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Stomatal responses to alterations of soil and air humidity in grapevines

by

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Spaltöffnungsreaktionen auf Veränderungen der Boden- und Luftfeuchtigkeit bei Reben

Zusammenfassung: Im Jahre 1985 wurde im Verlauf von 31 Tagesgängen die Assimilation und Transpiration ungestreßter (ψ_w vor Sonnenaufgang: −2 bis −3 bar) und zyklisch gestreßter (ψ_w vor Sonnenaufgang: −2 bis −8 bar) Riesling- und Silvanerreben gemessen:

1. Bei ungestreßten Reben lag die stomatäre Leitfähigkeit bei den Tageshöchstwerten der Assimilation (g bei A_{max}) des Rieslings unter der des Silvaners (−29 %). Die höhere Wassernutzungseffizienz (Assimilation/Transpiration, A/E bei A_{max}) des Rieslings ist überwiegend auf seine geringere Transpiration zurückzuführen. Wassermangel reduzierte bei beiden Sorten die stomatäre Leitfähigkeit bei A_{max}, woraus eine Abnahme der Assimilation und Transpiration bei A_{max} resultierte; das Verhältnis A/E bei A_{max} war vor allem bei Riesling infolge Wassermangelstreß erhöht.
2. g (bei A_{max}) und A_{max} korrelierten in allen Fällen positiv. Wassermangel führte bei Silvaner zu einem steileren Verlauf der Regressionsgeraden, woraus sich eine Erhöhung der Anpassungsfähigkeit an Trockenheit ableiten läßt. Bei Riesling führte Wassermangel zu einer Erhöhung des Korrelationskoeffizienten für g (bei A_{max}) und A_{max}. Diese enge Korrelation bei Wassermangel, das hohe A/E-Verhältnis bei A_{max} sowie der steile Verlauf der Regressionsgeraden lassen vermuten, daß Riesling vor allem bei Streß eine präzisere Stomataregulation und damit eine bessere Anpassungsfähigkeit an Trockenheit besitzt als Silvaner.
3. Bei ungestreßten Reben nahm das A/E-Verhältnis (Tagesmittelwerte) mit zunehmender Blatt-Luft-Wasserdampfdruckdifferenz (Δ_w) ab, wobei Riesling im allgemeinen höhere A/E-Werte besaß als Silvaner.

Im Jahre 1986 wurden Rieslingblätter bei konstanter Temperatur und Licht einem zunehmenden Δ_w ausgesetzt (13 bis 18 mbar · bar^{-1}):

4. Bei hohen Blattwasserpotentialen (−4 bis −6 bar) führten Veränderungen des Δ_w zu gleichzeitigen Abnahmen von g, A und E. Die Beziehung zwischen g und E verlief linear, die Beziehung zwischen g und A kurvilinear. Die optimale stomatäre Leitfähigkeit war dort gegeben, wo die marginale Transpirationsrate der marginalen Assimilationsrate entsprach; in diesem Bereich der stomatären Leitfähigkeit waren auch das A/E-Verhältnis und der Korrelationskoeffizient g (bei A_{max}) − A_{max} im Maximum.

Key words: leaf, stoma, transpiration, photosynthesis, water, drought, resistance.

Introduction

Stomata move in response to internal and environmental changes. These movements affect directly CO_2 uptake, water loss and leaf temperature. Studies of FARQUHAR and RASCHKE (1978) have shown that the surfaces within the leaves, e. g. the substomatal cavity, are completely wet. Therefore, under most circumstances a water vapor gradient exists between leaf and air which is considerably greater than the CO_2 gradient between the intercellular airspace and the air (SCHULZE 1986). This leads to a proportionally greater water loss than CO_2 uptake. According to RASCHKE (1979), frequently several hundred water molecules are lost from the plant for each CO_2 molecule taken up. It can be assumed that environmental conditions like soil water supply or air humidity affect the CO_2/H_2O ratio, i. e. the water use efficiency. From theoretical studies, COWAN and TROUGHTON (1971) concluded that the relationship between transpiration (E) and assimilation (A) is generally non-linear as stomatal conductance varies. According to FARQUHAR and SHARKEY (1982), this 'curvilinearity between E and A affects the requirement for an optimum relationship between the two'. SCHULZE and HALL (1982) postulated that correlation coefficients closer to one, for stomatal conductance (g) at maximal A versus maximal A, may indicate a more precise regulation of stomatal gas exchange.

The aim of this paper was to analyse the effects of soil and air humidity on water use efficiency and to determine the optimal relationship between assimilation and transpiration at varying stomatal conductance in grapevines.

Abbreviations used:

A	Net CO_2 assimilation rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
A_{max}	Maximum values of A during diurnal cycles with natural CO_2 concentration
E	Transpiration rate ($mmol \cdot m^{-2} \cdot s^{-1}$)
g	Stomatal conductance for water vapor ($mmol \cdot m^{-2} \cdot s^{-1}$)
g_{CO_2}	Stomatal conductance for CO_2 ($mmol \cdot m^{-2} \cdot s^{-1}$); $g_{CO_2} = g \cdot 0.64$
WUE	Water use efficiency, A/E ($\mu mol \cdot mol^{-1}$)
Δw	Leaf to air water vapor pressure difference, 'evaporative demand' ($mbar \cdot bar^{-1}$)
Ψpd	Predawn leaf water potential (bar)

Materials and methods

1-year-old Riesling and Silvaner vines were cultivated in 3-l plastic pots in the glasshouse. In June and July 1985, one half of the plants was daily irrigated ('unstressed') while the other half was irrigated only, when the predawn leaf water potential (ψ_{pd}) had reached -7 to -8 bar ('stressed'). At 6.00 h a. m., ψ_{pd} was determined by the pressure chamber technique as described earlier (DÜRING 1984). Subsequently, the gas exchange of fully expanded but not senescent leaves was registered 2 times/h to give 20 — 25 data sets/d; the duration of the experiment was 31 d. Besides assimilation and transpiration, air and leaf temperature, relative humidity and light intensity were registered by use of a portable steady-state porometer (H. Walz, D-8521 Effeltrich, FRG). Differentials of CO_2 and H_2O concentrations between cuvette (containing part of the leaf) and reference air streams as well as the climatic data were monitored continuously and stored in a data logger (DES, H. Walz) from where they were transmitted to a personal computer for further calculations. Following COWAN (1977) and CAEMMERER and FARQUHAR (1981), molar flux and molar conductance have been used for the sake of simplicity in the demonstration of relationships (see RASCHKE 1979).

In August 1986, leaves of potted Riesling plants were inserted into a Miniküvetten-System (H. Walz) and subjected to constant temperature (27.8 $\pm$ 0.5 °C) and light conditions (Osram HQI lamp, 400 W, 428 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the leaf surface). The leaf to air water vapor pressure difference (Δ_w) was linearly increased from 13.2 to 18.1 $mbar \cdot bar^{-1}$ within 92 min. The water potential of each leaf was determined after the experiment. The results presented are a typical example of a series of similar experiments.

Results and discussion

1. Responses to soil drought

In Table 1, the results on gas exchange of stressed and unstressed Riesling and Silvaner vines growing under glasshouse conditions (see 'Material and methods') are summarized. Average A, E, g and A/E values at the daily maximum assimilation (A_{max}) are drawn from 31 diurnal cycles with 20—25 measurements each. According to SCHULZE and HALL (1982) leaf conductance at which CO_2 assimilation is maximal (g at A_{max}) has a high ecological significance for understanding plant adaptations to their environment. Under the same environmental conditions, g (at A_{max}) of unstressed Riesling is distinctly lower than g (at A_{max}) of unstressed Silvaner (−29 %). It is evident that this leads to a lower transpiration (E at A_{max}) but not to a significant lower A_{max}. The higher transpiration rate of Silvaner at similar A_{max} values causes a lower WUE (A/E at A_{max}) of this variety. In unstressed vines, the correlation coefficient for g (at A_{max}) versus A_{max} does not indicate a very close relationship between both parameters. Due to reduced water supply during repeated stress and irrigation cycles, g (at A_{max}) is reduced in both varieties (Riesling −42 %, Silvaner −48 %). Higher values of g (at A_{max}) in Silvaner vines are associated with slightly higher A and distinctly higher E values at A_{max}. Water stress causes only a small increase of the ratio A/E at A_{max} in Silvaner but a significant increase in Riesling. This is due to the fact that in stressed Riesling vines E (at A_{max}) is much more reduced (−43 %) than A_{max} (−29 %), while in stressed Silvaner vines the reduction of A_{max} (−21 %) is similar to the rate of E (at A_{max}) (−23 %). As simultaneously in stressed vines the correlation coefficient A_{max} versus g (at A_{max}) is increased, to a small extent in Silvaner and to a high one in Riesling, a high correlation coefficient A_{max} versus g (at A_{max}) may in fact indicate a more precise functioning of stomatal action, as was assumed by SCHULZE and HALL (1982).

Table 1

Effects of soil humidity on assimilation (A), transpiration (E), stomatal conductance (g) and the water use efficiency (A/E) at the daily A maximum (A_{max}) and the correlation coefficient for A_{max} versus g at A_{max} · Averages from an experiment under glasshouse conditions; June, 11 to July, 18, 1985

Einfluß der Bodenfeuchtigkeit auf die Assimilation (A), Transpiration (E), stomatäre Leitfähigkeit (g) und Wassernutzungseffizienz (A/E) zum Zeitpunkt des täglichen A-Maximums (A_{max}) und der Korrelationskoeffizient A_{max}—g (bei A_{max}) · Mittelwerte eines Gewächshausversuches, 11. Juni—18. Juli 1985

	A	E	g	A/E	Correlation coefficient
	at A_{max}				A_{max}—g at A_{max}
Unstressed					
Riesling	5.6	1.02	52.7	5.49	0.63
Silvaner	5.7	1.40	74.5	4.07	0.78
Stressed					
Riesling	4.0	0.58	30.4	6.93	0.93
Silvaner	4.5	1.08	39.0	4.17	0.79

Fig. 1 illustrates the relationship between A_{max} and g (at A_{max}) of unstressed (control) and stressed Riesling and Silvaner vines. It is obvious that unstressed Riesling vines exhibit a steeper slope than the corresponding Silvaner vines. In Silvaner wines water stress leads to an increase of steepness of slope while that of Riesling remains nearly unchanged. Steeper slopes, as exhibited by Riesling and Silvaner (stressed), signify higher intrinsic water use efficiency and improved adaptation to dry habitats (SCHULZE and HALL 1982).

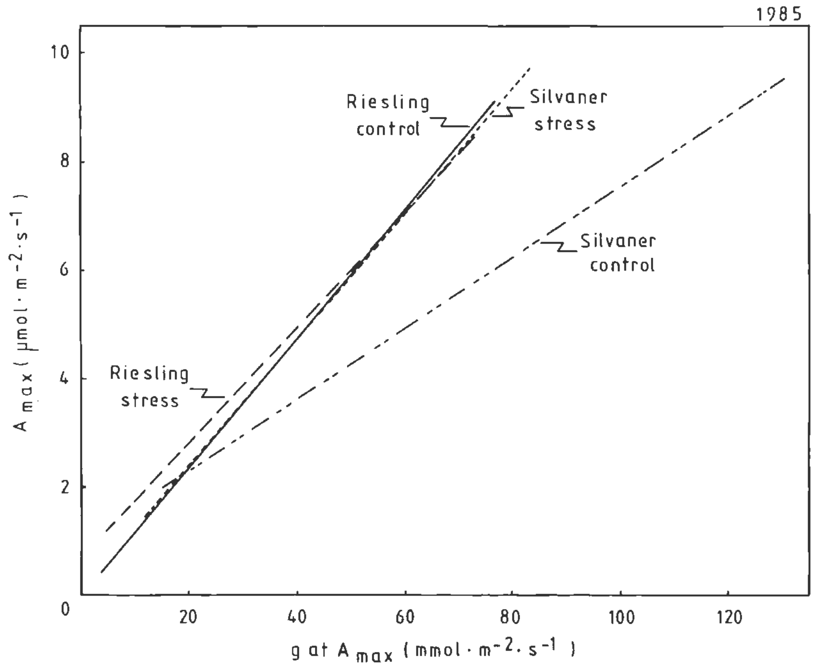

Fig. 1: Daily maximum values of assimilation (A_{max}) of unstressed (control) and stressed Riesling and Silvaner vines (glasshouse) related to stomatal conductance at A_{max}. — Riesling, control: $y = 1.12 + 8.83x$; stress: $y = -5.84 + 9.22x$. Silvaner, control: $y = -16.30 + 15.76x$; stress: $y = 0.42 + 8.56x$. — For correlation coefficients see Table 1.

Tageshöchstwerte der Assimilation (A_{max}) ungestreßter (Kontrolle) und gestreßter Riesling- und Silvaner-Reben (Gewächshaus), bezogen auf die stomatäre Leitfähigkeit bei A_{max}. — Die Korrelationskoeffizienten finden sich in Tabelle 1.

From these results, it appears that Riesling is superior to Silvaner with respect to drought tolerance due to its lower stomatal conductance leading to a lowering of water loss and an increase of A/E ratio. Moreover, Riesling is able to improve the precision of its stomatal action under drought stress. Silvaner gets adapted to drought by steepening its regression line A_{max} versus g (at A_{max}) close to that of Riesling. In both varieties drought reduced the 'benefit' (i. e. assimilation) and 'cost' (i. e. transpiration), raising at the same time the 'benefit to cost ratio', i. e. productivity.

Similar results with grapevines were obtained by EIBACH and ALLEWELDT (1984) who found at low water supply a reduction of A (−27 %) and E (−39 %) but an increase of productivity of +20 %.

2. Responses to air humidity

If stomata were uniformly open during all the day, transpiration would rise linearly with increasing evaporative demand. But grapevines subjected to a drought stress were shown to close their stomata at decreasing air humidity (DÜRING 1976). As in these experiments the leaf water potential was not determined, stomatal closure at decreasing air humidity might, at least in part, have been due to a lowered leaf water potential. In 1985, a preliminary analysis of environmental effects on stomatal action

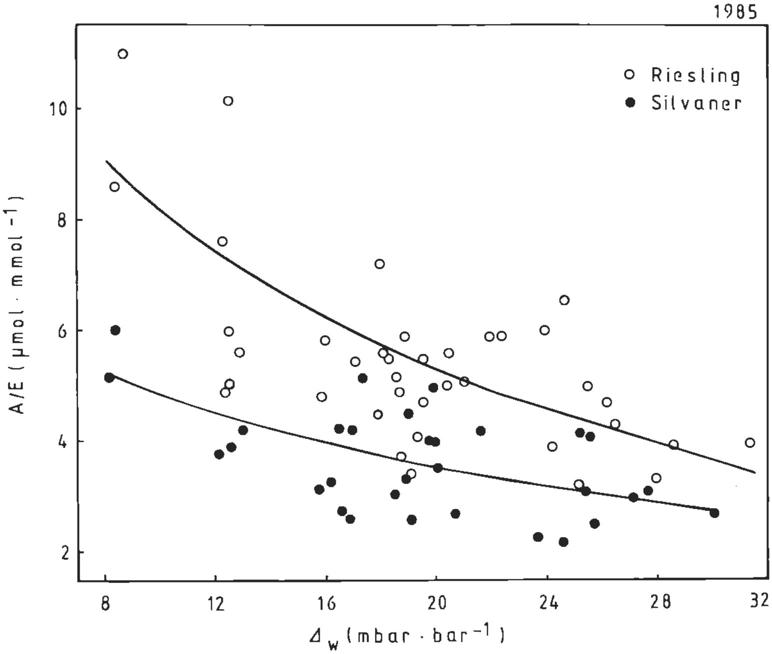

Fig. 2: The assimilation to transpiration ratio (A/E) related to the leaf to air water vapor pressure difference (Δ_w). The single values represent average daily values of 31 diurnal cycles. Unstressed Riesling and Silvaner vines under glasshouse conditions. — Riesling: $y = 17.43 - 4.05 \cdot \log x$, $r = -0.734$; Silvaner: $y = 9.02 - 1.83 \cdot \log x$, $r = -0.597$.

Das Verhältnis Assimilation : Transpiration (A/E), bezogen auf die Blatt-Luft-Wasserdampfdruckdifferenz (Δ_w). Die Einzelwerte sind Tagesmittelwerte aus 31 Tagesgängen. Ungestreßte Riesling- und Silvaner-Reben unter Gewächshausbedingungen.

showed that in daily irrigated, i. e. unstressed, vines increasing values of the leaf to air water vapor pressure difference (Δ_w) led to a decrease of the A/E ratio in Riesling and Silvaner vines, Riesling exhibiting a generally higher A/E ratio (Fig. 2); the data represent average daily values. As in natural environments, changes of Δ_w are associated with changes in temperature and light, the effect of one single factor (Δ_w) on stomatal gas exchange was examined in an experiment with Riesling leaves at constant temperature and light conditions. Δ_w was linearly increased as given under 'Material and methods'. As is shown in Fig. 3, an increase of Δ_w leads to a simultaneous decrease of g, A and E when Δ_w has passed 14—15 mbar · bar^{-1}. Stomatal closure at decreasing air humidity could not have been induced by a rapid water loss from the leaves, as measurements of the leaf water potential immediately after the experiment exhibited values in the range of −4 to −6 bar. When A and E are plotted against g, transpiration is found to increase in linear, photosynthesis in a non-linear manner (Fig. 4).

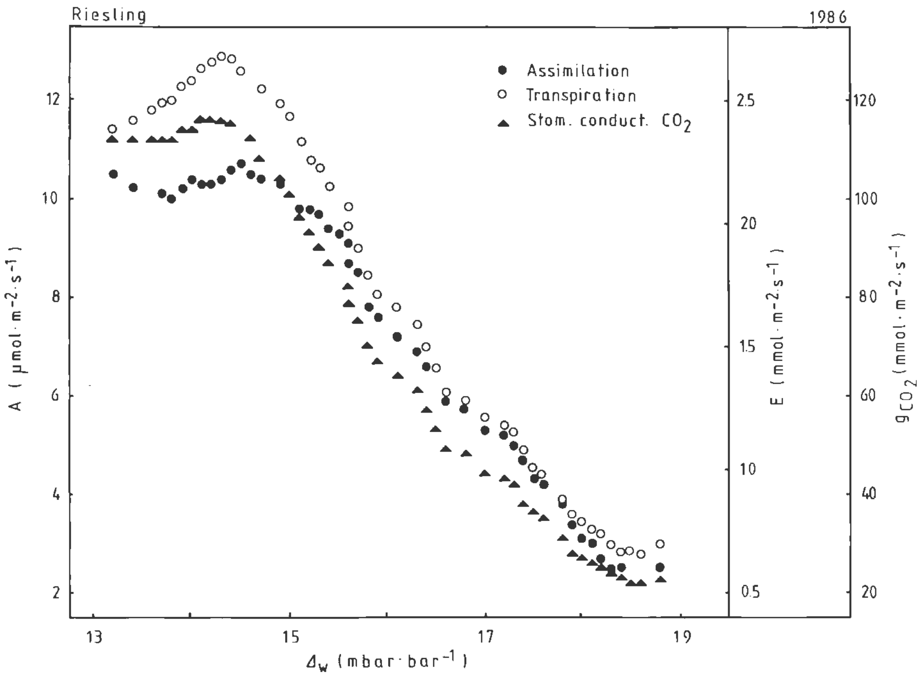

Fig. 3: The assimilation (A), transpiration (E) and stomatal conductance for CO_2 (g_{CO_2}) related to the leaf to air water vapor pressure difference (Δ_w). Potted Riesling plants.

Die Assimilation (A), Transpiration (E) und stomatäre Leitfähigkeit für CO_2 (g_{CO_2}) bezogen auf die Blatt-Luft-Wasserdampfdruckdifferenz (Δ_w). Topfpflanzen der Sorte Riesling.

According to FARQUHAR and SHARKEY (1982), the optimal conductance is given when the marginal 'cost' (water loss) equals the marginal 'benefit' (CO_2 gain). Under our experimental conditions, the optimal conductance is reached at approximately 50 mmol · m^{-2} · s^{-1}. Calculations indicate that the maximal A/E ratio, i. e. the highest water use efficiency, is reached at a stomatal conductance of approximately 40—70 mmol · m^{-2} · s^{-1}. This result demonstrates clearly that partial stomatal closure contributes to optimize water use efficiency of grapevines. Calculations of the correlation coefficient g versus A for increasing steps of g are summarized in Table 2. The highest correlation coefficients are found also at stomatal conductance values in the range of 40—70 mmol · m^{-2} · s^{-1}, i. e. in the range of maximum A/E values (see Fig. 3).

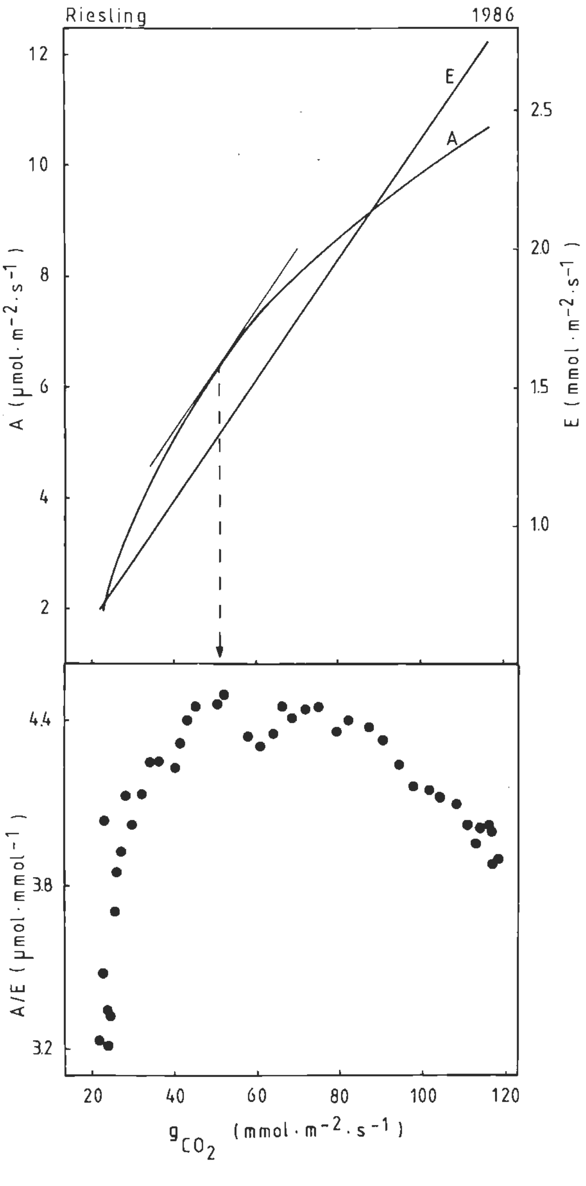

Fig. 4: The assimilation (A) and transpiration (E) related to the stomatal conductance for CO_2 (above) and the A/E ratio related to the stomatal conductance for CO_2 (below). The arrow denotes the stomatal conductance for CO_2, where the slope of A equals that of E and where the A/E ratio is maximum. Potted Riesling plants. — $A = f(g_{CO2}) : y = 15.24-0.19x$, $r = 0.998$; $E = f(g_{CO2}) : y = -9.39 + 45.36x$, $r = 0.999$.

Die Assimilation (A) und Transpiration (E), bezogen auf die stomatäre Leitfähigkeit für CO_2 (oben), und das Verhältnis A/E, bezogen auf die stomatäre Leitfähigkeit für CO_2 (unten). Der Pfeil deutet die stomatäre Leitfähigkeit für CO_2 an, bei der die Steigung von A und E gleich ist und bei der das A/E-Verhältnis Maximalwerte erreicht. Topfpflanzen der Sorte Riesling.

Correction of misprint

In the article of H. DÜRING, Vitis **26** (1), on p. 15, legend to Fig. 4, the 4th line must read:

maximum. Potted Riesling plants. — $A = f(g_{CO_2})$: $y = 15.24^{-0.19x}$, $r = 0.998$; $E = f(g_{CO_2})$: $y =$

Table 2

The water use efficiency (A/E ratio) and the correlation coefficient for g_{CO_2} versus A within different g_{CO_2} ranges · Potted Riesling plants (see Fig. 4)

Die Wassernutzungseffizienz (A/E-Verhältnis) und der Korrelationskoeffizient g_{CO_2} — A innerhalb verschiedener g_{CO_2}-Bereiche · Topfpflanzen der Sorte Riesling (vgl. Abb. 4)

g_{CO_2} mmol · m^{-2} · s^{-1}	A/E µmol · $mmol^{-1}$	Correl. coefficient g_{CO_2}—A
20— 30	3.69	0.91
30— 40	4.27	0.97
40— 50	4.38	0.99
50— 60	4.46	0.92
60— 70	4.37	0.99
70— 80	4.42	0.90
80— 90	4.35	0.94
90—100	4.22	0.83
100—110	4.12	0.94
110—120	3.96	−0.17

Conclusion

The results presented in this paper demonstrate that stomata of grapevines are an integral part within the framework of processes leading to an increase of adaptation to atmospheric and soil drought. Compared to mechanisms of adaptation to drought, like reduction of cell size or osmotic adjustment, the stomatal adaptations presented here belong to the group of short-term responses (DÜRING 1984). Although under most circumstances even a partial stomatal closure leads to a reduction of carbon gain, these reactions enable grapevines to survive under drought conditions and they guarantee the maintenance of vegetative growth and fruit production. EIBACH and ALLEWELDT (1984) note a close correlation between the assimilation/transpiration ratio and the transpiration coefficient (mg H_2O · g^{-1} dry matter) and conclude that measurements of gas exchange might provide useful informations when selecting drought tolerant grapevine scions. Our results confirm this statement. It is assumed that determinations of the A/E ratio, the correlation coefficient g (at A_{max}) versus A_{max} under drought stress conditions and the slope of the A_{max} versus g (at A_{max}) relation are useful parameters which may be considered in breeding programs to select drought tolerant cultivars. Moreover, it is concluded from preliminary results that g (at A_{max}) under near-optimal environmental conditions at ambient CO_2 concentrations may be a useful indicator of the photosynthetic capacity of a variety (DÜRING, unpublished).

Summary

In 1985, during 31 diurnal cycles the assimilation and transpiration of unstressed (predawn ψ_w: −2 to −3 bar) and cyclically stressed (predawn ψ_w: −2 to −8 bar) Riesling and Silvaner vines were recorded:

1. In unstressed vines, the average stomatal conductance at daily maximum assimilation (g at A_{max}) was lower in Riesling than in Silvaner (−29 %). The higher water use efficiency (assimilation to transpiration ratio, A/E at A_{max}) of Riesling was mainly due to its lower transpiration. At reduced water supply, g (at A_{max}) was reduced in both varieties causing a decline of A and E (at A_{max}); especially in Riesling the A/E ratio (at A_{max}) was increased due to water stress.
2. g (at A_{max}) and A_{max} were always positively correlated. In Silvaner, water stress led to a steeper slope of the regression line which indicates an increase of adaptation to drought; in Riesling, water stress caused a higher correlation coefficient. This closer correlation at water stress, the high A/E ratio (at A_{max}) and the steep slope of the regression line suggest that Riesling, especially under stress conditions, has a more precise functioning of stomatal action and herewith a higher adaptability to drought conditions than Silvaner.
3. In unstressed vines, the A/E ratio (daily average values) declined at increasing leaf-air water vapor pressure difference (Δ_w), Riesling exhibiting generally higher A/E values than Silvaner.

In 1986, Riesling leaves were subjected to increasing Δ_w (from 13 to 18 mbar · bar^{-1}) at constant light and temperature:

4. At high leaf water potentials (−4 to −6 bar), alterations of Δ_w led to simultanous decreases of g, A and E. Related to stomatal conductance, transpiration increased in a linear, assimilation in a curvilinear manner. The optimal stomatal conductance was given where the marginal transpiration rate equaled the marginal assimilation rate; the A/E ratio and the correlation coefficient g (at A_{max}) − A_{max} were found to be highest in that range of stomatal conductance.

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