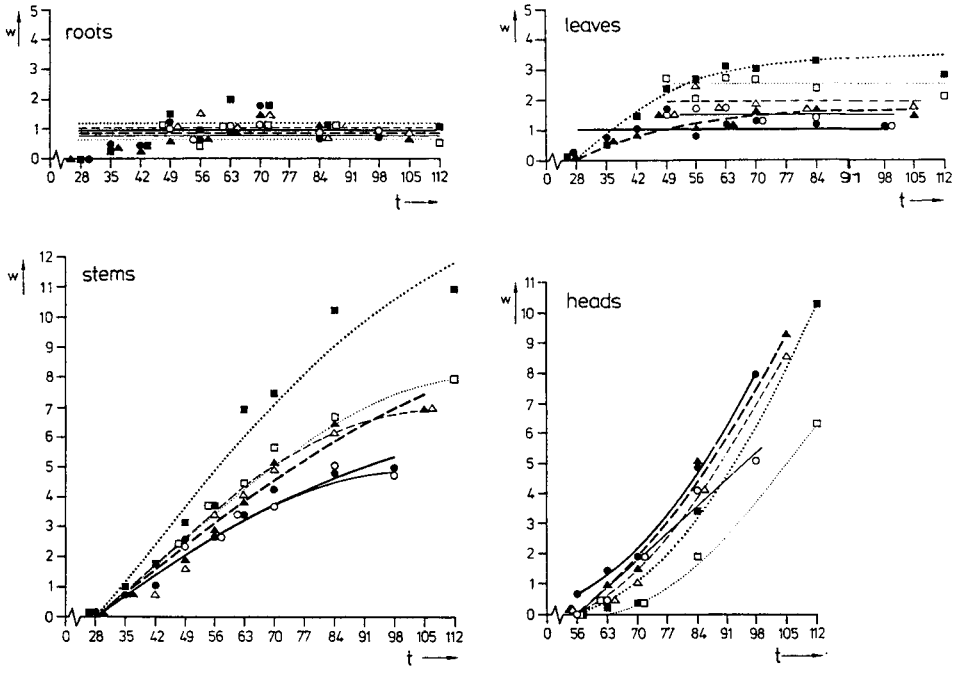

Fig. 1. Gemiddeld drooggewicht per plant (w) [10^{-3}.kg.plant^{-1}] in C en R bij D, M en W, tegen de tijd (t) [dag] van dag 28 tot dag 112. Het gebruik van de symbolen is als aangegeven in Tabel 2; ■... = C_W, □... = R_W, ▲-- = C_M, △-- = R_M, ●— = C_D, ○— = R_D. Voor de parameters van de regressiecurven zie Tabel 4.

Table 2. Student's t-test has been applied to test the significance of the differences between disease treatment and water potential levels. For C-R at D, M, and W and for the combinations C_W-C_M, C_W-C_D, and C_M-C_D, the regression of the difference between two concomitant values (y_i) per observation day (x_i) versus time (x) was calculated, using the regression equation $y_i = a + bx_i$. The t-values of the regression constants (a) and the regression coefficients (b) are tabulated in order to give an idea about the 'noise' in these data. There are n-2 = 4 degrees of freedom for t-tests of roots, leaves, stems and leaf area in the C-R combinations, and 7 for C_W-C_M, C_W-C_D and C_M-C_D. There were only 3 degrees of freedom for tests of heads in all combinations.
Symbols: C = uninfected plant; R = plant infected with rust: C_D, C_M and C_W = uninfected plants grown at D, M, and W (waterpotential levels, Table 1); roots = dry weight of roots per plant; leaves = dry weight of leaves per plant; stems = dry weight of stems per plant; heads = dry weight of heads per plant; leaf area = leaf area per plant.

	Roots		Leaves		Stems		Heads		Leaf area		Transpiration	
	a	b	a	b	a	b	a	b	a	b	a	b
$(C\text{-}R)_D$	0.29	0.04	−1.37	0.66	0.36	0.18	−0.32	1.94	−1.34	1.69	−5.81	5.02
$(C\text{-}R)_M$	−1.86	1.44	−1.02	0.39	−0.70	0.76	1.06	1.15	−0.23	0.10	−0.58	3.43
$(C\text{-}R)_W$	1.10	0.28	−0.11	1.95	0.96	2.38	−2.51	7.42	0.97	0.26	−18.10	10.00
C_W-C_M	0.32	0.16	0.09	3.40	−1.58	7.31	−1.28	0.85	0.76	1.42	13.37	5.02
C_W-C_D	−0.19	0.43	−0.42	4.18	−3.10	9.23	−2.08	2.02	0.73	1.69	− 4.41	18.81
C_M-C_D	−1.07	0.63	−1.38	3.00	−3.02	5.37	−5.83	7.83	−0.26	2.34	− 2.61	7.59

Tabel 2. De t-toets van Student is gebruikt om de verschillen te toetsen tussen ziektebehandelingsniveaus en niveaus van waterpotentiaal. Voor de combinaties C-R bij D, M en W en voor C_W-C_M, C_W-C_D, C_M-C_D, werd de regressie berekend van het verschil van twee bijeengevoegde waarden (y_i) per waarnemingsdag (x_i) tegen de tijd(x), middels de regressievergelijking $y_i = a + bx_i$. De t-waarden van de regressieconstanten (a) en de regressiecoëfficienten (b) zijn vermeld met het doel een indruk te geven van de 'ruis' in deze waarnemingen. Er zijn n-2 = 4 vrijheidsgraden voor de t-toets van roots, leaves, stems en leaf area in de C-R combinaties, en 7 voor die in C_W-C_M, C_W-C_D, C_M-C_D. In alle combinaties waren er slechts 3 vrijheidsgraden voor de toetsen van heads.
Symbolen: C = niet geïnfecteerde plant; R = plant geïnfecteerde met roest; C_D, C_M en C_W = niet geïnfecteerde planten opgegroeid bij waterpotentiaal D, M en W (Tabel 1); roots = drooggewicht van de wortels per plant; leaves = drooggewicht van de bladeren per plant; stems = drooggewicht van de stengels per plant; heads = drooggewicht van de aren per plant; leaf area = bladoppervlak per plant.

Growth. The results of measurements are given in Fig. 1. To test the significance of the differences between curves the 'difference method' described in Van der Wal and Cowan (1974) was used (Table 2). Six combinations of levels of disease treatment and water potential were studied for each response: (C–R) at D, M, and W; and C_W–C_M, C_W–C_D, and C_M–C_D. The decisions regarding significance of the effects are summarized in Table 3. The parameter values obtained after the application of various regression models on the data, are given in Table 4 together with the models used.

There was no effect of disease treatment, time, or water potential on root weight during the period from day 28 to harvest. The regression coefficients b (Table 3) did not differ significantly from zero. The absence of effects is possibly due to the inadequacy of the technique of root weight determination.

Time and water potential clearly affected dry weight of leaves per plant (Table 2 and 3). The weight of leaves per plant at W was twice that at D. No effect of disease could be shown.

For dry weights of stems, time and water potential effects were found. At D and M, final dry weights of stems were 5 and 7 g per plant respectively, but there was no

Table 3. The decisions about the significance of the differences between responses in the disease treatment and water potential combinations listed in Table 2. For symbols see Table 2. A + indicates significance, a – no significance at $P \leqslant 0.10$ (two tailed). The decisions are based on Student's t-values

	Roots		Leaves		Stems		Heads		Leaf area		Transpiration	
	a	b	a	b	a	b	a	b	a	b	a	b
$(C\text{-}R)_D$	–	–	–	–	–	–	–	–	–	–	+	+
$(C\text{-}R)_M$	–	–	–	–	–	–	–	–	–	–	–	+
$(C\text{-}R)_W$	–	–	–	–	–	+	+	+	–	–	+	+
$C_W\text{-}C_M$	–	–	–	+	–	+	–	–	–	–	+	+
$C_W\text{-}C_D$	–	–	–	+	+	+	–	–	–	–	+	+
$C_M\text{-}C_D$	–	–	–	+	+	+	+	+	–	+	+	+

Tabel 3. Beslissingen over de significantie van de verschillen tussen responsies bij de niveaus van ziektebehandeling en waterpotentiaal vermeld in Tabel 2. Voor de symbolen zie Tabel 2. Een + betekent significantie, een – geen significantie bij $P \leqslant 0.10$ (tweezijdig). De beslissingen berusten Student's t-waarden.

disease effect. In W, however, the effect of disease treatment was evident, final stem dry weights of C and R being 11 and 8 g per plant respectively.

Differences between curves of head dry weight were only found for $(C-R)_W$, and for C_M–C_D (Table 3). Analysis of variance applied to the yield data showed significant effects of disease and water potential ($p < 0.01$) on kernel number and kernel weight per plant (Table 7). In addition, an interaction of disease and water potential was demonstrable ($p < 0.05$). Kernel weight at M was only slightly reduced by rust infection (9%), whereas at D and W it was seriously reduced (c. 40%). At M, no reduction in kernel number was observed, but at D and W, the kernel number was severely reduced after rust infection (c. 30%). Average kernel weight was reduced by rust, most seriously in R_W. Fig. 2 shows the leaf area per plant versus time at the three water potential levels. The application of the 'difference method' on the data yielded only significance of the difference between C_M and C_D (Table 3). At D, the plants developed only c. 40% of the leaf area of plants at W. The effect of disease on turgescent leaf area is evident at W, but is hardly visible in M and D. The absence of significance of differences may be attributed to the segment of the curves compared.

Transpiration. At D, transpiration by C was only c. 40% of that at W (Fig. 3a); at M, it was c. 60%. The effects of disease varied with the water potential applied. At D, transpiration by R was less than that by C (Fig. 3b, Table 3), the period between day 49 and day 77 excepted. The result was a lower transpiration figure at harvest time. At M, the transpiration rate of R was greater than that of C during the whole period following infection. At W, the transpiration of C was higher than that of R, a short period after inoculation excepted. At harvest time the difference was c. 9%.

Infection type. The infection types varied with soil-water potential. Seven days after inoculation, type 3 was observed on flag leaves at D and W, type 2 at M. Some 14 days after inoculation the infection type at D changed to 4 and stayed at that level until ripening. At W the scores changed to 4 about 1 month after inoculation, but later type 3 was seen again. Seven days after inoculation type 2 was observed on plant at

Fig. 2. Mean turgescent leaf area (la) [10^{-2}.m^2.$plant^{-1}$] versus time [day] in C and R at D, M, and W. Symbols as in Fig. 1. The shape and position of the lines were obtained by eye-fitting.

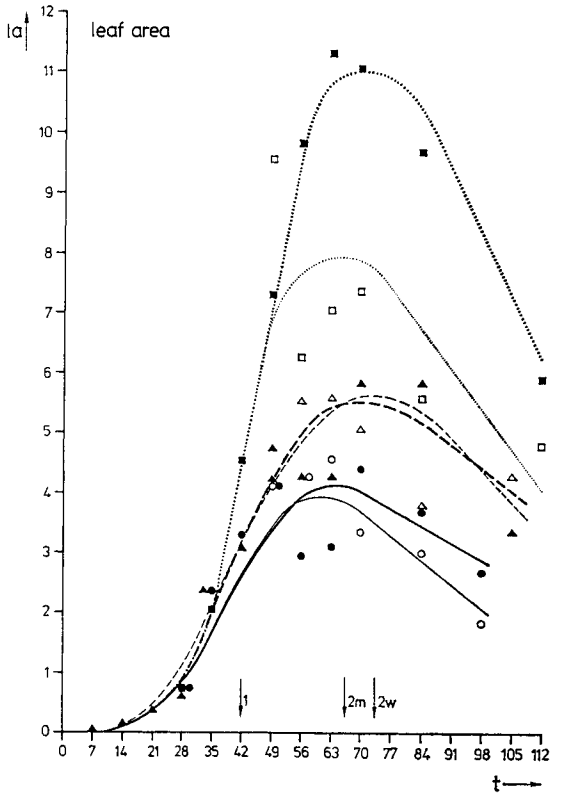

Fig. 2. Gemiddeld turgescent bladoppervlak (la) [10^{-2}.m^2.$plant^{-1}$] tegen de tijd [dag] voor C en R bij D, M en W. Symbolen als in Fig. 1. De lijnen zijn op het oog getekend.

M, but gradually the scores went up to 4. On the lower leaves, the infection type scores were usually one scale unit lower than the scores on flag leaves.

Pustule size. The largest pustules were found on plants at D, whereas at M the pustules were relatively small (Table 5). An analysis of variance showed a significant effect of time as well as of water potential treatment, both at the 1 % level.

Percentage of infection. Table 6 shows the percentages of infection versus time for each water potential treatment. The figures only represent the leaf area disrupted by open pustules, and they are calculated as weighed averages per leaf level per plant. Multiplication of these figures by the corresponding leaf area data per plant yields the total rusted area per plant. At M, the percentage of infection is lower than at D or W.

Spore production. Spore production (Fig. 4) was lowest at M, more at D, and highest at W. The effect of the second inoculation on spore production at W was more prominent than at M.

Table 4. Parameter values estimated by means of the calculation of the regression of dry matter and transpiration data [10^{-3} kg] on time [day]. The regression equations (REGR) used are given in the table. For symbols see Table 2. A * means that no relevant value has been estimated, due to certain properties of the computer programme used. It indicates that the variance of the data in comparison to the increase with time was too large to calculate a proper estimate. The regression curves are shown in Fig. 1 and 2. The transpiration regression was done from day 28 to harvest.

		D		M		W		REGR
		C	R	C	R	C	R	
roots	a	1.0	0.8	0.9	1.1	1.2	0.7	$y = a$
leaves	a	1.01	1.47	1.68	1.85	3.65	2.54	$y = a + be^{cx}$
	b	*	*	− 6.17	*	−11.80	*	
	c	*	*	−0.051	*	−0.041	*	
stems	a	10.26	6.08	15.48	7.31	18.47	9.61	$y = a + be^{cx}$
	b	−13.70	−12.90	−20.24	−41.91	−27.18	−22.80	
	c	−0.011	−0.025	−0.009	−0.041	−0.012	−0.024	
heads	a	2.77	26.59	− 9.48	− 3.76	− 5.02	− 3.36	$y = a + be^{cx}$
	b	0.70	−36.14	4.35	0.91	1.23	0.81	
	c	0.028	0.005	0.014	0.025	0.023	0.022	
transpi-	a	−1940	−1782	−3060	−3300	−4310	−3460	$y = a + bx^{cx}$
ration	b	61.7	59.6	88.5	95.3	131	111	

*Tabel 4. Parameterwaarden geschat door middel van de berekening van de regressie van droge stof en transpiratiemetingen [10^{-3}kg] op de tijd [dag]. De gebruikte regressievergelijkingen (REGR) zijn in de tabel vermeld. Voor de symbolen zie Tabel 2. Een * betekent dat geen relevante schatting is gemaakt wegens bepaalde eigenschappen van het gebruikte computerprogramma. Het betekent hier, dat de variantie in de gegevens in verhouding tot de toename in de tijd te groot was voor een goede schatting. De regressiecurven zijn te zien in Fig. 1 en 2. De regressie van de transpiratie gebeurde vanaf dag 28 tot de oogst.*

Table 5. Mean pustule size [$10^{-9}m^2$] of pustules on the second leaves of rusted plants versus time (t) at D, M and W. For the symbols see Table 1.

t	D	M	W
49	51	43	48
56	87	54	65
63	105	86	87
70	104	77	99

Tabel 5. Gemiddeld oppervlak van uredosori [$10^{-9}m^2$] op het tweede blad van met roest geïnfecteerde planten tegen de tijd (t) bij D, M en W. Voor symbolen zie Tabel 1.

Table 6. Percentage of infection of plants at D, M and W versus time. The figures are weighed means. For each leaf layer, the estimated percentage of infection was multiplied by the corresponding leaf area, and the sum of the products was divided by the total leaf area per plant.

t	D	M	W
49	3.5	1.4	3.0
56	8.9	1.4	5.8
63	7.2	1.6	3.3
70	7.0	2.9	2.2
84	6.0	4.4	5.5

Tabel 6. Het percentage aantasting van de planten bij D, M en W tegen de tijd. De getallen zijn gewogen gemiddelden per plant, berekend na bepaling van het aantastingspercentage per bladlaag en vermenigvuldigd met het bijbehorend bladoppervlak. De zo verkregen getallen werden opgeteld en gedeeld door het totale bladoppervlak per plant.

Fig. 3a. Mean transpiration [kg.plant^{-1}] in C and R at D, M, and W, versus time (t) [day] in the period from planting to harvest. For symbols see Fig. 1. Parameter values of the regression curves are given in Table 4.
Fig. 3b. Mean transpiration difference [kg.plant^{-1}] between C and R at D, M, and W, versus time (t) [day] in the period from day 49, one week after the first inoculation, to harvest. Arrows indicate inoculations. ↓1: first inoculation, ↓2M: second inoculation on R_M, ↓2W: second inoculation on R_W. ◐ — = $(C\text{-}R)_D$, ▲-- = $(C\text{-}R)_M$, ▯... = $(C\text{-}R)_W$.

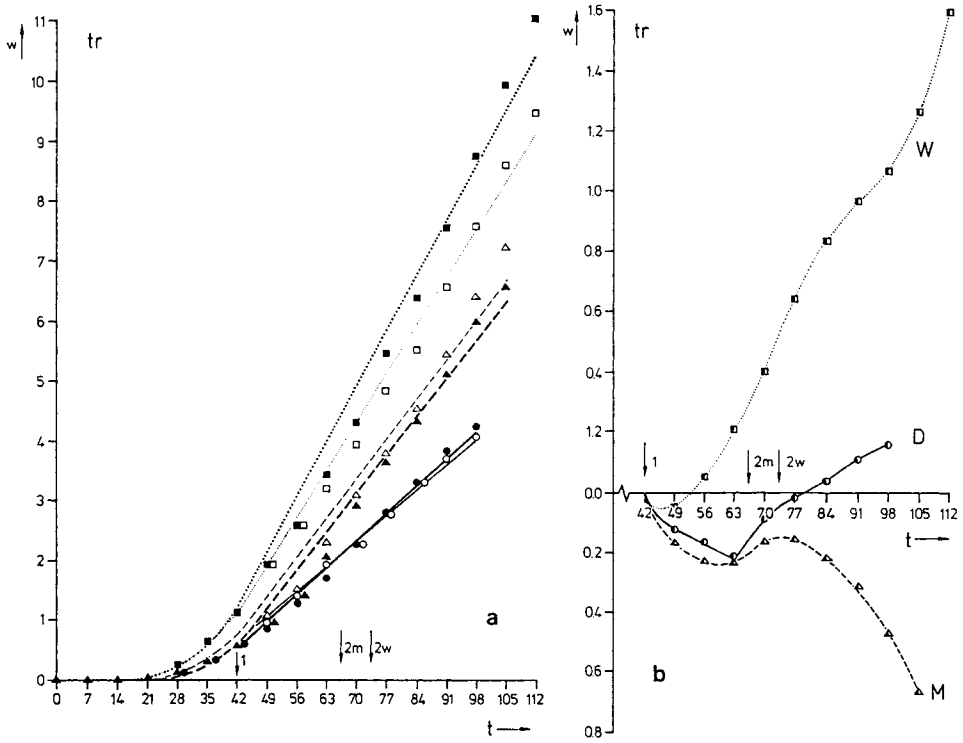

Fig. 3a. Gemiddelde transpiratie [kg.plant^{-1}] van C en R voor D, M en W tegen de tijd (t) [dag], van het uitplanten tot de oogst. Voor symbolen zie Fig. 1. De parameters van de regressiecurven worden gegeven in Tabel 4.
Fig. 3b. Gemiddeld verschil in transpiratie [kg.plant^{-1}] tussen C en R voor D, M en W, tegen de tijd (t) [dag] vanaf dag 49, één week na de eerste inoculatie, tot de oogst. Pijlen geven inoculaties aan. ↓1: eerste inoculatie, ↓2M: tweede inoculatie bij R_M, ↓2W: tweede inoculatie bij R_W. ◐ — = $(C\text{-}R)_D$, ▲-- = $(C\text{-}R)_M$, ▯... = $(C\text{-}R)_W$.

Resistance. When the figures of the responses of infection type, pustule size, and spore production are considered, they all indicate a more resistant reaction of the rusted plants at M, as compared with D and W.

Summary of results. The various aspects of the 'behaviour' of the uninfected and the diseased plant can be summarized as follows. From day 28 onwards, transpiration and leaf area had been greater at higher water potentials. Development was retarded at wetter soils. Increase in growth rate was related to decrease in 'development rate'. At the time of the first inoculation (day 42), leaf area per plant differed already. At D

Fig. 4. Mean spore production (w) [10^{-5}kg.plant^{-1}] of rusted plants at D,M, and W versus time (t) [day] in the period from day 49, one week after inoculation, to harvest. Symbols as in Fig. 1 and 3.

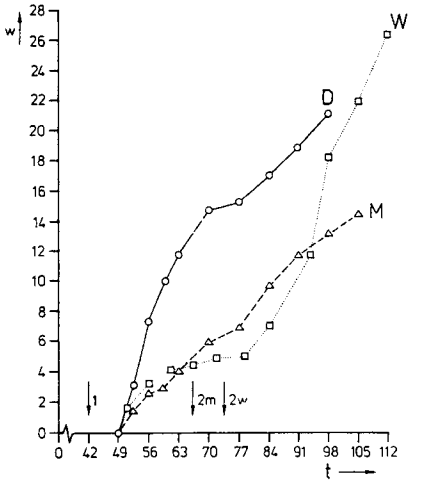

Fig. 4. Gemiddelde sporenproduktie (w) [10^{-5}.kg.plant^{-1}] van planten geïnfecteerd met roest bij D, M en W tegen de tijd (t) [dag] vanaf dag 49, één week na inoculatie tot de oogst. Symbolen als in Fig. 1 en 3.

and M, approximately half of the estimated maximum leaf area was reached by then, at W only 40%. Only at D the flag leaves were just visible. All plants were subjected to an equally dense 'shower' of spores. Seven days later, the percentage of infection at M was considerably lower than at D and W; the latter two did not differ much from each other in this respect. Because of the great reproducibility of the inoculation technique itself, the difference in percentage of infection can be explained as a difference in resistance. The increase in percentage of infection at M after the first inoculation was negligible, as compared with that at D and W. These figures suggest a higher resistance of plants at M as compared with those at D and W.

Transpiration of R had been greater than of C at all water potentials during the first seven days after inoculation. During the second week after inoculation, the transpiration of R at W was lower than that of C, related with lower scores of turgescent leaf area and stem weights of R. Growth had also been hampered by the rust. At D and M, transpiration of R was greater than that of C. At D, this remained so for a period of 35 days after inoculation, and at M for the full period after inoculation to harvest.

At D, rust grew rapidly; the percentage of infection increased and the sporulation rate was high. From day 63, and especially in the period from day 70 to day 77, sporulation rate was reduced. This coincides with an almost abrupt change in the transpiration figure of the difference C–R, and the beginning of a faster reduction in turgescent leaf area of R than of C. In the following period, the uninfected plant transpired more than the rusted plant at D. Sporulation rate is constant in that period, but lower than in the period before day 63.

At M, the growth of the rusted plant outrated the increase of the rusted area. The transpiration rate of R came again near to that of C, but, as result of the second

Table 7. Mean kernel weight [10^{-3}.kg.plant^{-1}], mean kernel number [plant^{-1}] and average kernel weight [10^{-6}.kg.kernel^{-1}] determined at harvest time for each of the six combinations of treatment levels.

	Kernel weight			Kernel number			Average kernel weight		
	D	M	W	D	M	W	D	M	W
C	6.2	7.3	7.8	174	189	202	35.7	38.6	38.7
R	3.9	6.6	4.5	117	198	154	33.5	33.4	29.3

Tabel 7. Gemiddeld korrelgewicht [10-^{3}.kg.plant^{-1}], gemiddeld korrelaantal [plant^{-1}] en het gemiddeld korrelgewicht [10^{-6}.kg.kernel^{-1}] bepaald bij de oogst voor elk van de zes combinaties van behandelingsniveaus.

infection, the rusted plants transpired much more than C, and this remained so until harvest. Sporulation rate increased after the second inoculation.

At W, the lower leaves lost their turgor rapidly from the second week after inoculation onwards. After day 56, the transpiration of the uninfected plant was greater than that of R. The growth of the heads was slowed down. A slight increase in transpiration rate of R was visible in the period from day 77 to 91, coinciding with an increase in sporulation rate. The sporulation rate decreased slightly in the period from day 98 to harvest time, in which period the difference in transpiration C–R increased further.

Where the transpiration of the rusted plant was initially greater and later lower than that of the control (at D and W), the kernel number of R was reduced. Only at M, kernel number of R was not lower than that of C.

In conclusion, morphogenesis of the wheat plant was largely affected by soil-water potential. In the case of drier soils, the development stages succeeded each other with shorter intervals, and axial development was reduced. Growth and transpiration became less at lower soil-water potentials. In the case of the rusted plants, lowest scores of percentage of infection, infection type, pustule size, and spore production were obtained at the intermediate soil-water potential M. The pattern of transpiration of rusted plants after infection was related to soil-water potential, but in all cases transpiration increased during the first week after infection. No reduction in kernel number by rust infection was found at M; yield reduction was minimal at M too, whereas considerable reductions in kernel number and yields were found at the other two water potentials.

Discussion

The three groups of plants showed differences in appearance greater than the usual differences between cultivars grown commercially in any particular area. Visitors often hardly believed that all plants belonged to the same cultivar and that the difference had been induced by varying soil-water potential only. In the present paper, as in the previous one (Van der Wal and Cowan, 1974), the ripening of the plants differed from that of a 'normal' crop in the field. Heat damage by the lamps led to early maturation of the heads (French: *échaudage*).

The effects of water potential on morphogenesis and resistance have been shown

beyond doubt within the framework of the situational factors chosen, i.e. under the conditions and with the cultivar-race combination described here. It is not known whether the conclusions with respect to resistance can be generalized and applied to other cultivars and other environmental conditions. Apparently, conditions for growth of the rust were different in the leaves of plants grown at different water potentials. These differences in growth conditions can be attributed to differences in physical properties of the leaves like leaf water potential and/or to differences in morphological and chemical composition of the leaves. There are two indications for effects of soil-water potential on the plant water potentials. Firstly, the transpiration of rusted plants increased after infection during the first week, as was found before (Van der Wal and Cowan, 1974). Secondly, the yield figures show a reduction of the number of kernels per plant of rusted plants at D and W, but not at M. Under the present environmental conditions, 'water stress' was likely to occur (Fischer, 1973). The plants grown at the three levels of soil-water potential apparently differed enough in 'state' to show different responses to the 'extra water stress' caused by the rust infection.

Samenvatting

Een ecofysiologische benadering van 'schade', geïllustreerd aan het systeem tarwe, bruine roest en kafjesbruin.
III. Effecten van de waterpotentiaal van de grond op ontwikkeling, groei, transpiratie, symptomen en sporenproduktie van tarweplanten, geïnfecteerd met bruine roest

De invloed van een milieufactor, de waterpotentiaal van de grond, op de ontwikkeling en groei van de tarweplant, en op de waard-parasiet verhouding, werd onderzocht onder klimaatkamer-omstandigheden. Niet geïnfecteerde planten (C) werden vergeleken met planten die met roest geïnfecteerd waren (R). De waterpotentiaal werd gesteld op drie niveaus: $-1025\ J.kg^{-1}$ (D, droog, nabij het verwelkingspunt), $-425\ J.kg^{-1}$ (M, matig nat, een tussenwaarde), en $-250\ J.kg^{-1}$ (W, nat, nabij het verzadigingspunt).

Er werd een duidelijk effect van de waterpotentiaal op de ontwikkeling, groei en transpiratie van de tarweplant (zomertarwe, 'Kolibri') gevonden. De planten doorliepen de opeenvolgende ontwikkelingsstadia met kortere tussenpozen naarmate de waterpotentiaal lager was (Tabel 1). Ook werd de ontwikkeling van zij-assen minder bij afnemende waterpotentiaal. Groei en transpiratie waren geringer bij lagere waterpotentialen (Fig. 1 en 2, Tabel 2 en 3).

Infectietype, aantastingsgraad, maat van sporenhoopjes en sporenproduktie werden beïnvloed door de waterpotentiaal van de grond. De laagste waarden werden waargenomen voor geïnfecteerde planten die groeiden bij $-425\ J.kg^{-1}$ (M). Dit duidt op een verschil in resistentie tussen de planten, gerelateerd aan de waterpotentiaal van de grond waarop zij groeiden (Fig. 3, Tabel 5 en 6).

Verschillen in waterpotentiaal in de grond kunnen blijkbaar niet alleeen verschillen in ontwikkeling, groei en transpiratie van de plant, maar zij kunnen ook verschillen in resistentie van de plant teweegbrengen.

Het effect van de roestinfectie op de korrelopbrengst bleek eveneens samen te hangen met de waterpotentiaal (Tabel 7). Bij alle drie waterpotentialen verminderde het gemiddeld korrelgewicht door de roest en bij D en W ook het korrelaantal, maar niet

bij M. Het verloop van het verschil in transpiratie tussen C en R, het patroon in de afname van het turgescente bladoppervlak, en het effect van de roest op het korrelaantal, doen vermoeden dat bij roestinfectie ook veranderingen van de waterpotentialen in de plant (zoals het turgescent blijven van nog niet gekoloniseerd plantweefsel, het al dan niet afstoten van jonge vruchten van belang zijn bij het ontstaan van 'schade'.

Acknowledgments

The authors are indebted to Mr A. H. Gerritsen for his interest and assistance in the operation of the climate chamber. The services of the Drawing Office and the University Computer Centre are much appreciated. Mr H. J. A. van Beckum's correction of the English text is gratefully mentioned. Dr J. C. Zadoks' continuous interest has been stimulating.

References

Boyer, J. S., 1969. Measurement of the water status of Plants. Ann. Rev. Plant Physiol. 20: 351–364.

Cowan, M. C. & Zadoks, J. C., 1973. Relations between soil water potential and disease in wheat seedlings infected by *Puccinia recondita*. Neth. J. Pl. Path. 79: 1–4.

Fischer, R. A., 1973. The effect of water stress at various stages of development on yield processes in wheat: In: Plant response to climatic factors. Ecology and conservation. Proc. Uppsala Symp. 1970, 5, pp. 233–241, Unesco 1973.

Gates, D. M., 1968. Transpiration and leaf temperature. Ann. Rev. Plant Physiol. 19: 211–248.

Johnston, C. D. & Miller E. C., 1940: Modification of diurnal transpiration in wheat by infections of *Puccinia triticina*. J. Agric. Res. 61 (6): 427 444.

Mehta, Y. R. & Zadoks, J. C., 1970. Uredospore production and sporulation period of *Puccinia recondita* f.sp. *triticina* on primary leaves of wheat. Neth. J. Pl. Path. 76: 267–276.

Wal, A. F. van der & Cowan, M. C., 1974. An ecophysiological approach to crop losses exemplified in the system wheat, leaf rust, and glume blotch. II. Development, growth, and transpiration of uninfected plants and plants infected with *Puccinia recondita* f. sp. *triticina* and/or *Septoria nodorum* in a climate chamber experiment. Neth. J. Pl. Path. 80: 192–214.

Weiss, F., 1924. The effect of rust infection upon the water requirement of wheat. J. Agric. Res. 27: 107–118.

Zadoks, J. C., Chang, T. T. & Konzak, C. F., 1974. A decimal code for the growth stages of cereals. Eucarpia Bull. 7, 10 pp.

Address

Laboratorium voor Fytopathologie, Landbouwhogeschool, Binnenhaven 9, Wageningen, the Netherlands.