

CO₂ assimilation and photorespiration of grapevine leaves: Responses to light and drought

by

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CO₂-Assimilation und Lichtatmung bei Blättern von Reben: Reaktionen auf Licht und Trockenheit

Zusammenfassung: Der Einfluß von Lichtintensität (Photonenfluß, PFD) und Wassermangelstreß auf den Gaswechsel wurde bei Freiland- und Gewächshaus-kultivierten Rebsorten untersucht:

1. Bei Blättern von Freilandreben (Riesling) wurde der Lichtkompensationspunkt mit $9 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ermittelt; die Lichtsättigung der Photosynthese (A) lag bei $0,55 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Bei höherem PFD ($0,55$ — $2,25 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) stieg A weiterhin geringfügig an; dieser Anstieg ist vermutlich auf die mit dem PFD zunehmende interzelluläre CO₂-Konzentration (c_i) zurückzuführen. Die Lichtnutzung (A/PFD) nahm mit zunehmendem PFD ab. Die Lichtatmung (R_L) lag im Bereich von $13,7$ — $16,1 \%$ von A (mit Ausnahme von $\text{PFD} < 0,17 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).
2. Bei bewässertem, im schattierten Gewächshaus (PFD maximal $400 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) kultivierten Reben waren A, A/PFD und die Carboxylierungseffizienz (A/c_i) geringer als bei Freilandpflanzen. Hohe PFD-Dosen führten bei diesen Pflanzen zu einer geringfügigen Abnahme von A. Die Wassernutzungseffizienz (A/E) war bei Trollinger ($4,7 \mu\text{mol CO}_2 \cdot \text{mmol H}_2\text{O}^{-1}$) am höchsten, es folgten Riesling mit $4,6$ und Phoenix mit $3,6 \mu\text{mol CO}_2 \cdot \text{mmol H}_2\text{O}^{-1}$. R_L (in % von A) war bei den Gewächshausreben gegenüber den Freilandreben auf 20% erhöht.
3. Bei Gewächshausreben, die einem Wassermangelstreß ausgesetzt waren ($\psi_{pd} = -7,5 \text{ bar}$), war die maximale CO₂-Assimilation (A_{max}) vermindert. PFD bei A_{max} war bei gestreßten Reben von 725 auf $520 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ herabgesetzt. Das A/E-Verhältnis war bei Wassermangel in allen Sorten erhöht. R_L war unter Streßbedingungen vermindert, aber in einem geringeren Umfang als A, sodaß die R_L -Rate (in % von A) auf 35 — 52% anstieg.
4. 3 d nach der Wiederbewässerung gestreßter Reben hatten sich die stomatare Leitfähigkeit für CO₂ (g_{CO_2}) und A noch nicht vollständig vom Streß erholt; eine völlige Erholung war 5 d nach der Bewässerung bei Riesling und Phoenix, nicht jedoch bei Trollinger festzustellen.

Key words: leaf, stoma, photosynthesis, respiration, transpiration, light, water, drought, resistance, variety of vine.

Introduction

Grapevine productivity as the difference between the amount of photosynthetic and respiratory activity is strongly governed by the efficiency with which the photosynthetic apparatus operates under the prevailing conditions and its ability to cope with environmental stresses (OSMOND *et al.* 1980). In recent years, several reports on the effects of light, temperature and water supply to the photosynthetic rate of grapevine leaves have been presented (KRIEDEMANN and SMART 1971; HOFACKER 1976; KRIEDEMANN and DOWNTON 1981; EIBACH and ALLEWELDT 1984; DOWNTON *et al.* 1987; DURING 1987). However, to our knowledge photorespiration has not yet been determined quantitatively in grapevines. This is probably due to theoretical and technical problems associated with the determination of the photorespiration rate (OGREN 1984; SHARKEY 1988).

In recent years, a better understanding of the biochemical pathway of photorespiration allowed the calculation of rates of photorespiration from the kinetics of ribulose-1,5-biphosphate carboxylase/oxygenase (RuBPcase) (SHARKEY 1988); for details see LAING *et al.* 1974; FARQUHAR and VON CAEMMERER 1982). The aim of this paper was to determine photosynthetic and respiratory responses of vines to light intensity and to study the light-water stress interaction of several grapevine varieties.

Material and methods

Plants

Experiment 1: In July 1987, the effects of light intensity (PFD, photon flux density) on gas exchange were studied using fully expanded but not senescent leaves of 13-year-old field-grown ungrafted grapevines (variety Riesling). After a series of rainfalls, the plants were fully supplied with water (average $\psi_{pd} = -1.5$ bar).

Experiment 2: 2-year-old *Vitis vinifera* varieties Riesling and Trollinger and the interspecific variety Phoenix were cultivated in pots under glasshouse conditions (maximum light intensity $400 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) until the experiment was started on May, 13 1988. Plants were selected for uniform growth (stem length 1.10 m). Gas exchange was measured at various photon flux densities (0—1330 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Experimental details are given below:

Stage	Day of experiment (d)	Soil water capacity (%)	Predawn water potential (-bar)
a: Irrigated control	0—1	80—100	1—2
b: Stress	10	45— 50	7—8
c: Recovery	13	80—100	1—2
d: Recovery	15	80—100	1—2

Gas analysis

Fully expanded but not senescent leaves were inserted into a cuvette chamber of the Minicuvette-system (produced by H. Walz, D-8521 Effeltrich, F. R. of Germany) and sealed by a lid containing two layers of glass (Sanalux). Inside air temperature of the chamber was held at $25 (\pm 0.2) ^\circ\text{C}$, the leaf to air water vapor pressure difference was kept constant at a dew point of $17 ^\circ\text{C}$ (61 % air humidity). Illumination was provided for the enclosed part of the leaf with a 12 V 75 W projector lamp (General Electric) fixed to the top of the light filter system which can be connected to the lid of the chamber. Light intensity was varied with gray filters inserted below the light bulb. Stepwise change of filters resulted in a response curve of CO_2 assimilation to photosynthetic active radiation between 95 and $2250 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Equilibration time after change of light intensity was approximately 10—15 min. CO_2 and H_2O exchange of the enclosed part of the leaf was measured in an open flow system according to the differential gas analysis procedures. In order to eliminate errors in CO_2 measurement due to cross sensitivity to water vapor the measuring and reference air streams after transpiration measurement passed through a water vapor trap (dew point of $2 ^\circ\text{C}$). The calculations of gas exchange parameters are based on the propositions made by VON CAEMMERER and FARQUHAR (1981) and SHARKEY (1988).

Abbreviations used:

A	CO ₂ assimilation ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
A _{max}	Maximum CO ₂ assimilation at light saturation and under ambient CO ₂ concentration
R _L	Photorespiration ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
R _D	Dark respiration ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
g _{CO₂}	Stomatal conductance for CO ₂ ($\text{mmol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
c _a	Ambient CO ₂ concentration (ppm)
c _i	Intercellular CO ₂ concentration (ppm); $c_i = c_a - (A/g_{\text{CO}_2})$
PFD	Photon flux density, 'light intensity' ($\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
A/PFD	Photon yield ($\mu\text{mol CO}_2 \cdot \mu\text{mol quanta}^{-1}$)
A/E	Water use efficiency, CO ₂ assimilation/transpiration ratio ($\mu\text{mol CO}_2 \cdot \text{mmol H}_2\text{O}^{-1}$)
A/c _i	Carboxylation efficiency ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{ppm CO}_2^{-1}$)
Ψ _{pd}	Predawn water potential (bar)

Results

1. Experiments with field-grown vines

To study the effects of light intensity of field-grown Riesling vine leaves on the outer part of the canopy were exposed to various photon flux densities. As shown in Fig. 1, dark respiration of the leaves was low (i.e. close to 0); the light compensation point was found at $9 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which is in accord with the results of RÜHL *et al.* (1981) who measured in *Vitis* spp. light compensation points ranging from 450 to 750 lx. CO₂ assimilation increased rapidly when light intensity increased; light saturation of photosynthesis was reached at $0.55 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. A further increase of light intensity up to $2.25 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ raised the rate of CO₂ assimilation only slightly (+ 14.8 %). The light response of CO₂ assimilation led to a rapid decrease of photon yield (A/PFD) from $0.0424 \mu\text{mol CO}_2 \cdot \mu\text{mol quanta}^{-1}$ at $95 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ to $0.0058 \mu\text{mol CO}_2 \cdot \mu\text{mol quanta}^{-1}$ at $2250 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Calculation of the rate of photorespiration indicates that increasing light intensity caused a rapid increase of photorespiratory CO₂ loss up to PFD of $0.55 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, while at higher light intensities photorespiration remained fairly constant at $1.7 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

The rate of photosynthesis related to the rate of photorespiration was almost constant from 0.17 to $2.25 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, i.e. $13.7 (\pm 1.0) \%$ of the CO₂ assimilation falls to photorespiration. Only at lower PFD the ratio was slightly higher. (Similar results were obtained with field-grown plants of Phoenix and Gf.Ga-47-42 where under the same ambient conditions the rate of photorespiration was 16.1 and 15.0 % of A, respectively).

An increase of light intensity from 0 to $0.55 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ led to a decrease of the intercellular CO₂ concentration due to the rapidly increasing CO₂ demand at an almost constant stomatal conductance for CO₂. At higher light intensities, at almost constant A and increasing g_{CO₂}, internal CO₂ concentration increased again.

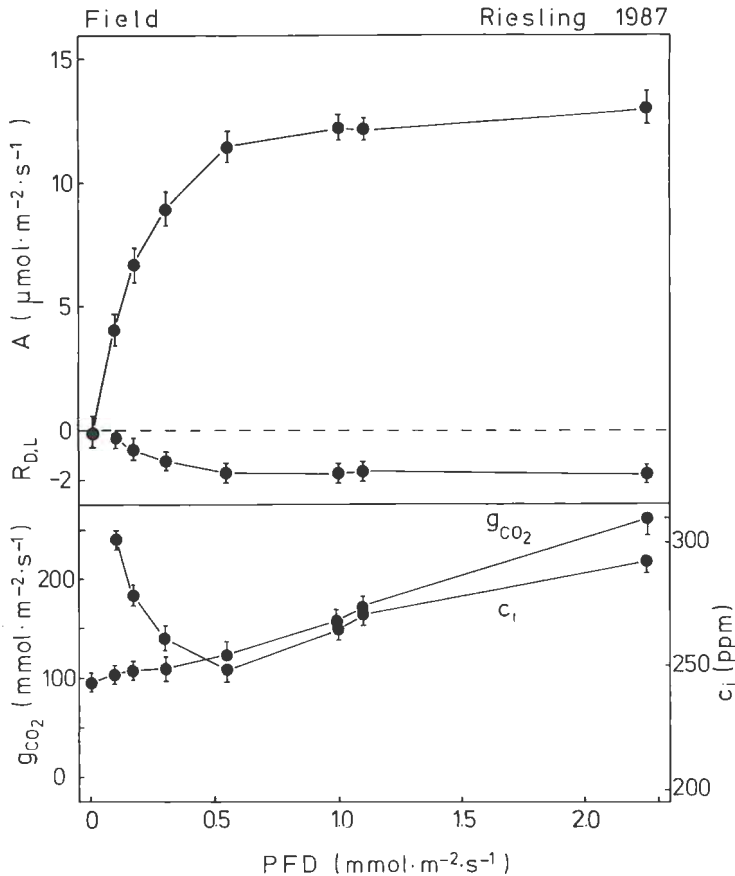


Fig. 1: CO_2 assimilation (A), dark respiration (R_D), light respiration (R_L), stomatal conductance for CO_2 (g_{CO_2}) and intercellular CO_2 concentration (c_i) of leaves of field-grown Riesling vines as a function of light intensity (PFD). The vertical bars indicate least significant differences at the 5% level.

Photosynthese (A), Dunkelatmung (R_D), Lichtatmung (R_L), stomatische Leitfähigkeit für CO_2 (g_{CO_2}) und interzelluläre CO_2 -Konzentration (c_i) von Rieslingblättern in Abhängigkeit von der Lichtintensität (PFD). Freilandpflanzen. Senkrechte Balken: Grenzdifferenzen bei $P = 5\%$.

2. Experiments with glasshouse-grown vines

a) Light effects at high leaf water potential

The CO_2 assimilation of fully irrigated vines (varieties Phoenix, Riesling and Trollinger) grown in a shaded glasshouse increased with increasing PFD (Fig. 2,a; data of Phoenix and Trollinger not shown). The light compensation point was determined at 6 (Trollinger), 11 (Riesling) and 24 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Phoenix). Maximum CO_2 assimilation (A_{max}), maximum photon yield (A/PFD at 95 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and maximum carboxylation efficiency (A/c_i at 1000 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were lower in glasshouse-grown vines compared to field-grown ones (Table 1).

At $\text{PFD} > 0.55 \text{ mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ the assimilation rate decreased slightly. Increases of PFD were closely correlated to increases of stomatal conductance, while

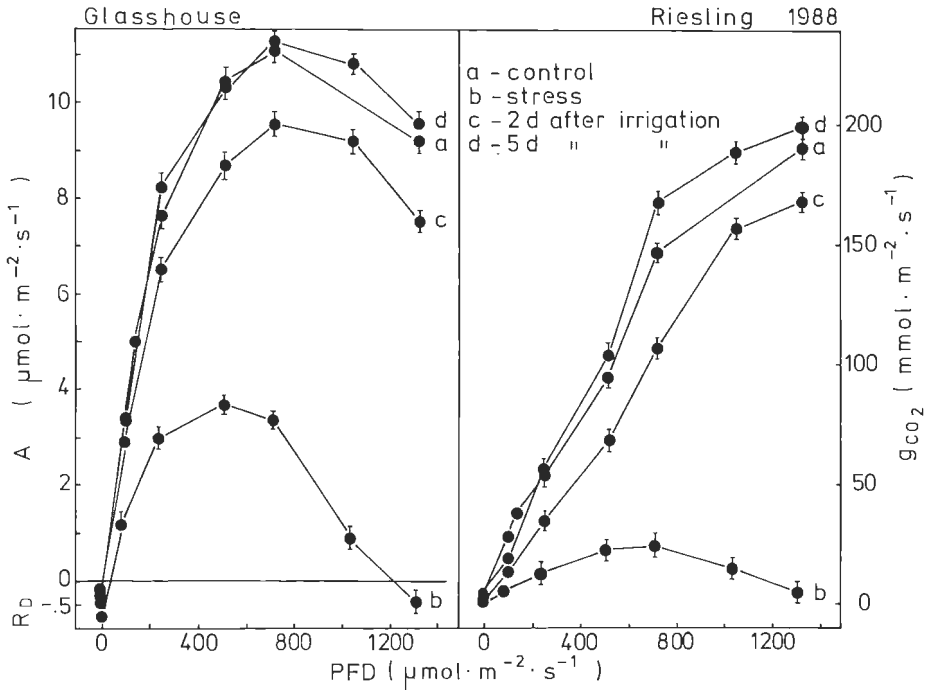


Fig. 2: CO₂ assimilation (A), dark respiration (R_D) and stomatal conductance for CO₂ (g_{CO_2}) of leaves of irrigated (a), stressed (b) and recovering (c, d) Riesling vines. Glasshouse experiment. Values of A and g_{CO_2} are significant at the 5 % level (exceptions: a and d). The vertical bars indicate least significant differences at the 5 % level.

Photosynthese (A), Dunkelatmung (R_D) und stomatäre Leitfähigkeit für CO₂ (g_{CO_2}) von Blättern bewässerter (a), gestresster (b) und sich erholender (c, d) Rieslingreben. Gewächshausversuch. Die A- und g_{CO_2} -Werte sind signifikant unterschiedlich für P = 5 % (Ausnahme: Varianten a und d). Senkrechte Balken: Grenzdifferenzen bei P = 5 %.

the correlation coefficient for g_{CO_2} versus A was slightly lower (Table 2, a). Stomatal conductance for CO₂ at A_{max} differs widely from 116 (Trollinger) to 147 (Riesling) and 193 $mmol \cdot m^{-2} \cdot s^{-1}$ (Phoenix). As a consequence, the A/E ratio at A_{max} is higher in Trollinger and Riesling (4.7 and 4.6 $\mu mol CO_2 \cdot mmol H_2O^{-1}$) compared to Phoenix (3.5 $\mu mol \cdot CO_2 \cdot mmol H_2O^{-1}$).

Calculation of the rate of photorespiration does not show substantial varietal differences. Approximately 20 % of the CO₂ assimilation falls to photorespiration indicating a slightly higher proportion of photorespiration in glasshouse-grown plants (Table 3).

b) Light effects at low leaf water potential

After 10 d of withholding irrigation, the leaves had decreased their predawn water potential to $-7.5 (\pm 1)$ bar, the soil water capacity was reduced to 45–50 %. Under stress conditions the light compensation point had moved to higher light intensities (Riesling 38, Phoenix 50, Trollinger 61 $\mu mol quanta \cdot m^{-2} \cdot s^{-1}$; Fig. 2, b).

Table 1

Maximum CO₂ assimilation, photon yield and carboxylation efficiency of Riesling and Phoenix vines grown in the glasshouse and under field conditions

Maximale Photosynthese, Lichtnutzung und Carboxylierungseffizienz von Riesling- und Phoenixreben aus dem Gewächshaus und aus dem Freiland

Conditions	Variety	Maximum		
		Assimilation ¹⁾ ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	Photon yield ²⁾ ($\mu\text{mol CO}_2 \cdot \mu\text{mol quanta}^{-1}$) $\times 10^3$	Carbox. efficiency ³⁾ ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1} \cdot \text{ppm CO}_2^{-1}$) $\times 10^3$
Glasshouse	Riesling	11.4 (± 0.4) ⁴⁾	36.8 (± 1.0)	44.0 (± 0.6)
	Phoenix	10.3 (± 0.4)	30.9 (± 1.2)	38.4 (± 1.0)
Field	Riesling	13.0 (± 0.6)	42.4 (± 0.8)	46.4 (± 0.9)
	Phoenix	15.1 (± 0.8)	54.3 (± 1.8)	62.2 (± 1.2)

1) At 725 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (glasshouse).

At 2250 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (field).

2) At 95 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

3) At 250 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (glasshouse).

At 550 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (field).

4) Values in parentheses are confidence limits at the 5 % level.

The rate of A_{max} was reduced compared to irrigated plants by 62 % (Phoenix), 47 % (Trollinger) and 37 % (Riesling). It should be noted that in all three varieties the PFD where A reached its maximum was reduced from 725 to 520 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. In contrast to irrigated vines, under stress conditions stomata opened only to a small extent and stomatal conductance decreased at PFD > 725 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in Riesling, and > 520 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in Phoenix and Trollinger. The obviously synchronous behaviour of A and g_{CO_2} under stress conditions is verified by the increase

Table 2

Correlation coefficients of light intensity (PFD) versus stomatal conductance (g_{CO_2}) and g_{CO_2} versus CO₂ assimilation (A) · Glasshouse-grown vines

Korrelationskoeffizienten zwischen Lichtintensität (PFD) und stomatärer Leitfähigkeit (g_{CO_2}) sowie zwischen g_{CO_2} und Photosynthese (A) · Gewächshausreben

Stage	Correlation	Riesling	Phoenix	Trollinger
a	PFD — g_{CO_2}	0.979	0.946	0.999
	g_{CO_2} — A	0.808	0.817	0.741
b	PFD — g_{CO_2}	-0.023	0.151	0.087
	g_{CO_2} — A	0.909	0.905	0.948
c	PFD — g_{CO_2}	0.992	0.995	0.920
	g_{CO_2} — A	0.756	0.727	0.740
d	PFD — g_{CO_2}	0.968	0.992	0.992
	g_{CO_2} — A	0.838	0.712	0.677

Table 3

CO₂ assimilation (A), photorespiration (R_L) and photorespiration as a proportion of CO₂ assimilation of unstressed and water-stressed grapevines cultivated in the glasshouse · Measurements at 250 μmol quanta · m⁻² · s⁻¹

Photosynthese (A), Photorespiration (R_L) und Photorespiration bezogen auf die Photosynthese bei ungestreift und Wassermangel-gestreift Gewächshausreben · Messungen bei 250 μmol quanta · m⁻² · s⁻¹

Parameter Treatment	Riesling	Trollinger	Phoenix
A (μmol · m ⁻² · s ⁻¹)			
Unstressed	7.64	7.61	7.07
Stressed	2.96	4.35	2.90
R _L (μmol · m ⁻² · s ⁻¹)			
Unstressed	1.46	1.64	1.43
Stressed	1.02	1.51	1.52
R _L (as % of A)			
Unstressed	19.1	21.6	20.2
Stressed	34.5	34.7	52.4

Differences between values of unstressed and stressed treatments are significant at the 5 % level.

of the correlation coefficient A versus g_{CO_2} (Table 2, b), indicating an increased coordination between stomatal action and CO₂ assimilation. This increased coordination is also reflected by the increased A/E ratio at A_{max} which is highest in Phoenix (7.9) followed by Trollinger (7.0) and Riesling (6.6 μmol · mmol⁻¹).

Table 3 shows that the rate of photorespiration of stressed vines is lower compared to irrigated vines (exception: Phoenix) and that R_L (in % of A) increased under water stress conditions.

c) Light effects at recovery from stress

After recording the light effects at low leaf water potential, all plants were fully irrigated. 3 d later, the predawn water potential was again close to 0 at a soil water capacity in the range of 80—100 %. As shown in Fig. 2,c, the light compensation point in all varieties was close to 0 and A_{max} was reached (similar to the control) at PFD = 725 μmol quanta · m⁻² · s⁻¹. Thereafter A decreased slightly. 3 d after irrigation, the values of A_{max} were still lower than those measured before stress. Stomatal conductance increased together with PFD up to 1330 μmol quanta · m⁻² · s⁻¹. Similar results were obtained for Trollinger and Phoenix. It is obvious that 3 d after irrigation CO₂ assimilation and stomatal conductance of all three varieties had not yet completely recovered from previous stress conditions. The A/E ratio at A_{max} was still higher compared to that of the control plants (Riesling 4.9, Phoenix 4.6, Trollinger 5.0 μmol CO₂ · mmol H₂O⁻¹). Complete recovery was achieved only 5 d after irrigation in Riesling and Phoenix but not in Trollinger where A_{max} was still reduced by 19 % (Fig. 2, d). The correlation coefficient PFD— g_{CO_2} had increased again while that of g_{CO_2} —A was slightly lowered 3 and 5 d after watering compared to the values recorded under stress conditions (Table 2, c and d).

Discussion

The results clearly show that light intensity induces reactions of stomata, photosynthesis and photorespiration. In field-grown vines, stomatal conductance and — as a consequence — c_i continuously increased at PFD > 550 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. It is supposed that in our experiments stomatal sensitivity to increasing intercellular CO_2 concentration was reduced at high PFD and thus stomatal conductance was mainly a direct stomatal response to light (SHARKEY and RASCHKE 1981).

As in the field experiment the vines were fully supplied with water, this stomatal reaction appears to be advantageous for the vines: to saturate their photosynthetic apparatus with respect to CO_2 the c_i values should be as high as possible. In fact, we observed under field conditions in Riesling (and other varieties, data not shown) a slight increase of CO_2 assimilation when PFD was raised from 1000 to 2250 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ which may be — *inter alia* — a consequence of the higher c_i values observed at high PFD. Compared to field-grown vines, irrigated glasshouse-grown vines exert lower photosynthetic rates at the same light intensity. As shown in Table 1, the reduced CO_2 assimilation under glasshouse conditions is associated with a lower biochemical capacity for CO_2 assimilation. The rate of photorespiration (as % of CO_2 assimilation) determined in field-grown plants corresponds to that given by OGREN (1984) who calculated a photorespiratory CO_2 release of about 15 % of the rate of net CO_2 fixation for plants with minimal stomatal diffusive resistance. The higher rate of photorespiration (as % of A) found in leaves of glasshouse-grown and especially of stressed vines may possibly find its explanation in the reduced stomatal conductance to CO_2 in these plants which have lowered the internal CO_2/O_2 ratio and thereby the carboxylation/oxygenation ratio (LAWLOR and FOCK 1975; OGREN 1984). In glasshouse-grown vines CO_2 assimilation declined at PFD > 750 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ although at high PFD stomatal conductance and intercellular CO_2 concentration increased. This suggests a non-stomatal inhibition of CO_2 assimilation. In experiments with Sultana, KRIEDEMANN (1968) observed a similar depression of photosynthesis when glasshouse-grown vines were exposed to high light intensities. In our experiments, the leaves were exposed to high PFD less than 30 min only. As no pigment bleaching or destruction due to high PFD became visible and the depression of CO_2 assimilation was reversible, it is assumed that the reduced rate of photosynthesis at high PFD is caused by a transient photoinhibition according to the definition of POWLES (1984). While in our experiments the high PFD effects were studied at optimum temperature, under field conditions high PFD would normally be associated with high temperature.

Under stress conditions stomatal conductance was distinctly reduced, especially at PFD > 725 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. According to the results of RASCHKE (1975), abscisic acid (ABA) which accumulates in leaves during wilting increases the sensibility of stomata to CO_2 . Although the ABA content of the wilted leaves was not determined, it is suspected that in our experiments stomatal closure at high PFD may have been induced by an ABA-mediated sensibilisation of stomata to internal CO_2 which increased in unstressed and stressed leaves in parallel to increasing light intensity. The depression of CO_2 assimilation at high PFD was obviously intensified by water stress. An interaction between high light intensity and water stress has been observed by several authors (for literature: POWLES 1984). It is suggested that both kinds of stress, high light intensity and water stress, cause an inactivation of primary photochemistry of the photosystem II reaction centers. BJÖRKMAN and POWLES (1984) and LUDLOW and BJÖRKMAN (1984) conclude that water stress predisposes the leaves to photoinhibition. Our preliminary experiments indicate that in vine leaves subjected to water stress and

high PFD the maximum of delayed fluorescence (BLAICH 1988) was considerably reduced for several hours.

After rewatering the stressed plants, the recovery of stomatal conductance and photosynthesis was delayed by several days. A similar delay of photosynthetic recovery after water stress has been reported by LIU *et al.* (1978). While in their experiments with *Vitis labruscana* stomatal opened within 1 h after rewatering, a complete photosynthetic recovery was found only after 3 d. Results of RÜHL and ALLEWELDT (1983) indicate that stress intensity and duration strongly affect the recovery of photosynthesis and transpiration of vine leaves. For *Nerium Oleander*, BJÖRKMAN and POWLES (1984) calculated a recovery period after a severe combined water and light stress of even 17 d. Our observation that 3 d after rewatering both CO₂ assimilation and stomatal conductance are still reduced may be beneficial for the simultaneous consideration of the carbon and water economy of the vines. The possibility that residual ABA is effective in coordinating CO₂ uptake and water loss a couple of days after rewatering cannot be excluded (MANSFIELD and DAVIES 1981; RASCHKE, pers. communication).

Summary

The effects of light intensity (photon flux density, PFD) and water stress on the gas exchange of grape vine varieties grown under field and glasshouse conditions were studied:

1. The light compensation point of leaves of field-grown Riesling was determined at 9 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the light saturation of CO₂ assimilation (A) was reached at 0.55 $\text{mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. At higher PFD (0.55—2.25 $\text{mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) A increased slightly; this increase is assumed to be due to the increasing intercellular CO₂ concentration (c_i) at high PFD. Photon yield (A/PFD) decreased with increasing PFD. The rate of photorespiration (R_L) ranged from 13.7 to 16.1 % of A (except at PFD < 0.17 $\text{mmol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).
2. Irrigated vines grown in a shaded glasshouse (maximum PFD 400 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) exerted lower rates of A, A/PFD and carboxylation efficiency (A/ c_i) compared to field-grown plants. At high PFD the rate of A of these plants was slightly decreased. The water use efficiency (A/E) was highest in Trollinger (4.7) followed by Riesling (4.6) and Phoenix (3.5 $\mu\text{mol CO}_2 \cdot \text{mmol H}_2\text{O}^{-1}$). Compared to field-grown vines R_L (% of A) of glasshouse-grown vines increased to 20 %.
3. Glasshouse-grown vines subjected to water stress ($\psi_{pd} = -7.5$ bar) showed reduced maximum rates of A (A_{\max}). PFD at A_{\max} was lowered in stressed vines from 725 to 520 $\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. At water stress, the A/E ratio was increased in all varieties. The rate of R_L was reduced under stress conditions, but to a smaller extent than A. Therefore R_L (as % of A) increased to 35—52 %.
4. 3 d after rewatering stressed vines, stomatal conductance for CO₂ (g_{CO_2}) and A had not fully recovered from stress; a complete recovery was observed only 5 d after rewatering in Riesling and Phoenix but not in Trollinger.

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