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

IV. Water flow and leaf-water potential of uninfected wheat plants and plants infected with Puccinia recondita f.sp. triticina

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Abstract

Effects of leaf rust (*Puccinia recondita* Rob. ex Desm. f.sp. *triticina* Eriks.) infection of spring wheat (*Triticum aestivum* L.) plants 'Kolibri' on transpiration rate and leaf-water potential were studied during growth in a climate chamber at various soil-water potentials. The water potentials ranged from —210 J.kg^{-1} to —1025 J.kg^{-1}. Rust infection has been found to increase the transpiration rate. The magnitude and duration of the increase depended on soil-water potential and the time (growth stage) of inoculation.

The transpiration rate of uninfected heads was affected by rust infection of the leaves, also depending on soil-water potential and infection time. Overall resistance of the plants to water flow was determined; sudden changes in resistance due to rust infection concur with high crop losses due to abortion of kernels. Leaf-water potentials were calculated and found to vary in uninfected plants from -1740 J.kg^{-1} at the lowest soil-water potential to -580 J.kg^{-1} when water was plentiful. At high soil-water potential, the leaf-water potential of rusted plants was lower than that of uninfected plants, but this was not so at low soil-water potentials. The effects of leaf-water potential on rust growth and water flow through leaves and heads are discussed. Suggestions about the application of the results to breeding for tolerance (= resistance to loss) and, eventually, to prevention of loss by rust in semi-arid areas are given.

Introduction

Water moves from the soil through the plant to the atmosphere along a gradient of potential energy (Boyer, 1969). The rate of water flow is determined by the magnitude of this potential gradient and the resistances along the path of movement. When water is plentiful in the soil, the major resistance to water flow is at the plant-air

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[1] I. A simple and accurate balance for the continuous measuring and recording of (evapo-)transpiration of plants in indoor experiments. Neth. J. Pl. Path. 80 (1974) 77–84 (P. Tegelaar and A. F. van der Wal).

II. Development, growth, and transpiration of uninfected plants and plants infected with *Puccinia reconditz* f.sp. *triticina* and/or *Septoria nodorum* in a climate chamber experiment. Neth. J. Pl. Path. 80 (1974) 192–214 (A. F. van der Wal and M. C. Cowan).

III. Effects of soil-water potential on development, growth, transpiration, symptoms, and spore production of leaf rust infected wheat. Neth. J. Pl. Path. 81 (1975) 1–13 (A. F. van der Wal, H. Smeitink and G. C. Maan).

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boundary. As soil-water potential declines, the resistance to water movement in the soil becomes an important part of the overall resistance to water flow (Rijtema, 1965; Yang and De Jong, 1972).

In uninfected plants, the rate of transpiration and of water uptake are controlled by the adjustment of resistance in the stomata and in the roots (Hopmans, 1971). After inoculation of wheat (*Triticum aestivum* L.) leaves with leaf rust (*Puccinia recondita* Rob. ex Desm. f.sp. *triticina* Eriks.), the transpiration rate of the infected plants increases (Van der Wal and Cowan, 1974; Van der Wal et al., 1975). This increase apparently caused by decrease in the resistance at the leaf-air boundary, may affect the leaf-water potential, and possibly the rate of photosynthesis. After heading the separate effects of leaf infection on water flow through the leaves, and on water flow through the heads can be considered.

In this paper an attempt is made to estimate these two flows in uninfected plants and in plants with rusted leaves. Leaf-water potentials are calculated for these plants grown at various soil-water potentials.

Materials and methods

The experimental data discussed here are those obtained in previous experiments. The treatment 'extra wet' (EW = c. –210 $J.kg^{-1}$) was described by Van der Wal and Cowan (1974), the treatments 'wet' (W = c. –250 $J.kg^{-1}$), 'medium' (M = c. –425 $J.kg^{-1}$), and 'dry' (D = c. –1025 $J.kg^{-1}$) were described by Van der Wal et al. (1975). The lowest water potential was near the wilting point for wheat. Leaf-water potential was calculated using the equation of Gardner and Ehlig (1962) for plants in pot experiments:

$$\psi_l - \psi_s = E_t(R_{pl} + b/k)$$

where ψ_l = leaf-water potential [$J.kg^{-1}$], ψ_s = soil-water potential [$J.kg^{-1}$], E_t = transpiration rate [$kg.m^{-2}.day^{-1}$], R_{pl} = resistance to liquid flow through the plant [day], b = a function of root density and rooting depth [m], k = soil capillary conductivity [$m.day^{-1}$]. Inserting the dimension [m^3] in place of the dimension [kg] the conductivity values expressed as [$kg.m^{-1}.day^{-1}$] can be approximated as [$m.day^{-1}$].

Direct measurement of leaf-water potential by thermocouple psychrometry (Spanner, 1951; Monteith and Owen, 1958) was considered. Among the difficulties discussed more fully by Boyer (1969) are the generation of heat and water vapour as products of respiration, especially in heavily infected samples of leaf tissue (Shaw and Samborski, 1957). The relation between capillary conductivity k and soil-water potential for peat soil (Rijtema, 1965) leads to an estimate of k of 2×10^{-6} $m.day^{-1}$ for treatment EW, 1.7×10^{-6} $m.day^{-1}$ for W, 10^{-6} $m.day^{-1}$ for M, and 0.2×10^{-6} $m.day^{-1}$ for D. The value of b was estimated to be less than 10^{-3} m, using the relation b = $1/4\pi az$ (Rijtema, 1965) where a is the root density [m^{-2}] in metres root length per m^3 soil, and z is the rooting depth [m]. Estimates for root density were obtained from root weight and root diameter data, whereas bucket depth was used for z. The maximum of b/k in EW was 500 days. Yang and De Jong (1972) published values for R_{pl} for wheat growing in an artificial environment, ranging from 32 to 59×10^3 days. At EW, W, M, and D, the values of b/k were 500, 590, 1000, and 5000 days, or c. 1%, 1.2%, 2% and 10% of R_{pl}, respectively, and these values were entered into the calculation.

From the data given by Yang and De Jong for 'Thatcher' growing in soil of high water potential at 24 °C and 65 % relative air humidity, R_{pl} was taken as 41×10^3 days.

Results

Transpiration of uninfected plants. Fig. 1 illustrates the relation between turgid leaf area and transpiration rate, both expressed per plant. At D and M, the relation between leaf area and transpiration rate was approximately linear up to the time of the appearance of the first spikelets. Heading was not synchronous. In lower order axes, heads appeared earlier than in higher order ones. Leaf area was still increasing during the heading period. At W and EW, leaf areas were 2 to 3 times those of D and M, and the transpiration rate per unit leaf area decreased in the period before heading. The effect is probably the result of mutual shading of leaves and reduced ventilation. Just before heading, the transpiration rates per unit leaf area at EW, W, M, and D were respectively 0.4, 0.7, 1.1 and 1.4 $kg.m^{-2}.day^{-1}$.

The increase in transpiration rate during the heading period is partly caused by transpiration of the heads and peduncles, and partly by greater transpiration of the upper leaves. Physical considerations suggest that the latter effect was smaller than the former. With the progress of ripening, turgid leaf area decreased (lower leaves first) and the heads started yellowing. At any value of turgid leaf area, the difference in transpiration rate before and after heading can be attributed mainly to the transpiration of the heads.

If the experiment had been continued until complete ripeness of the plants, the transpiration rate/leaf area curve would have fallen to the origin (see Fig. 1, EW, rust). However, the last samples were taken when the three lowest order axes reached stage 92 (Van der Wal et al., 1975). A number of green or partly green heads and leaves were still present at that time. Early termination of the experiment explains the 'truncated' appearance of the upper parts of the graphs.

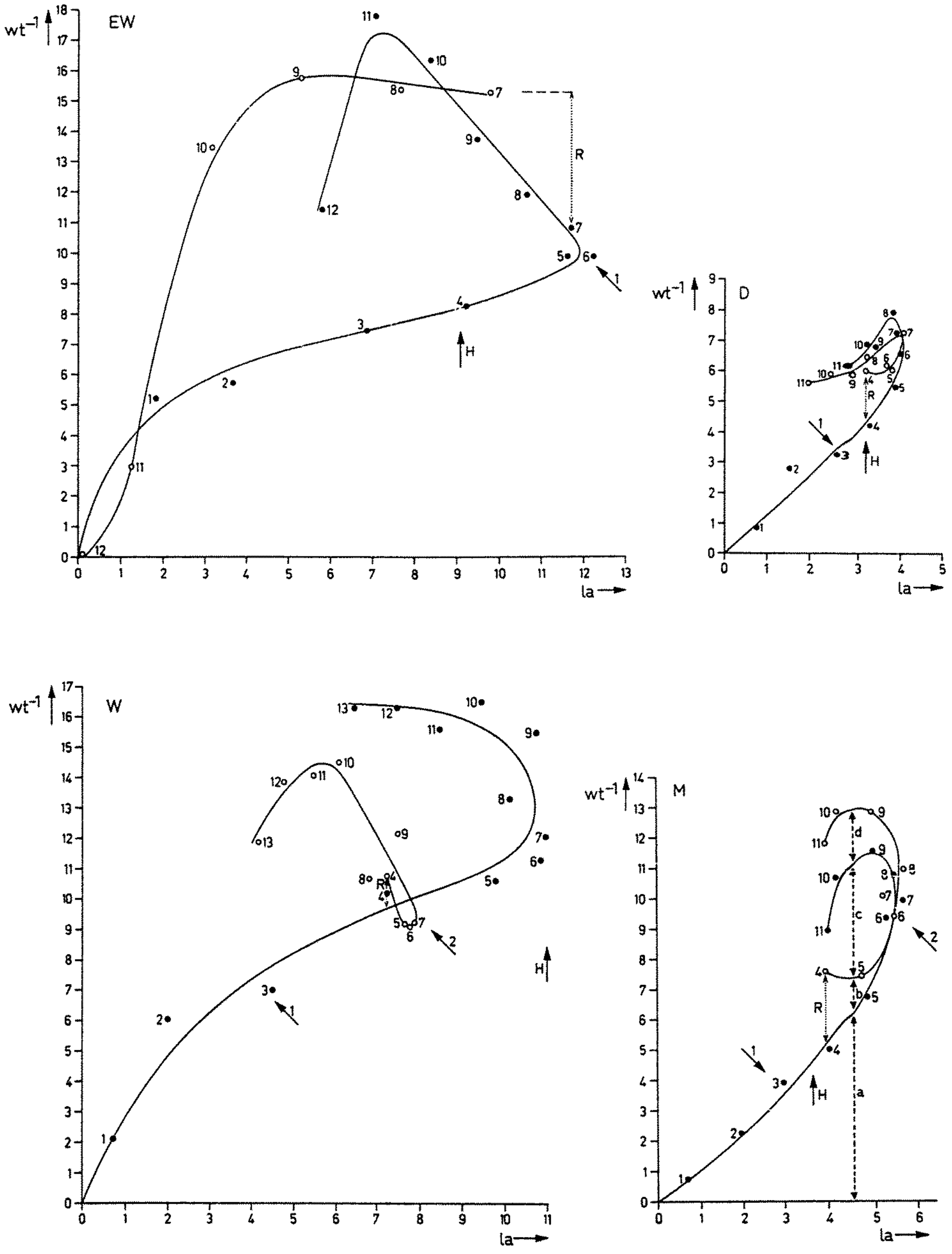
An estimate for the proportion of the plant water flow that moves through the heads can be derived from Fig. 1 by taking the difference in transpiration rate before and after heading at one leaf-area value. As an example, increase in transpiration $b + c$ (Fig. 1, M) is about half the total transpiration $a + b + c$. At the end of flowering or at the waterripe stage, head transpiration accounts for c. 30 to 40 % of the total transpiration.

Transpiration of rusted plants. Rust infection initially increased transpiration rate (Fig. 1, circles). The size of the effect was related to the water potential of the soil.

At M, the transpiration rate of the leaves increased after rust infection. Apart from the rise in the level of transpiration, the shape of the curve for the infected plant was almost the same as that for the uninfected one. The transpiration rate of the heads seemed not to have changed, there was no reduction in kernel number, and the loss was only 9 % (Van der Wal et al., 1975). Close examination of the curves suggests that the rise in transpiration after the first inoculation decreased gradually, but was restored after the second inoculation.

At D, the reduction in turgescent leaf area in the infected plant proceeded faster than in the uninfected plant, and the pattern of transpiration rate after heading deviated from that in the uninfected plant. The maximum value of transpiration in the infected plant was lower than in the uninfected one. Transpiration of the heads seemed to be lower in rusted plants than in uninfected plants. A reduction in kernel number was found and loss was considerable.

At W, the transpiration rate in the rusted plant rose after inoculation but this rise lasted only for one week, after which the transpiration rate rapidly became lower than



that of the uninfected plant, and remained so to the end of the experiment. During c. 20 days, just before and after heading, the loss of turgid leaf area, mainly due to collapse of the lower leaves, was matched by the increase in turgid leaf area by growth of the upper leaves. Heads developed, transpiration rate increased again, but at no time equalled that of the uninfected plant. Towards the end of the experiment (from point 10 onwards, early milky ripe), senescence in the uninfected plants proceeded faster than in the rusted plants, but the latter ended with a far lower leaf area. The steep increase in transpiration rate of the infected plants was a result of the combined effect of heading and the second inoculation. As in D, the maximum transpiration rate of the rusted plants was less than that of the uninfected plants, and the transpiration of the heads in the rusted plants was impeded. The reduction in kernel number and the loss were considerable.

At EW, the heads had already emerged before inoculation. Leaf area had reached its maximum at inoculation time, and the transpiration rate of the infected plant was greater than that of the uninfected control plant. The reduction in kernel number was not different from that of the control, but the loss was c. 20% (Van der Wal and Cowan, 1974).

Leaf-water potential decreased with decreasing soil-water potential and with time after heading, in both rusted and uninfected plants (Table 1). Differences in leaf-water potential between rusted and uninfected plants were large at EW, but small at W, M and D. It has been shown previously (Cowan and Zadoks, 1973) that uredospore production was reduced in wheat seedlings grown in soil of low water potential. This supports the finding that at high soil-water potentials rust growth was most rapid (Van der Wal et al., 1975: Fig. 4). When saturation of the soil was approached, leaf-water potential declined steeply soon after infection, and little green leaf area was recorded four weeks after inoculation (EW).

In conclusion, diagrams of transpiration rate versus turgid leaf area for plants at various soil-water potentials showed changes in the transpiration pattern after infec-

Fig. 1. Transpiration rate (wt^{-1}) [10^{-2}.kg.day^{-1}.plant^{-1}] versus turgid leaf area (la) [10^{-2}.m^{2}.plant^{-1}] at the four soil-water potentials: –1025 J.kg^{-1} (D = dry), –425 J.kg^{-1} (M = intermediate), –250 J.kg^{-1} (W = wet), and –210 J.kg^{-1} (EW = extra wet).
● = uninfected plants, ○ = rusted plants. ↑ H = heading, ↑ 1, ↑ 2 = inoculations. A second inoculation was applied at M and W to adjust the infection percentage of M and W to that of D. The numbers near the dots indicate the successive sampling times. Sampling was usually done at weekly intervals. Identical numbers refer to samples of uninfected and rusted plants taken at the same time. For further explanation see text.

Fig. 1. Transpiratiesnelheid (wt^{-1}) [10^{-2}.kg.dag^{-1}.plant^{-1}] uitgezet tegen het turgescente bladoppervlak (la) [10^{-2}.m^{2}.plant^{-1}] bij de vier grondwaterpotentialen: –1025 J.kg^{-1} (D = droog), –425 J.kg^{-1} (M = een tussenwaarde), –250 J.kg^{-1} (W = nat), en –210 J.kg^{-1} (EW = extra nat).
● = niet geïnfecteerde planten, ○ = planten geïnfecteerd met roest. ↑ H = het in aar komen; ↑ 1, ↑ 2 = inoculaties. Een tweede inoculatie werd gedaan bij M en W om het verschil in aantastingsgraad bij M en W t.o.v. D te verkleinen. De getallen bij de punten geven de opeenvolgende bemonsteringstijdstippen aan. De periode tussen twee opeenvolgende bemonsteringen was meestal 1 week. Gelijke getallen duiden gelijktijdig genomen monsters van niet geïnfecteerde planten en planten met roest aan. Voor een nadere toelichting zie de tekst.

Table 1. Values of leaf-water potentials (ψ_l) [$J.kg^{-1}$] calculated for 28 and 56 days after the first inoculation at the four soil-water potentials (ψ_s). R: rusted plants; C: uninfected plants ; *: plants already harvested. Day 28 corresponds with point 7 (Fig. 1) for D, M, W, and 10 for EW; day 56 with 11 (D, M, W).

Treatment		ψ_s	ψ_l 28	ψ_l 56
EW	C	– 210	– 580	*
	R	– 210	–2480	*
W	C	– 250	– 605	– 725
	R	– 250	– 640	– 855
M	C	– 425	– 910	–1025
	R	– 425	– 900	–1140
D	C	–1025	–1480	–1740
	R	–1025	–1485	–1860

*Tabel 1. Waarden van de waterpotentialen in het blad (ψ_l) [$J.kg^{-1}$] berekend voor 28 en 56 dagen na de eerste inoculatie bij de vier grondwaterpotentialen (ψ_s). R: met roest geïnfecteerde planten; C: niet geïnfecteerde planten; *: planten reeds geoogst. Dag 28 komt overeen met punt 7 (Fig. 1) voor D, M, W, en 10 voor EW; dag 56 met 11 (D, M, W).*

tion which were related to soil-water potential. At a soil-water potential of –425 $J.kg^{-1}$, a minimal deviation from the pattern of the uninfected plant due to disease, was found, together with greatest resistance to rust and minimal loss. Leaf-water potential was calculated as –900 $J.kg^{-1}$ for leaves of plants grown at a soil-water potential of –425 $J.kg^{-1}$. Only at the high soil-water potential (–210 $J.kg^{-1}$) there was a rapid decrease in leaf-water potential after infection.

Discussion

R_{pl} refers to the resistance to liquid flow through the plant per unit leaf area. Evidence has been obtained which indicated that R_{pl} is constant at high flow rates (Hailey et al., 1973). Transpiration rate per unit leaf area depends on leaf diffusion resistance, boundary layer resistance, absorption of radiation energy, and air humidity. Overall plant resistance depends also on growth stage of the plant (viz. before and after heading), and plant habit. At higher soil water potentials, a greater leaf area per plant was developed, with greater mutual shading, greater interference with air flow, and therefore a lower transpiration rate per unit leaf area. In other words, plant habit affected resistances in the gaseous phase of the water transport. However, R_{pl} (the resistance in the liquid phase of the water transport) was considered constant for all water potentials.

When soil-water potential was low, leaf-water potential, growth and transpiration rates of both infected and uninfected plants were less than the corresponding values in plants growing in soil at high water potentials. Growth of the rust, however, was retarded on plants growing on soil with low water potential. Minimum loss occurs at a soil-water potential of c. –400 $J.kg^{-1}$ and a corresponding leaf-water potential of c. –900 $J.kg^{-1}$. It seems that tolerance (= resistance to loss) to rust has an optimum soil-water potential. This conclusion applies to the cultivar-race combination under the conditions of the present experiments. Such an optimal soil-water potential, with reference to loss and not to yield, may be a varietal property. If this hypothesis is correct, soil-water potential measurement may become a new tool in tolerance breeding.

Infection of the leaves altered in most cases the pattern of transpiration of the plant (Fig. 1). If it is assumed that the transpiration per unit turgid leaf area before and after heading did not change much, the water flow through the heads must have decreased. Since kernel number reduction at D and W in rusted plants was associated with reduction in water flow through the heads, it may be concluded that the head water potential decreased because of reduced water supply resulting in abortion of kernels.

The nature of loss, caused by rust infection can partly be explained by water shortage in the heads. Reduced photosynthesis was reported as the result of rust infection, after an initial period of increased photosynthesis (Shaw, 1964), but this effect is confined to an area of a few mm beyond the rust pustule. Other effects, such as an increase in auxin concentration, may influence growth and development of the entire infected plant (Shaw, 1964). Changes in translocation after rust infection have been shown (Doodson et al., 1965). Insufficient supply of assimilates to the heads may also cause kernel number reduction.

Transpiration and photosynthesis are usually closely related (De Wit, 1958). When c. 30% of transpiration of the plant is contributed by the heads, a comparable contribution by the heads to the total photosynthesis of the plant is probable. The contribution made by the heads to the total photosynthesis of plants in a crop ranges from 20% to 50% depending on solar elevation, the highest percentage occurring at zero elevation (Puckridge, 1972). The figure of 30% quoted here for transpiration is consistent with these data.

If it is permitted to generalize from the climate chamber to the field situation, two possible applications of the results reported above are worth mentioning. First, a more dynamic view of tolerance (= resistance to loss) can be of use in solving breeding problems. Tolerance to rust is a result of biological processes, not a static property. Since it has been shown that rust development in wheat seedlings is dependent on soil water potential (Cowan and Zadoks, 1973) and that leaf-water potential and rust growth are associated in mature plants, a knowledge of leaf-water potential as a response of the plant to its environment may become an essential step in the development of new selection methods for tolerance to rust. Secondly, wheat grows within a wide range of soil-water potentials and responds to changes in these potentials. It may be that the increased water loss occurring after rust infection will not be injurious to the crop if the crop is irrigated at the right time. Water might therefore be used in place of fungicides to prevent loss caused by rust, under semi-arid conditions.

Samenvatting

Een ecofysiologische benadering van 'schade', geïllustreerd aan het systeem tarwe, bruine roest en kafjesbruin.

IV. Transpiratiepatroon en bladwaterpotentiaal van niet geïnfecteerde tarweplanten en planten geïnfecteerd met Puccinia recondita f.sp. triticina

In dit artikel wordt verder ingegaan op de transpiratie van niet geïnfecteerde tarweplanten (*Triticum aestivum* L.) 'Kolibri' en planten geïnfecteerd met roest (*Puccinia recondita* Rob. ex Desm. f.sp. *triticina* Eriks.). Allereerst wordt het transpiratiepatroon van wel en niet geïnfecteerde planten vergeleken bij vier grondwaterpotentialen (Fig. 1). Bladoppervlak en transpiratiesnelheid, beide uitgedrukt per plant, werden tegen elkaar uitgezet. Bij de twee laagste waterpotentialen, –1025 $J.kg^{-1}$ en –425 $J.kg^{-1}$, zijn de transpiratiesnelheden recht evenredig met het bladoppervlak, althans tot het in aar komen. Bij de hogere waterpotentialen (–250 en –210 $J.kg^{-1}$) neemt de transpiratiesnelheid per eenheid van bladoppervlak af naarmate er meer blad gevormd wordt, waarschijnlijk als gevolg van onderlinge beschaduwing en geringere ventilatie van de bladeren.

Uit het verschil tussen de transpiratiesnelheid voor en na het in aar komen bij een gelijk turgescent bladoppervlak werd een schatting gemaakt van het aandeel van de aren in de transpiratie van de plant. Dit bleek 30 tot 40% te zijn bij het einde van de bloei/waterrijpheid.

Het transpiratiepatroon van de plant na infectie week minimaal af van dat van de niet geïnfecteerde plant bij een grondwaterpotentiaal van –425 $J.kg^{-1}$. Alleen de grootte van de transpiratiesnelheid verschilde, niet de vorm van de curve (Fig. 1). Bij deze waterpotentiaal trad geen reductie op in het aantal korrels per plant en de schade was gering. Ook de resistentie was hier maximaal (Van der Wal et al., 1975). De berekende bladwaterpotentiaal was –900 $J.kg^{-1}$. Zowel bij de laagste als bij de twee hoogste grondwaterpotentialen week het transpiratiepatroon van de plant na infectie sterk af van dat van de niet geïnfecteerde plant. Bij –1025 en bij –250 $J.kg^{-1}$ trad reductie van het aantal korrels op, terwijl de schade aanzienlijk was. De berekende waterpotentialen in het blad waren 28 dagen na de eerste infectie respectievelijk –1485 en –640 $J.kg^{-1}$ (Tabel 1). Bij –210 $J.kg^{-1}$ nam het turgescent bladoppervlak snel af na infectie. Hoewel geen effect van de infectie op het korrelaantal werd gevonden, mogelijk omdat pas na de bloei was geïnfecteerd, bleek de schade groot te zijn (Van der Wal en Cowan, 1974). Een hoge bladwaterpotentiaal laat blijkbaar een relatief hoge groeisnelheid van de schimmel in het blad toe. Hierdoor wordt de transpiratie aanvankelijk sterk verhoogd, met snelle uitdroging van het blad als gevolg.

Aangezien groei van waardplant en pathogeen blijkbaar in hoge mate samenhangen met de waterpotentialen in het blad, kan een studie als deze bijdragen tot een beter begrip van tolerantie (= resistentie tegen schade). In semi-ariede gebieden zou misschien door irrigatie op het juiste ogenblik de schade als gevolg van roestaantastingen beperkt kunnen worden.

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References

Boyer, J. S., 1969. Measurement of the water status of plants. A. Rev. Pl. 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.

Doodson, J. K., Manners, J. G. & Myers, A., 1965. Some effects of yellow rust (*Puccinia striiformis*) on ^{14}carbon assimilation and translocation in wheat. J. exp. Bot. 16: 304–317.

Gardner, W. R. & Ehlig, C. F., 1962. Impedance to water movement in soil and plant. Science 138: 522–523.

Hailey, J. L. et al., 1973. Resistance to water flow in *Vigna sinensis* L. (Endl.) at high rates of transpiration. Crop Sci. 13: 264–267.

Hopmans, P. A. M., 1971. Rhythms in stomata opening of bean leaves. Meded. Landbouwhogeschool Wageningen 71 (3): 86 pp.

Monteith, J. L. & Owen, P. C., 1958. A thermocouple method for measuring relative humidity in the range 95% to 100%. J. scient. Instrum. 35: 443–446.

Puckridge, D. W., 1972. Photosynthesis of wheat under field conditions. V. The effect of solar elevation on the distribution of photosynthetic activity with the crop canopy. Aust. J. agric. Res 23: 397–404.

Rijtema, P. E., 1965. An analysis of actual evapotranspiration. Thesis Wageningen/Agric. Res. Rep. 659: 107 pp.

Shaw, M., 1964. The physiology and host-parasite relations of the rust. A. Rev. Phytopath. 2: 259–294.

Shaw, M. & Samborski, D. J., 1957. The physiology of host-parasite relations. III. The pattern of respiration in rusted and mildewed cereal leaves. Can. J. Bot. 35: 389–407.

Spanner, D. C., 1951. The Peltier effect and its use in the measurement of suction pressure. J. exp. Bot. 2: 145–168.

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 plant and infected with *Puccinia recondita* f.sp. *triticana* and/or *Septoria nodorum* in a climate chamber experiment. Neth. J. Pl. Path. 80, (1974) 192–214.

Wal, A. F. van der, Smeitink, Hanneke & Maan, G. C., 1975. An ecophysiological approach to crop losses, exemplified in the system wheat, leaf rust and glume blotch. III. Effects of soil-water potential on development, growth, transpiration, symptoms, and spore production of leaf rust-infected wheat. Neth. J. Pl. Path. 81 (1975) 1–13.

Wit, C. T. de, 1958. Transpiration and crop yields. Versl. landbouwk. Onderz. 64 (6) 88 pp.

Yang, S. L. & Jong, E. de, 1972. Effects of aerial environment and soil-water potential on the transpiration and energy status of water in wheat plants. Agron. J. 64: 574–578.

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