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Transpiration Rate and Intercellular Diffusive Resistance in the Tobacco Leaf

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Dedicated to Academician S. Prát on the occasion of his 80th birthday

Abstract. The increase in the measured transpiration rate in tobacco leaves due to the experimentally decreased humidity of the bulk air was found to be significantly lower than the theoretical value calculated from the change of water vapour concentration gradients. Boundary layer and stomatal diffusive resistances remained unchanged under experimental conditions with no change of net photosynthetic CO_2 uptake. This suggests an increase in intercellular diffusive resistance with an increase in water vapour concentration gradient which is the driving force of water vapour diffusive part of transpiration flux.

The increase can be ascribed to the lengthening of intercellular diffusive pathway as steeper water vapour concentration gradient in intercellular spaces results in an increased evaporating surface of intercellular cells thus moving the effective plane of vaporization in leaf mesophyll further inwards. Due to different and independent changes of concentration gradients for water vapour and CO_2, different length of intercellular diffusive pathways for CO_2 and water vapour may be expected.

The decreased humidity of the air surrounding the leaf results in an increased gradient of water vapour concentration which is the driving force of diffusive flux of water vapour across the air boundary layer, stomata and intercellular spaces in the leaf mesophyll. This diffusive flux starts at the intercellular cell wall surfaces where saturated water vapour concentration (corresponding to the leaf temperature) may be assumed.**

The flux ends at the external boundary of the still air boundary layer where water vapour concentration of the bulk air may be expected. The distribution of serial diffusive resistances along this diffusive pathway (intercellular resistance r_i, stomatal resistance r_s and boundary layer resistance r_a) determines the distribution of the water vapour concentrations. Existence of any intercellular resistance results in water vapour gradients within intercellular spaces which become the steeper the higher is the overall gradient which is determined, *ceteris paribus*, primarily by external air humidity.

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** The decrease in saturated air humidity due to the water potential at cell surface being lower than zero is negligible under normal conditions

The steepness of these gradients not only determines the rate of the diffusive flux (corresponding to the transpiration rate) but may also affect the proportion of the intercellular spaces where water vapour concentration is lower than saturated. This may lengthen the effective pathway which in turn may result in an increase in the intercellular portion of diffusive resistance in the leaf (r_i).

We wondered how far a slight decrease of external air humidity (*e.g.* by 10% r.h.) could change the calculated sum of $r_s + r_i$ under conditions of unchanged r_s as checked by simultaneous measurement of net photosynthetic CO_2 uptake. Any changes of $(r_i + r_s)$ could be detected by comparing the measured experimental increase in transpiration rate with its theoretical increase, calculated on the basis of increased gradient of water vapour concentration. r_s (and of course r_a) being constant, changes of r_i can be found.

Material and Methods

Adult attached leaves of tobacco plants (*Nicotiana tabacum* L. cv. 'Wisconsin 38') grown in Mitscherlich pots in a greenhouse were used. Transpiration rate and net photosynthetic CO_2 uptake of adaxial leaf surface were measured in an open system with a differential infrared analyser (URAS 2, Hartmann and Braun) using bilateral air-conditionned and ventilated assimilation chambers according to JARVIS and SLATYER (1966) at an irradiance 280 W m^{-2} (400—700 nm) and at [CO_2] 320 µl l^{-1}. The change of water vapour gradient was induced by the decrease in external effective air humidity from about 75 to 65 per cent at 25.0 °C. The sum of $r_s + r_i$ was calculated from $r_s + r_i = (c_{sat} - c_a)/E - r_a$, where c_{sat} is saturated concentration of water vapour at the leaf temperature (measured with a miniature thermistor bead), c_a water vapour concentration of the ambient air at the air temperature, E the transpiration rate measured and

TABLE 1.

MEAN ($\bar{x} \pm s_{\bar{x}}$) TRANSPIRATION RATES (E), SUM OF STOMATAL AND INTERCELLULAR DIFFUSIVE RESISTANCES ($r_s + r_i$) AND NET PHOTOSYNTHETIC CO_2 UPTAKE (P_N) OF ADAXIAL LEAF SURFACES IN THE AIR OF 75% EFFECTIVE RELATIVE HUMIDITY (SUBSCRIPTS 1) AND 65% EFFECTIVE RELATIVE HUMIDITY (SUBSCRIPTS 2). THE AVERAGE r_a WAS 0.56 s cm^{-1}.

Dimension	E_1	$E_{2exp.}$	$E_{2theor.}$
µg cm^{-2} s^{-1}	1.614 ± 0.036	1.925 ± 0.045	2.447
mg dm^{-2} h^{-1}	581 ± 13	693 ± 17	738
per cent	100	119.23	127.1
	$(r_s + r_i)_1$	$(r_s + r_i)_2$	
s cm^{-1}	3.77 ± 0.09	7.33	
percent	100	114.9	
	P_{N1}	P_{N2}	
ng cm^{-2} s^{-1}	27.37 ± 0.72	27.59 ± 0.69	
mg dm^{-2} h^{-1}	9.85 ± 0.26	9.93 ± 0.25	
per cent	100	100.8	

r_a boundary layer resistance determined as usual from evaporation of a dummy evaporating filter paper surface placed in the assimilation chamber in the same conditions as experimental lea ves

Results

26 measurements of transpiration rate and net photosynthetic CO_2 uptake at about 75 and subsequently at about 65 per cent average effective relative air humidity were used for calculations. In all cases no significant

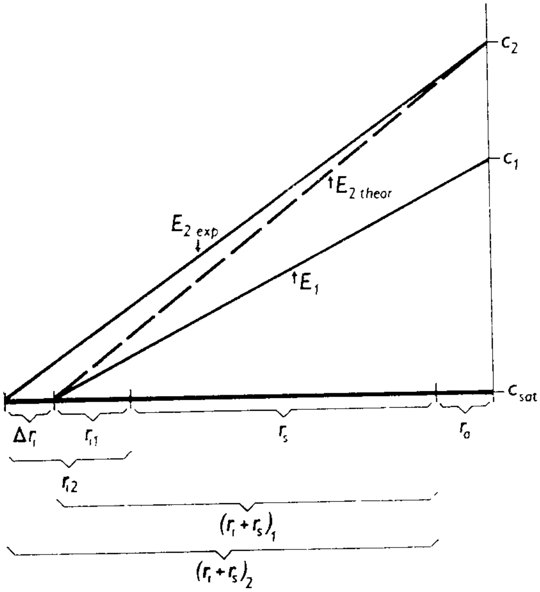

Fig. 1. Scheme showing the dependence of transpiration rates (slopes of the E lines) on water vapour concentration gradients (c) and water vapour diffusive resistances (r). Values with subscripts 1 correspond to initial values with about 75 per cent effective relative humidity of the bulk air, values with subscript 2 are values with relative humidity decreased to about 65 per cent.
Slope of E_{2teor} is the theoretical value calculated from the change of c_1 to c_2. Slope of $E_{2exp.}$ denotes the experimentally found transpiration rate at c_2 bulk air humidity. (c_{sat} is the saturated water vapour concentration at the leaf temperature.) r_a and r_s are the boundary layer and stomatal diffusive resistances respectively, found to be constant under the experimental conditions used. r_i are the calculated intercellular diffusive resistances, Δr_i being the calculated increase in intercellular resistance due to the gradient of bulk air humidity increased from c_1 to c_2.

change in net CO_2 uptake took place (Table 1). After subtracting the experimentally determined boundary layer resistance in the same experimental conditions the sum $r_s + r_i$ was calculated as above. The observed increase in transpiration rate was compared with the theoretical one, calculated from the increase in the gradient of water vapour concentration ($c_{sat} - c_a$). The increase in the transpiration rate found experimentally was in all cases lower than that expected from calculations using the change in effective water vapour concentrations. The transpiration rate measured, instead of being on the average by 27.1 per cent higher in the lower air humidity (as calculated from the increase of the above gradients of water vapour concentration) was only 19.3 per cent higher. The explanation is an increase in intercellular resistance r_i as r_s remained unchanged, see unchanged net photosynthetic CO_2 influx. The increase in $(r_s + r_i)$ calculated was, on the average, 14.0 percent of the initial value.

Discussion

When the overall difference of water vapour concentration on the diffusive pathway (intercellular cell walls → bulk air) is increased, transpiration rate is bound to increase in proportion to the increase of that difference. In all cases leaf and air temperature measured with sufficient accuracy (0.1 °C at least) must be taken into account. An experimentally induced increase in the overall difference of water vapour concentration by about 27 per cent (from the average of 8.48 g cm^{-3} to 10. 78 g cm^{-3} at 25 °C) resulted in our experiment only in an about 19 per cent increase in transpiration rate. No significant change of net photosynthetic CO_2 uptake was detected (at the average level of 9.86 mg CO_2 $dm^{-2}h^{-1}$ a statistically insignificant increase by 0.8 per cent was found) so that no change of r_s could be supposed. In case of no change in the position of the effective sinks for CO_2 (*sensu* JONES and SLATYER 1972, SLAVÍK 1975a, b) to be expected, r_i pertinent to CO_2 flux can be supposed to be constant. As no significant change of net photosynthetic CO_2 uptake was found in the above experiments, r_s which is in all cases common to both CO_2 and water vapour fluxes can be supposed to be constant. Any change in the sum $r_s + r_i$ calculated for water vapour flux is to be attributed solely to a change in r_i to water vapour flux.

The most plausible explanation for an increased r_i with an increased overall gradient of water vapour concentration is the lengthening of the intercellular diffusive pathway in the leaf mesophyll. As stated above, any increase in the overall water vapour concentration gradient results in an increased water vapour gradient in the intercellular spaces, which means that zones of air humidity lower than saturated are "penetrating" deeper into the interconnected intercellular spaces. In other words we may say that the effective evaporation plane inside the leaf, representing an averaged evaporating cell wall surface, where actual vaporization takes place, is moving the more inwards the higher is the water vapour gradient. This movement will result in a lengthening of the intercellular diffusive pathway which in turn will result in an increased intercellular diffusive resistance r_i.

The observed increase in the calculated sum $r_s + r_i$ by 14.9 per cent with r_s alone remaining unknown but constant (and with transpiration rate increased by 19 per cent), corresponds to an increase of r_i higher than this, depending on the ratio r_i/r_s.

The suggested change in the effective length of the diffusive pathway of water vapour in the intercellular spaces due to changes in the gradients of water vapour concentration thus results in an increase of r_i. This would also mean that r_i values for water vapour and for CO_2 may differ (in addition to different diffusive coefficients) due to different effective length of intercellular diffusive pathways. The effective intercellular pathway of water vapour depends on the localization of the effective vaporization plane (source of water vapour), while the effective intercellular pathway of CO_2 depends on the localization of the effective sink plane for CO_2 (see again Jones and Slatyer 1967 and Slavík 1975). Both planes may move as a result of a changing "activity" of sources or sinks as influenced by changes of the pertinent concentration gradients.

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B. Slavík (Praha): **Rychlost transpirace a intercelulární difusní odpor v listu.** — Biol. Plant. **17** : 400—404, 1975.

Vzestup měřené rychlosti transpirace listů tabáku následkem snížené vlkosti vzduchu byl průkazně nižší než teoretická hodnota, vypočtená podle změny gradientu koncentrace vodní páry. Difusní odpor hraniční vrstvy vzduchu a průduchů zůstal nezměněn, o čemž svědčil nezměněný čistý fotosynthetický příjem kysličníku uhličitého.

Z uvedeného vyplývá, že zvýšeným gradientem koncentrace vodní páry, který je hnací silou transpirace, se zvětšil intercelulární difusní odpor. Jeho zvětšení je zřejmě důsledkem prodloužení intercelulární difusní dráhy, protože strmější gradient koncentrace vodní páry v intercelulárních prostorech způsobí zvětšení výparného povrchu buněk v intercelulárách, které má za následek posunutí efektivní roviny výparu dále dovnitř listového mezofylu. Následkem rozdílných, navzájem nezávislých změn koncentračních gradientů vodní páry a CO_2 může být očekávána různá efektivní délka difusní cesty v intercelulárách pro oba plyny.