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Diurnal changes in water relations and abscisic acid in field grown *Vitis vinifera* cvs.

I. Leaf water potential components and leaf conductance under humid temperate and semiarid conditions

by

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Der Tagesgang des Wasserhaushaltes und der Abscisinsäure bei *Vitis-vinifera*-Sorten im Freiland

I. Die Komponenten des Blattwasserpotentials und die stomatäre Leitfähigkeit unter gemäßigt humiden und semiariden Bedingungen

Zusammenfassung. — Unter den gemäßigt humiden Klimabedingungen Deutschlands (Geilweilerhof) und im semiariden Klima Südaustraliens (Adelaide) wurden der diurnale Verlauf des Wasserpotentials (ψ_w) und seiner Komponenten, das osmotische Potiential (ψ_s) und das Turgorpotential (ψ_p), sowie die stomatäre Leitfähigkeit untersucht; hierzu wurden die Sorten Riesling und Silvaner miteinander verglichen, die sich offenbar hinsichtlich ihrer Anpassungsfähigkeit an Trockenheit unterscheiden.

1. Auf dem Geilweilerhof lag das ψ_w vor Sonnenaufgang nahe bei 0 bar, und die stomatäre Leitfähigkeit war sehr niedrig. Mit zunehmender Lichtintensität und Temperatur öffneten sich die Stomata am Vormittag. Um 15 Uhr begannen die Stomata sich zu schließen, wobei die stomatäre Leitfähigkeit bei Silvaner rascher abnahm als bei Riesling. Mit Ausnahme des späten Nachmittags lag das ψ_w des Silvaners im Tagesverlauf geringfügig unter dem des Rieslings.
2. Unter den semiariden Bedingungen Adelaides betrug das ψ_w vor Sonnenaufgang -6 bar (Riesling) bzw. -7 bar (Silvaner); es nahm um 10 Uhr rasch auf -14 bar (Riesling) bzw. -16 bar (Silvaner) ab; die stomatäre Leitfähigkeit hatte zu dieser Zeit Maximalwerte erreicht, die bei Riesling deutlich höher lagen als bei Silvaner. Danach nahm die stomatäre Leitfähigkeit bei Riesling rasch, bei Silvaner etwas langsamer ab. Die ψ_w-Werte blieben bis zum späten Nachmittag niedrig, wobei Silvaner stets geringere Werte aufwies als Riesling.
3. Während ψ_s keine deutlichen Veränderungen im Tagesverlauf erkennen ließ, nahmen die ψ_p-Werte insgesamt ab; die ψ_p-Werte des Silvaners lagen hierbei stets unter denen des Rieslings. Unter semiariden Bedingungen lag ψ_p bereits ab 10 Uhr nahe bei 0 bar.
4. Unter semiariden Bedingungen waren die ψ_s-Werte der Blätter grundsätzlich vermindert, was auf eine osmotische Anpassung hindeutet. Bei Riesling war das osmotische Potential niedriger und die Gewebeelastizität höher als bei Silvaner.
5. Unter semiariden Bedingungen löste der Traubenbehang einen Anstieg der ψ_s-Werte und eine Abnahme der ψ_p-Werte bei Silvaner, nicht jedoch bei Riesling aus.

Introduction

As a part of the soil-plant-atmosphere continuum, grapevines like many other crop plants have to be adapted to dry air and soil conditions, i. e. to be drought tolerant in order to produce a sufficient yield. Besides other morphological and physiological

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adaptations, the ability of a plant to maintain a positive, or even constant, turgor (ψ_p) as water potential (ψ_w) decreases is a generally accepted criterion of drought tolerant cultivars (TURNER 1979). A positive turgor is a prerequisite for growth, many enzymatic reactions (HSIAO 1973), and ion and assimilate partitioning (GEIGER 1975), and is thus essential for yield formation. To maintain a positive turgor over a wide range of leaf water content grapevines are able to close their stomata and to lower transpiration (DÜRING 1976, 1978). Besides that, some plants are known to actively accumulate solutes during stress, thereby decreasing their osmotic potential, a process called osmotic regulation (KAUSS 1979) or osmotic adjustment (TURNER 1979). A high tissue elasticity also contributes to the maintainance of a positive leaf turgor potential (WEATHERLEY 1970). While a reduction of stomatal transpiration within certain limits will markedly reduce photosynthesis, the carbon required for osmotic adjustment may have its origin not only in photosynthesis but also in organic acid or carbohydrate metabolism and thus represents only a small proportion of current assimilates (TURNER 1979).

In order to study the mechanisms of response to drought in two grape cultivars known to differ in their adaptation to drought, the diurnal changes of water relations, i. e. water potential and its components and leaf conductance of Riesling and Silvaner, were analysed under field conditions in a humid temperate and in a semiarid climate. In addition, the effects of fruit load on some of these parameters were studied in the vines grown in the semiarid environment.

Material and methods

a. Vines grown in Australia

11-year-old ungrafted grapevines (*Vitis vinifera,* cvs. Riesling and Silvaner) were used in the 2nd half of January and in February 1981 at the Claremont orchard of the Waite Agricultural Research Institute at Glen Osmond, Adelaide, South Australia. According to COOMBE and MONK (1979) the average rainfall is 629 mm/year. Drip-irrigation (ca. 150 mm) had been applied from October to December. As there was no measurable rainfall for 4 weeks before and during the experiment, and 1981 turned out to be an extremely hot year many grape varieties showed considerable water stress. All experiments were carried out using fruit-bearing vines. On January, 20th, the clusters of one half of the plants were detached; this took place in the period of rapid sugar accumulation (Riesling: 14.9, Silvaner 12.4 °Brix by refractometer), the average fruit load per vine being 6.03 kg (Riesling) and 7.24 kg (Silvaner). The diurnal changes of water relations were estimated on fully expanded but not senescent leaves from the mid-one-third of the shoots from January, 19th to 22nd.

b. Vines grown in Germany

7-year-old ungrafted Riesling (clone 90) and Silvaner (clone 64) vines were used from August, 18th to 20th 1981, at the Bundesforschungsanstalt für Rebenzüchtung Geilweilerhof, Germany. The average rainfall here is 780 mm/year and in 1981 54.5 mm were measured within the 4 weeks before the experiments.

Leaf conductance was determined using a Lambda Li 60 Diffusion porometer, leaf xylem water potential was measured with a pressure bomb (SCHOLANDER *et al.* 1965). The osmotic potential (ψ_s) was determined by a Wescor psychrometer (HR-33) and a Vogel osmometer (OM 801). Turgor potential was calculated from the water potential and the osmotic potential, $\psi_p = \psi_w - \psi_s$. To estimate water loss at $\psi_p = 0$ leaves from the field were collected from 9 to 10 a. m.; the petiole was kept under water in a water-containing plastic bag. This was transferred to the dark for 16 h allowing relative water content (RWC) of the leaves to reach 100 %. After measuring ψ_s of fully turgid leaves, ψ_w and the leaf weight were determined alternately during wilting. Light intensity was measured by a Lambda Li 185A Quantummeter. The water saturation deficit of the air (WSD_{air}) is the saturation water content of the air at leaf temperature minus the absolute air humidity.

Abbreviations:

ψ_w	=	water potential
ψ_s	=	osmotic potential
ψ_p	=	turgor potential
RWC	=	relative water content
WSD_{air}	=	water saturation deficit of the air

Results

Under humid temperate conditions no stress symptoms were to be detected in either variety, but under semiarid conditions, Silvaner vines appeared to be stressed: Shoot length of Silvaner was distinctly reduced compared to Riesling. Only Silvaner showed leaf folding and changes in leaf angle during the day, a characteristic of water stress (SMART 1974) and leaf senescence started earlier in Silvaner than in Riesling.

1. Diurnal changes under humid temperate conditions

Starting at predawn (7—8 °C, $WSD_{air} \simeq 0$) at Geilweilerhof water potential was close to 0 and leaf conductance was low but increased after 8 a. m. to reach its maxi-

Table 1

The osmotic potential at RWC = 100 % and the water loss of detached leaves at $\psi_p = 0$ of Riesling and Silvaner under the Geilweilerhof and Adelaide conditions

Das osmotische Potential bei RWC = 100 % und der Wasserverlust abgeschnittener Blätter bei $\psi_p = 0$ bei den Sorten Riesling und Silvaner unter den Bedingungen des Geilweilerhofes und Adelaides

Cultivar	Osmotic potential at RWC = 100 % (-bar)		Water loss (%) at $\psi_p = 0$	
	Geilweilerhof	Adelaide	Geilweilerhof	Adelaide
Riesling	9.4	15.1	5.5	5.5
Silvaner	8.4	11.6	2.3	1.8

mum at noon, while ψ_w decreased to −7 (Riesling) and −8 bar (Silvaner), respectively by 11 a. m. (Fig. 1). With increasing light intensity, leaf temperature reached a first maximum at 11 a. m. while the WSD_{air} increased to 15 g · m^{-3}. After that period distinct reductions in light intensity were observed due to midday clouds. As a consequence leaf conductance started to decline immediately (Silvaner) or some 3 h later

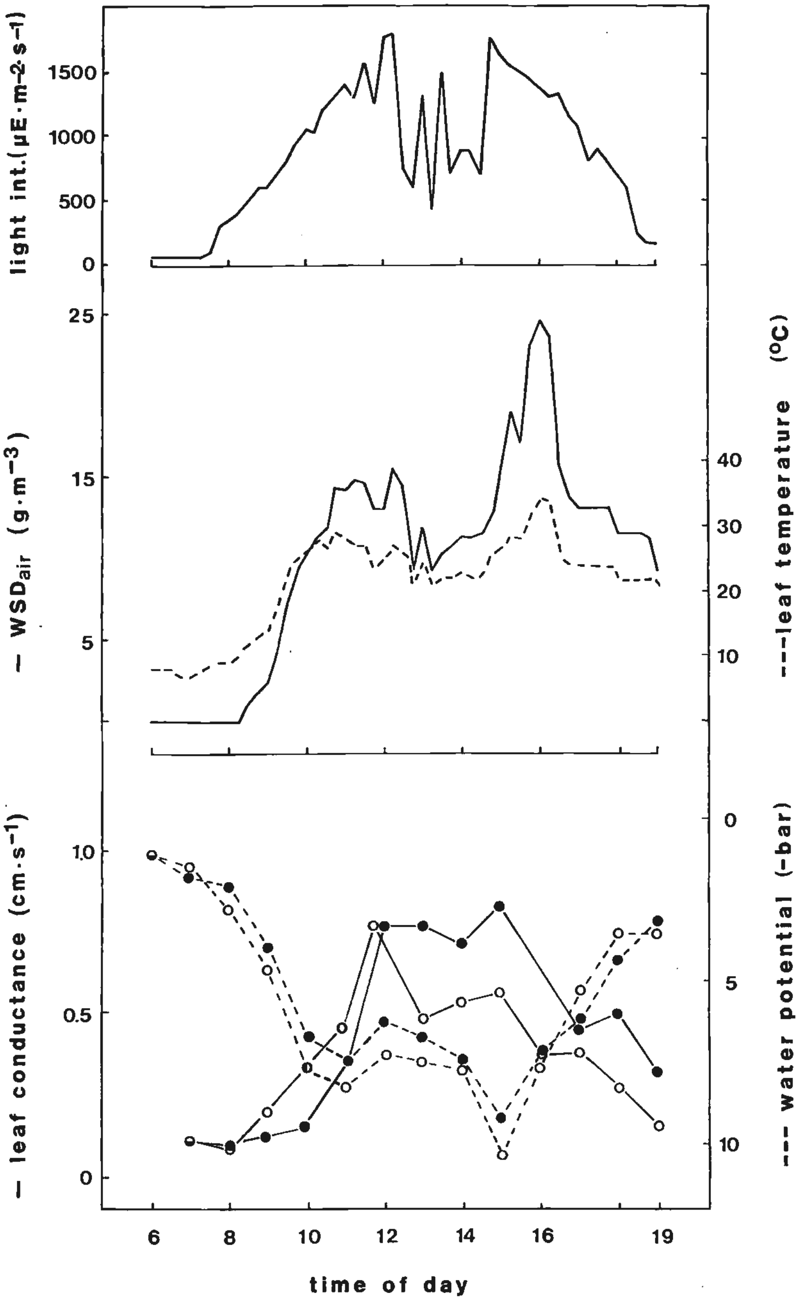

Fig. 1: Diurnal changes in light intensity, leaf temperature, water saturation deficit of the air, stomatal conductance and water potential of Riesling (●) and Silvaner leaves (○) at Geilweilerhof.

Der Tagesgang der Lichtintensität, der Blattemperatur, des Wassersättigungsdefizits der Luft, der stomatären Leitfähigkeit und des Wasserpotentials von Riesling- (●) und Silvanerblättern (○) auf dem Geilweilerhof.

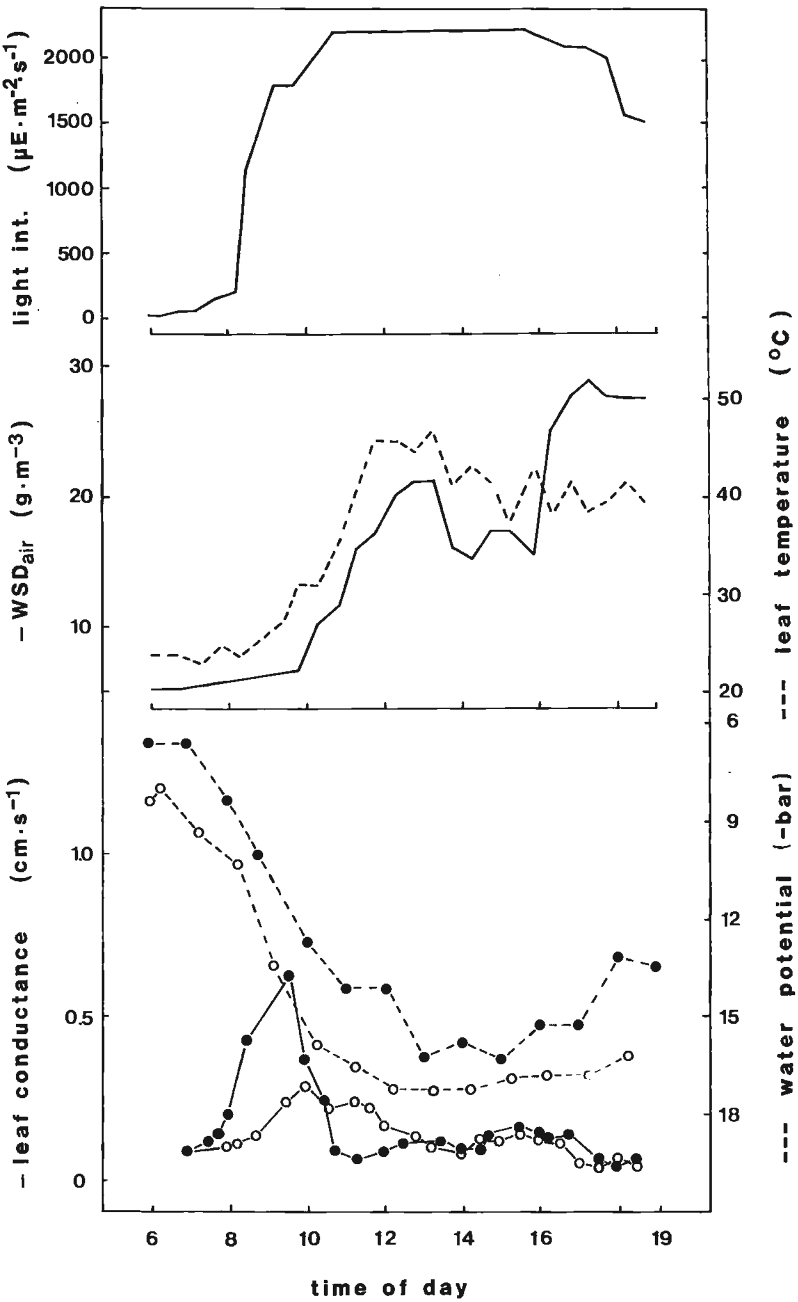

Fig. 2: Diurnal changes of light intensity, leaf temperature, water saturation deficit of the air, stomatal conductance and water potential of Riesling (●) and Silvaner leaves (○) at Adelaide.

Der Tagesgang der Lichtintensität, der Blattemperatur, des Wassersättigungsdefizits der Luft, der stomatären Leitfähigkeit und des Wasserpotentials von Riesling- (●) und Silvanerblättern (○) in Adelaide.

(Riesling). In both cultivars ψ_w reached its minimum at 3 p. m. and thereafter it increased again to approximately reach the predawn values by the evening.

2. Diurnal changes under semiarid conditions

Under the semiarid conditions of South Australia at predawn (leaf temperature 24 °C, $WSD_{air} \approx 0$), ψ_w declined rapidly from −6 bar (Riesling) and −7 bar (Silvaner) to −14 bar (Riesling) and −16 bar (Silvaner) at 10 p. m. (Fig. 2). With increasing light intensity leaf conductance at that time had reached its maximum which in Riesling is distinctly higher than in Silvaner. Thereafter conductance declined rapidly in Riesling and more slowly in Silvaner.

3. Osmotic and turgor potential changes

Distinct diurnal changes of ψ_s were not observed, but there was a marked difference in ψ_s between Geilweilerhof and Adelaide. Measurements of ψ_s at full turgidity indicated lower (more negative) values under semiarid conditions (Table 1). While there was only a small difference between Riesling and Silvaner at Geilweilerhof, at Adelaide the ψ_s values at RWC 100 % were distinctly more negative in Riesling than in Silvaner.

Table 2

Effects of fruit load on the leaf water, osmotic and turgor potential (bar) of Riesling and Silvaner vines · Location: Adelaide · Time of sampling: 6 to 7 a.m.

Der Einfluß des Traubenbehangs auf das Blattwasserpotential, das osmotische Potential und das Turgorpotential (bar) von Riesling- und Silvanerreben · Standort: Adelaide · Zeitpunkt der Probenahme: 6—7 Uhr

Cultivar	+Fruit			−Fruit		
	ψ_w	ψ_s	ψ_p	ψ_w	ψ_s	ψ_p
Riesling	−6.6	−15.8	9.2	−6.2	−14.2	8.0
Silvaner	−9.8	−12.5	2.7	−7.1	−14.4	7.3

Calculations of ψ_p of Riesling and Silvaner at dawn under humid temperate conditions indicate that ψ_p is close to its maximum. Under semiarid conditions ψ_p of Riesling and Silvaner had not reached its maximum during the night, the predawn ψ_p of Silvaner being much lower than that of Riesling (Riesling 9.3 bar, Silvaner 2.7 bar). In the period from 9 to 11 a. m. ψ_p generally decreased under humid and semiarid conditions, Silvaner again being lower in ψ_p than Riesling. At Adelaide ψ_p of Silvaner was close to 0 at this time (Fig. 3). In contrast to Silvaner under semiarid conditions ψ_p of Riesling, even in the afternoon, was above 0.

4. Leaf elasticity and effects of fruit load

The determination of the water loss during wilting at the moment when $\psi_w = \psi_s$, i. e. at turgor 0, indicates that under both environmental conditions turgor 0 of Riesling leaves was reached only when the leaves had lost 5.5 %, while in Silvaner the leaves had lost 2.3 % (Geilweilerhof) or 1.8 % (Adelaide) at turgor 0 (Table 1). Both determina-

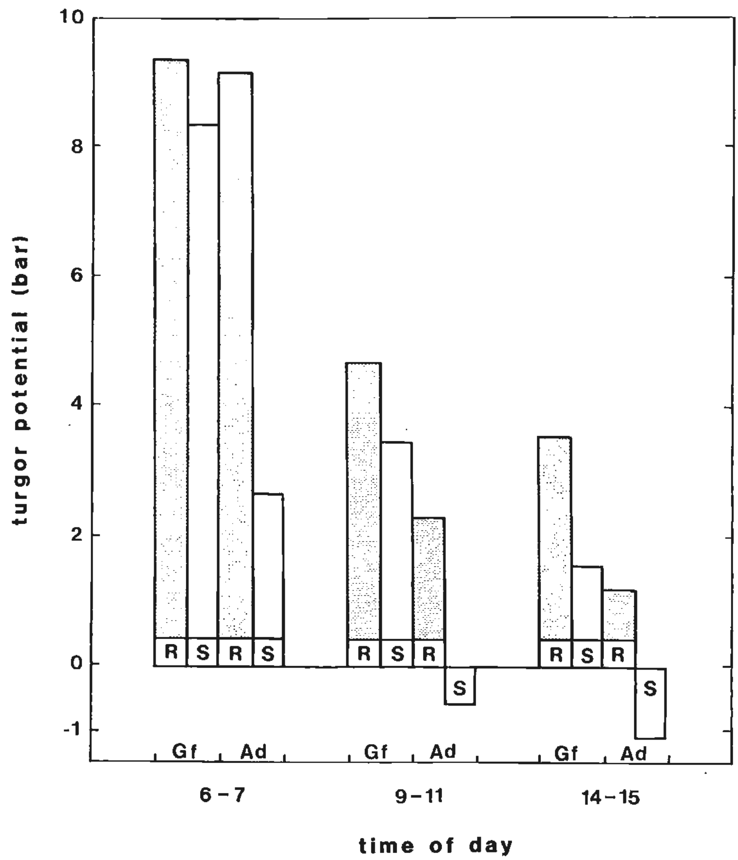

Fig. 3: Diurnal changes of the leaf turgor potential of Riesling (R) and Silvaner grapes (S) under humid temperate (Gf) and semi-arid conditions (Ad). Locations: Geilweilerhof (Gf), and Adelaide (Ad).

Der Tagesgang des Blatturgorpotentials von Riesling- (R) und Silvanerreben (S) unter gemäßigt humiden (Gf) und semiariden Bedingungen (Ad). Standorte: Geilweilerhof (Gf) und Adelaide (Ad).

tions indicate that Riesling leaves have a higher tissue elasticity than Silvaner leaves. Meanwhile this has also been confirmed by specific measurements of the elastic modulus indicating a distinctly higher elasticity in Riesling compared to Silvaner (DÜRING, in preparation).

Table 2 shows the effects of fruit load on ψ_w, ψ_s and ψ_p under Adelaide conditions. While in Riesling there was no distinct difference in ψ_w of fruit-bearing and fruitless vines, fruit-bearing vines of Silvaner were more stressed than fruitless vines. Fruitload increased ψ_s and decreased ψ_p in Silvaner but not in Riesling.

Discussion

The results indicate that under humid temperate and semiarid conditions in the morning the internal and the ambient water status of the atmosphere are favorable to stomatal opening. During the night the leaf water potential increased and the WSD_{air}

was close to 0 at sunrise. Thus stomata opened when the light intensity exceeded about 1000 μE. At maximum leaf conductance under the Adelaide conditions the water potential has declined to about −12 bar (Riesling) and −15 bar (Silvaner). It is supposed that the stomatal closure which followed may be due to the low water status of the leaves and the increasing WSD_{air}. KRIEDEMANN SMART (1971) showed that under Australian conditions the rate of photosynthesis of Thompson Seedless and Syrah (Australian synonym Shiraz) vines was maintained until ψ_w reached −13 to −15 bar and then declined rapidly. This corresponds to our results.

Under the Geilweilerhof conditions the onset of the stomatal opening process seems to be limited not by the internal water status but by reductions in the light intensity due to midday clouds. Under these conditions stomatal closure in the afternoon may be caused by both the decrease of light intensity and the high WSD_{air} values. These results agree with those of LANGE and MEYER (1979) who report that at increasing soil water deficiency the daily period of positive net photosynthesis of grapevines was restricted more and more to some hours in the morning; they suppose that the following stomatal closure is due to the decrease of leaf water potential while at a sufficient soil water supply the diurnal changes of stomatal action are mainly dependent on the air humidity. According to COWAN (1977) stomatal regulation dependent on air humidity optimises water loss related to photosynthesis, as a humidity dependent "feedforward" control of stomatal resistance avoids ineffective water loss when the WSD_{air} is high (SCHULZE *et al.* 1975, FARQUHAR *et al.* 1980).

A comparision of the stomatal behaviour of Riesling and Silvaner under stress conditions indicates that the stomatal opening of Riesling is restricted to a relative short period in the morning when the WSD_{air} values are still low, while the stomata of Silvaner start to open later and to a smaller degree in a period of increasing water demand of the atmosphere. The ability of a plant to maintain a positive turgor as water potential decreases is an important adaptation to water deficits. A positive turgor over a wide range of leaf water contents may be caused by a low osmotic potential at high water contents or by a high tissue elasticity (WEATHERLEY 1970, TURNER 1979). Our results indicate that the osmotic potential of Riesling at sufficient water supply and especially under stress conditions is lower than that of Silvaner, stress conditions inducing osmotic adjustment in both cultivars to a different extent. As the tissue elasticity was shown to be distinctly higher in Riesling this cultivar seems to be more adapted to drought conditions (a) by its better ability to avoid drought due to its stomatal regulation, (b) by its lower osmotic potential and (c) by its higher tissue elasticity. In addition the water status, especially turgor, was shown to be less affected by fruit load in the case of Riesling than in that of Silvaner. This negative influence of fruit load on turgor may at least in part be explained by its stomatal opening effect which has been observed in grapevines by LOVEYS and KRIEDEMANN (1974), DÜRING (1978) and EIBACH (1981).

Summary

Diurnal changes of water potential (ψ_w) and its components (ψ_s, ψ_p) and leaf conductance were analysed under the humid temperate climate of Germany (Geilweilerhof) and the semiarid climate of South Australia (Adelaide) comparing the two cultivars, Riesling and Silvaner, which appear to differ in their adaptation to drought.

1. At Geilweilerhof predawn water potential was close to 0 and leaf conductance very low. Stomata opened during the morning as light intensity and temperature

increased. At 3 p. m. stomata started to close, leaf conductance declining earlier in Silvaner than in Riesling. ψ_w of Silvaner was slightly lower during the day than that of Riesling except during the late afternoon.

2. Under the semiarid conditions of Adelaide predawn ψ_w was −6 bar (Riesling) and −7 bar (Silvaner); it decreased rapidly to −14 bar (Riesling) and −16 bar (Silvaner) at 10 a. m.; leaf conductance at that time had reached its maximum which in Riesling was distinctly higher than in Silvaner. It rapidly declined thereafter in Riesling and more slowly in Silvaner. ψ_w remained low until the late afternoon, Silvaner always having lower values than Riesling.
3. While there were no distinct diurnal changes in the osmotic potential (ψ_s), turgor potential (ψ_p) decreased during the day, ψ_p of Silvaner always being lower than that of Riesling. After 10 a. m., under semiarid conditions, ψ_p of Silvaner was close to 0.
4. The osmotic potential of leaves was generally lower under semiarid conditions indicating osmotic adjustment. In Riesling, the osmotic potential was generally lower and tissue elasticity higher than in Silvaner.
5. Under semiarid conditions fruitload increased ψ_s and lowered ψ_p in the leaves of Silvaner but not in Riesling.

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