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Transpiration of Spring Barley under Nitrogen and Phosphorus Deficiency during Leaf Wilting

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Abstract. In an open gas exchange system with a thermocouple psychrometer the transpiration rate of the first leaf in 8-day plants of spring barley was measured in dependence on the water saturation deficit (ΔW_{sat}). The plants were cultivated in Richter's nutrient solution, either complete, or deficient in nitrogen or phosphorus. The cuticular transpiration (as measured in the dark) was unaffected by N and P deficiency. The N deficiency reduced the transpiration rate by increasing stomatal resistance since full water saturation of the leaf (67% rate of the control variant) up to stomatal closing at $\Delta W_{sat} = 14\%$. The P deficiency does not affect the transpiration rate at initial phases of wilting, but the stomata close only at a higher ΔW_{sat} (25%) than those in the control.

The reduction in the transpiration rate under water stress is brought about mainly by changes in stomatal resistance (HSIAO 1973). At P deficiency both the decrease in the transpiration rate (in *Festuca arundinacea*, *Camellia sinensis*, *Arctium minus*) and the increase or no changes (*Picea sitchensis*) were recorded (BRADBURY and MALCOLM 1977, NAGARAJAH and RATNASURIYA 1978, PITCAIRN and GRACE 1982).

Under full water saturation of the leaf the nitrogen deficiency causes a reduction in the transpiration rate by increasing stomatal resistance, *e.g.* in *Beta vulgaris*, *Manihot esculenta*, *Camellia sinensis* (YOSHIDA and CORONEL 1976, NAGARAJAH 1981). In wilting *Phaseolus vulgaris* SHIMSHI (1970) found an increase in transpiration rate due to N deficiency. At low nitrogen doses a higher transpiration rate was recorded in *Festuca arundinacea* exposed to high wind speed (PITCAIRN and GRACE 1982). It is thus probable that in nitrogen deficient plants the stomata are on the one hand open to a smaller extent, on the other when closed, their aperture is not so tight as in the controls (SHIMSHI 1970).

Our experiments aimed at examining the changes in transpiration rate in spring barley due to short-term wilting, as affected by nitrogen and phosphorus deficiency in mineral nutrition.

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MATERIAL AND METHODS

The measurements were performed in primary leaves of 8-day spring barley plants (*Hordeum vulgare* L., cv. Spartan), cultivated in nutrient solutions according to Richter — complete (R), minus nitrogen (N) and minus phosphorus (P), under constant conditions of photon fluence rate (170 μeinstein m^{-2} s^{-1}, 400 to 700 nm), photoperiod (18 h light, 6 h darkness), temperature (22 $\pm$ 2 °C) and relative air humidity (40—60%).

The rate of transpiration was investigated in an open gas exchange system; for the measurement of dew point of the air we used a thermocouple psychrometer according to SLATYER and BIERHUIZEN (1964). The dew point of air entering the leaf chamber was maintained at a constant value of 1 °C. The leaf temperature was measured by means of a thermocouple on the abaxial leaf surface. The leaf chamber was irradiated by an incandescent lamp through a water filter at a photon fluence rate of 200 μeinstein m^{-2} s^{-1}. The air flow through the leaf chamber amounted to 8.3 cm^3 s^{-1} (linear rate approximately 0.9 cm s^{-1}). Our measurements involved:

1) Rate of transpiration E_t of the irradiated, fully water-saturated leaf.

2) Rate of transpiration E_c of saturated leaves in the dark. This value is considered as the rate of cuticular transpiration.

3) Transpiration rate of leaves without water supply, ΔW_{sat} being determined by subtracting the water transpired from the mass of a fully saturated leaf.

The calculation of stomatal resistance was made on the basis of the model of finite resistance elements (GATES 1968). The resistance of boundary layer was determined from the rate of evaporation of a moist filter paper (60 s m^{-1}).

RESULTS

The curves for the dependence of E_t on ΔW_{sat} are characteristic by their maximum, which is identical in all variants at $\Delta W_{sat} = 6\%$ (Fig. 1). E_t in the variant N is significantly lower both under full water saturation (67% of the value R), and in the maximal value obtained (56% of R). The increase in E_t at $\Delta W_{sat} = 6\%$ against full saturation amounts to 54% in the control and variant P, and to 29% in the variant N. E_t decreases to the value for E_c in the variant N at $\Delta W_{sat} = 14\%$, in the variant P at $\Delta W_{sat} = 25\%$, but at $\Delta W_{sat} = 20\%$ in the control.

The ratio E_c/E_t under full saturation is relatively high, amounting to 22.2% in the variant N, to 16.4% in P, and to 15.6% in the control. This ratio maintains the high level even at the maximum E_t obtained, and does not fall below 10% (R — 10.2%, N — 17.2%, P — 10.8%).

The stomatal resistance r_s (Fig. 2) of the variant N in the whole interval of ΔW_{sat} investigated was higher than that in R and P variants. The variant P differs significantly from the control by a less steep increase in r_s only since $\Delta W_{sat} = 13\%$. The value for r_s reaches that for the cuticular resistance r_c at $\Delta W_{sat} = 11.5\%$ in the variant N, at $\Delta W_{sat} = 21.5\%$ in P, and at $\Delta W_{sat} = 15.5\%$ in the control.

E_c was not affected either by the deficiency in mineral nutrients, or by water deficit. The effect of both these factors thus became evident mainly in the stomatal resistance and thus in E_t.

DISCUSSION

Maximum E_t value is obtained under a low ΔW_{sat} value (6%), since the opening of stomata is highest at a certain low ΔW_{sat} (STÅLFELT 1955).

The reduction in the transpiration rate under nitrogen deficiency (plants without water stress), as caused by an increase in r_s, has already been demonstrated (YOSHIDA and CORONEL 1976, NAGARAJAH 1981). According

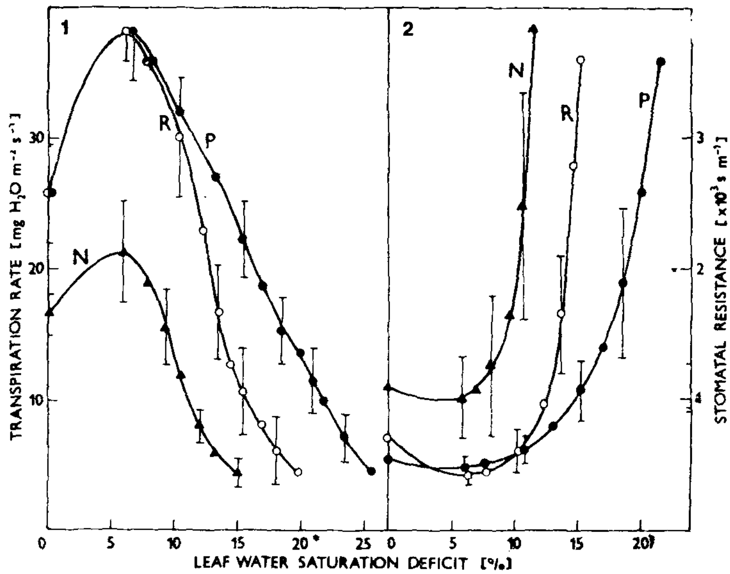

Fig. 1. The effect of N and P deficiencies on the transpiration rate under increasing water saturation deficit. Mean values from 7 repetitions, vertical line segments are confidence intervals ($\alpha = 0.05$).

Fig. 2. The effect of N and P deficiencies on the value of stomatal resistance for H_2O transfer under increasing water saturation deficit. Mean values from 7 repetitions, vertical line segments are confidence intervals ($\alpha = 0.05$).

to our results the N deficiency suppresses transpiration within the entire ΔW_{sat} interval up to stomatal closing. An opposite result is referred to only by CETL and PENKA (1958) in spring barley cv. Valtický, and by SHIMSHI (1970) in wilting leaves of *Phaseolus vulgaris*, this being explained by the fact that due to water stress, the stomata in the nitrogen-deficient variant are not tightly closed. This was not observed in our experiments; on the contrary, the stomatal closing in the variant N occurred at a substantially lower ΔW_{sat} than in the other variants.

A more rapid closing of stomata with a rising ΔW_{sat} under nitrogen deficiency (similarly as in ageing) was also observed by RADIN (1981). The stomata in the control are closed at $\Delta W_{sat} = 15\%$. This corresponds to the data of MILLAR *et al.* (1968) who found in barley the stomatal closing at $\Delta W_{sat} = 5-15\%$, in dependence on the ontogenetic phase. The variant P differs from the control only in the phase of stomatal closing (Figs. 1, 2). The specific dry mass and specific fresh mass under full water saturation were not affected by N and P deficiency. Unlike ATKINSON (1973) we did not observe any changes in tissue hydration under P deficiency. The values of r_s

we obtained under full saturation are relatively high in comparison with literature data for barley: thus GATES (1968) refers to 50–100 s m^{-1}, PAZOUREK (personal communication) approximately 100 s m^{-1}. The higher value for r_s may be caused by a lower irradiance during the measurement; moreover, when calculating r_s we also took the cuticular transpiration into consideration. Neglecting the cuticular transpiration in the calculation of r_s, if, in barley, the former makes up to 40% of the total transpiration (MILLAR *et al.* 1968), may reduce the r_s calculated as much as 1.7 times (HÁK and NÁTR 1984). One may presume that with increasing ΔW_{sat} the resistance of the mesophyll walls also increases, and so-called "incipient drying" takes place (SLAVÍK 1958). However, though the resistance of the mesophyll walls increases with ΔW_{sat} (JARVIS and SLATYER 1970), its relative significance decreases with the rising ΔW_{sat}, for r_s also markedly increases with ΔW_{sat}. Thus the resistance of the mesophyll walls is only a negligible constituent of the total resistance (HSIAO 1973).

We ascribe the reduction in transpiration in the variant N to the increase in r_s. However, it is not clear as yet to what extent this increase is caused by a factually reduced stomatal aperture or by other anatomical changes. Under the same cultivation conditions as in the present experiments, PAZOUREK and NÁTR (1981) revealed a considerable increase in stomatal density in the first leaf of N deficient spring barley (129.5% in comparison with the control), the P deficiency being without effect. It is usually assumed that r_s is inversely proportional to stomatal density, but one must keep in mind that there exists an interference between adjacent stomata which reduces transpiration, and the significance of which increases with a decreasing distance of stomata (COOK and VISKANTA 1968). The values for the cuticular transpiration are characteristic by high variability (HOLMGREN *et al.* 1965). Moreover, we are aware of the fact that the measuring of cuticular transpiration in the dark is affected by the risk of incomplete stomatal closing (STÅLFELT 1955, HOLMGREN *et al.* 1965). Apparently also with regard to the high variability of cuticular transpiration and to the low ΔW_{sat}, we were not able to observe in the course of measuring any reduction in the cuticular transpiration with increasing ΔW_{sat} (SLAVÍK 1958).

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BOOK REVIEW

EGAN, H., PREUSSMANN, R., O'NEILL, I. K., EISENBRAND, G., SPIEGELHALDER, B., BARTSCH, H. (ed.): ENVIRONMENTAL CARCINOGENS SELECTED METHODS OF ANALYSIS. VOL. 6: N-NITROSO COMPOUNDS. — International Agency for Research on Cancer, Lyon 1983. 508 pp. US $ 40.00.

The existence of N-nitroso compounds in the environment represents a serious problem in environmental health hazard studies. A large number of compounds are involved and they or reactants capable of forming them, are widely distributed. The IACR has published since 1972 several specific volumes, dealing with the genotoxic effects of N-nitroso compounds and with analytical methods for their detection. This volume is a manual concerned with selected methods of analysis of N-nitroso compounds. The introductory chapters comprise reviews of the public health hazards of environmental N-nitroso compounds, problems of contamination and artifact formation in nitrosamine sampling and analysis, and of hazards in handling these compounds. Chapter II presents methods of analysis of volatile N-nitrosamines in air, tobacco and tobacco smoke, in malt and malt-based beverages, in animal feed and food, further in rubber and plastic commodities and in pesticides. In chapter III general clean-up and analysis procedures for non-volatile N-nitroso compounds (*e.g.* nitrosodiethanolamine, nitrosoamino acids) are given in detail. The modern methods for the separation and detection of volatile and non-volatile nitroso-compounds, *i.e.* gas chromatography, high-performance liquid chromatography, mass spectrometric analysis, voltammetry, polarography and the use of TEA (termal energy analyzer) are described in chapters IV and V.

This publication makes available a complete set of methods for the analysis of N-nitroso compounds for those engaged in research and in setting regulations. An excellent hand-ready manual.

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