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Stomatal adaptation of grapevine leaves to water stress

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S u m m a r y: Stomata of grapevine leaves respond to the evaporative demand of the atmosphere and to changes of soil water. Leaf epidermis and roots are regarded as sensors of air and soil humidity. Besides a hydraulic communication between soil and leaf, non-hydraulic signals represent a metabolic communication between roots and stomata: stomatal conductance, and thereby the rate of CO₂ assimilation, of turgid vine leaves declined when part of the roots was subjected to progressively drying soil.

Under water stress conditions stomata of leaves reduce transpiration and fully account for putative non-stomatal inhibition of CO₂ assimilation. They enable vine leaves to optimize their CO₂ uptake to water loss ratio (water use efficieny) under sometimes rapidly changing ambient and internal conditions. A close correlation between CO₂ assimilation and stomatal conductance indicates a precise functioning of stomatal action and thereby a high water use efficiency, this correlation coefficient which is generally high in grapevines was demonstrated to increase under water stress conditions. As a screening, the CO₂ assimilation to stomatal conductance ratio and the CO₂ assimilation to transpiration ratio provide valuable information on the water economy of grapevine varieties under drought conditions.

Key words: leaf, stoma, root, photosynthesis, transpiration, water use efficiency, drought, resistance, variety of vine, selection.

In periods of drought, leaves of grapevines are faced with a dilemma: CO₂ assimilation from the atmosphere requires an intensive gas exchange, on the other hand the prevention of excessive water loss demands a reduction of gas exchange. Both, CO₂ uptake and water loss are regulated mainly by turgor-operated valves, the stomata. The ratio of CO₂ assimilation rate of a leaf to its transpiration rate, the water use efficiency (WUE), gives information about the economy of

Table 1: Gas exchange and water use efficiency of field-grown grapevine varieties

	Phoenix	Ga – 47 – 42	Riesling
A, μmol·m ⁻² ·s ⁻¹	16,3	11,9	10,8
g_{co2} , mmol·m ⁻² ·s ⁻¹	126	104	58
E, $mmol \cdot m^{-2} \cdot s^{-1}$	4,9	3,5	1,8
c ₁ , ppm	220	236	164
A/E	3,3	3,4	6,0
A/g _{co2}	0,129	0,114	0,186
c_1/c_a at constant Δ_w	0,63	0,67	0,47
WUE	low	low	high

transpirational water loss and, therefore, may help to identify drought tolerant varieties. As is shown in Fig. 1, stomatal conductance of grapevine leaves controles the rate of transpiration and has been reported to fully account for the inhibition of photosynthesis under water stress conditions (Downton et al. 1988). Measurements of gas exchange of field-grown cultivars Phoenix, Gf. Ga-47-42 and Riesling (drought tolerant) indicate that at light saturation, ambient CO, concentration and favourable air humidity and temperature the rate of photosynthesis (A), stomatal conductance for CO₂ (g_{CO2}), and transpiration (E) are highest in Phoenix and lowest in Riesling; values of the intercellular CO, concentration (c_i) were distinctly lower in Riesling. From these results, the water use efficiency (WUE) can be derived as the A/E, A/g_{CO2} or c/c_a ratio (at constant leaf to air water vapour pressure difference) (Table 1). All three parameters confirm the high WUE of Riesling which can be ascribed to its low stomatal conductance (DÜRING 1987; DURING and KLINGENMEYER 1987). Partly closed stomata obviously lower the rate of photosynthesis by decreasing intercellular concentration. But this reduction is relatively small compared to transpiration, thus the WUE of Riesling is increased. Fig. 1 demonstrates that air humidity affects stomatal conductance, an increasing leaf to air water vapour pressure difference leading to a decrease of A, E and g. It is interesting to note that the correlation coefficients A_{u} -g and g-A increase in water stressed vines, in Riesling more than in Silvaner leaves (Table 2). This indicates a higher sensitivity of Riesling leaves to changes in air humidity and also an improved tuning between stomatal conductance and CO, assimilation under soil water stress: Stomata operate more precisely (Düring 1988).

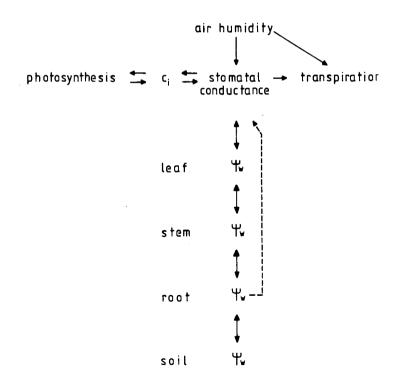


Fig. 1: Stomata of vine leaves play a central role in optimizing gas exchange under changing conditions of ambient soil and air humidity.

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The traditional view of the stomatal response to soil drying is that the leaf water potential and turgor decline, thereby promoting stomatal closure. In a root split experiment we have shown that besides hydraulic communications between roots and stomata (Fig. 1) non-hydraulic signals are sent from the roots to the leaves which induce stomatal closure. Although the water potential and turgor of the root split plant indicate a high leaf water status, the stressed part of its roots is suggested to have induced stomatal closure (Fig. 2). These preliminary results indicate that stomatal closure of grapevine leaves can occur independently of any change in leaf turgor but varies as a function of the amount of available soil water. From experiments with other plants it is suggested that roots as sensitive organs measure the available soil water and communicate via chemical signals with the stomata to optimize photosynthesis and transpiration. The ability to sense changes of the available soil water and to induce stomatal closure before the leaf water potential declines is assumed to be part of the adaptation mechanisms occurring between drought tolerant rootstocks and scions.

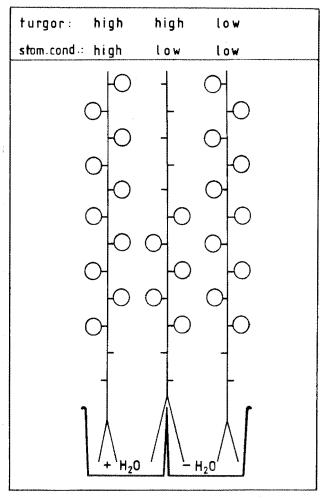


Fig. 2: Root split experiments with 1-year-old Trollinger vines. The root split plant was partly defoliated to compensate its limited water supply.

Table 2: Correlation coefficients of the leaf to air water vapour pressure difference (Δ_{w}) versus stomatal conductance (g) and of g versus CO₂ assimilation (A) of unstressed and stressed Riesling and Silvaner vines

		correlation coefficient		
variety		air humidity — stom. conductance	stom. conductance – CO ₂ assimilation	
Riesling	unstressed	- 0,39	+ 0,63	
	stressed	- 0,82	+ 0,93	
Silvaner	unstressed	- 0,40	+ 0,78	
	stressed	- 0,72	+ 0,79	

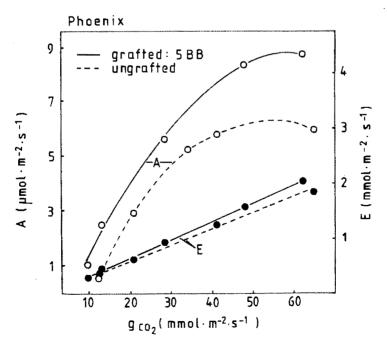


Fig. 3: CO₂ assimilation (A) and transpiration (E) of leaves of ungrafted and grafted Phoenix vines under glasshouse conditions.

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Under glasshouse and field conditions several irrigated scion varieties grafted to Kober 5 BB showed higher rates of photosynthesis compared to ungrafted varieties due to a higher carboxylation efficiency (Fig. 3). But only in 1- and 2-year-old vine varieties this higher CO₂ assimilation rate led to increases of the WUE.

In further experiments we will examine the effects of increasing water stress on gas exchange of grafted and ungrafted scions.

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On the mechanism of vine resistance to low temperatures

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A b s t r a c t: Frost resistance of grapevine is based on its high water confining capacity formed by osmotic forces in result of protective matters being stored in protoplast and with the help of structure ability to lower water activity in prefrozen cells. Colorimetric investigations have shown that before being injured the tissues of the plant contain a high amount of supercooled water. The degree and rate of ice nucleation in tissues depend on their hydration level at the prefrozen period. The low water content promotes the supercooling state of water within living cells of the plant for a longer period and ice nucleation in cells occurs at lower temperatures.

In rehydrated cuttings of frost resistant varieties the first peak – an exothermal rise connected with the beginning of extracellular ice formation after supercooling – is observed at -6 °C. The second low temperature exotherm (LTE) is observed at -22 to -24 °C, corresponding to considerable damage of buds and tissues. In case of dehydrated cuttings (for 5-6 %) the first peak is not observed. The first insignificant peaks are registered at -14 °C, which is perhaps connected with the beginning of extracellular ice formation, for at -14 °C the tissues and buds are alive.

The second exotherm rise is noted only at -26 to -28 °C, when the beginning of strong damages is observed; otherwise the intracellular ice formation begins.

High resistance to low temperatures in frost resistant grapevine varieties is conditioned by higher water confining capacity of cells and more intensive water supercooling in the range of critical temperatures.

Such a mechanism of cell protection does not provide high frost resistance since supercooling state is useful only in moderate frost weather while it is dangerous in long-term hard frosts.