

Article

Variability among Young Table Grape Cultivars in Response to Water Deficit and Water Use Efficiency

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Abstract: Climate change will lead to higher frequencies and durations of water limitations during the growing season, which may affect table grape yield. The aim of this experiment was to determine the variability among 3-year old table grape cultivars under the influence of prolonged water deficit during fruit development on gas exchange, growth, and water use efficiency. Six own rooted, potted table grape cultivars (cv. ‘Muscat Bleu’, ‘Fanny’, ‘Nero’, ‘Palatina’, ‘Crimson Seedless’ and ‘Thompson Seedless’) were subjected to three water deficit treatments (Control treatment with daily irrigation to 75% of available water capacity (AWC), moderate (50% AWC), and severe water deficit treatment (25% AWC)) for three consecutive years during vegetative growth/fruit development. Water deficit reduced assimilation, stomatal conductance, and transpiration, and increased water use efficiencies (WUE) with severity of water limitation. While leaf area and number of leaves were not affected by treatments in any of the tested cultivars, the response of specific leaf area to water deficit depended on the cultivar. Plant dry mass decreased with increasing water limitation. Overall, high variability of cultivars to gas exchange and water use efficiencies in response to water limitation was observed. ‘Palatina’ was the cultivar having a high productivity (high net assimilation) and low water use (low stomatal conductance) and the cultivar ‘Fanny’ was characterized by the highest amount of total annual dry mass as well as the highest total dry mass production per water supplied during the experiment (WUE_{DM}). Hence, ‘Fanny’ and ‘Palatina’ have shown to be cultivars able to cope with water limiting conditions and should be extensively tested in further studies.

Keywords: water limitation; dry mass partitioning; assimilation; intercellular CO_2 ; stomatal conductance; leaf water potential

1. Introduction

Climate change and the resulting alterations in temperature, precipitation as well as frequency and duration of extreme weather events, have a huge impact on crop production worldwide and will result in positive and negative changes in the quality and quantity of agricultural products [1]. Water will be one of the most limiting factors for agricultural crop production [2]. According to the IPCC [3], the central and southern part of Europe will have a higher risk of summer droughts due to increasing temperatures and annual precipitation decreases [3]. Additionally, more frequent and intense heat waves will occur all over Europe [3]. High temperatures and decreasing water availability might make Southern Europe unsuitable for wine as well as for table grapes, while northern and central Europe may offer better growing conditions. Increasing temperatures in northern and central

Europe will result in an enlarged production area, which will continue to extend further north [4–6]. Climate conditions in regions from France and Germany will likely resemble to those located in the Mediterranean Basin [7]. Due to very high annual yields and high water requirements, table grape production has already been affected and will be more affected in the future by water shortages [8].

Adaptations of table grape production to changing environmental conditions are possible but will require additional irrigation, time-consuming breeding, or the selection of drought tolerant cultivars, which are able to cope with limited water availability. Until now, most research in the field of water limitation was done on vines and very few studies exist for table grapes, such as ‘Crimson Seedless’ [9,10] and ‘Thompson Seedless’ [11]. From our knowledge, no screening was done yet on the cultivars cultivated in Germany, especially with regard to their physiological and growth response to water deficit, their ability to use water efficiently, and their potential to grow under water limiting conditions in the future. Within several studies, grapevine cultivars showed a high variability to water limitation on leaf and on whole-plant level parameters. This was demonstrated under water-stress [12–14] and also under non-stressed conditions [15,16]. Screenings can be based on direct or indirect measurements for the determination of water limitation on the physiological level. Non-destructive gas exchange measurements on a single leaf are often used as an indicator for the detection of water stress in plants, as stomatal closure is one of the first adaptable plant responses to water limitation, and will result in limiting plant water losses [17,18]. While protecting plants against water loss, the closure of stomata will also reduce the amount of assimilated carbon [18], which can decrease yield and reduce the quality of table grapes. Furthermore, additional observations on the plant-level are important to evaluate the impact of water deficit on table grape cultivars, as grapevines adapt to water limitation by decreasing leaf area, reducing the number of leaves, and limiting growth rate [19,20]. Water use efficiency (WUE) can be calculated on a single-organ or on whole canopy scale. On leaf-scale, WUE can be distinguished between intrinsic WUE (WUE_i) and instantaneous WUE (WUE_{inst}). WUE_i represents the link between net assimilation of CO_2 (A_n) and the stomatal conductance of water (g_s) [21] and WUE_{inst} of A_n and transpiration (E). Both leaf-level WUE are used as parameters to characterize genetic as well as environmental effects [16,22,23]. Plant-level WUE is expressed as the accumulation of biomass per water lost/used [24,25] and shows the response of the plant during the growing season. In contrast to leaf-level WUE, plant-level WUE is not based on a single gas exchange measurement at a specific time and environmental conditions. The main objective of the present work was to determine the influence of water deficit on growth, physiology, and WUEs of six 3-year old table grape cultivars and to identify possible cultivars able to cope with water limitation.

2. Materials and Methods

2.1. Plant Material and Treatments

The experiment was conducted from 2014 to 2016 on potted, own rooted table grapes in a greenhouse of the University of Hohenheim, Germany. Overall, six table grape cultivars (‘Muscat Bleu’, ‘Nero’, ‘Fanny’, ‘Palatina’, ‘Crimson Seedless’, and ‘Thompson Seedless’) subjected to three water deficit levels were tested with eight replications/plants per combination (six cultivars \times three treatments \times eight replications). For the current study, only data of 2016 was analyzed. For experimental setup, a non-resolvable block design was chosen as it allows to cover a potential temperature gradient within the greenhouse.

The plant material of the table grape cultivars ‘Thompson Seedless’ and ‘Crimson Seedless’ originated from Israel (The Volcani Center, ARO, Bet-Dagan, Israel), while the other cultivars were obtained from Germany (Rebveredlung Kühner, Lauffen, Germany). One-bud cuttings of all cultivars were grown in sand, kept hydrated until they grew 4 to 6 leaves and developed a sufficient root. Twenty-four plants per cultivar were transplanted in 7-L pots with six kilograms of a loam, sand, and peat mixture (40:50:10, % per volume) in July 2014, with a maximum water holding capacity

of 37.8%. During the consecutive three-year experiment, plants were kept at field capacity before and after stress treatment. Additionally, plants were fertilized biweekly with 1 g Hakapos® Blue (N 15% + P 10% + K 15% + Mg 2%) (CAMPO EXPERT, Münster, Germany) and 0.1 g Fetrilon®¹ Combi (BASF, Ludwigshafen, Germany). Treatments and experiment information (timeframe, no. of weeks of water deficit treatment, and BBCH) are summarized in Table 1. The first water deficit treatment started in 2014, after an establishment phase of 16 weeks. In the second year, water was limited during vegetative growth starting at an average shoot height of 60 cm and 6 to 8 leaves for 10 weeks. Furthermore, grapevines developing inflorescences were defruited before the treatments started. In 2016, table grapes were kept well-watered during flowering and water deficit treatments started at fruit set and ended at harvest. Over the entire three-year experiment, plants were maintained with only one shoot, attached to bamboo sticks.

Table 1. Characterization of water deficit treatments and experimental information from 2014 to 2016.

		Water Deficit Treatment		Daily Irrigation to	
		Control		75% AWC	
		Moderate		50% AWC	
		Severe		25% AWC	
Year	Timeframe	Weeks of Water Deficit		BBCH (at the Beginning of Water Deficit)	
2014	22.9. – 29.10.	5.5		19	
2015	12.5. – 21.7.	10		16–18	
2016	15.6. – 16.9.	12		71	

In 2014, one bud cuttings were planted. 2014 & 2015: Only vegetative growth. AWC was determined gravimetrically for each pot. AWC, available water content; BBCH, Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie.

For determining the water usage of every plant during the imposition of water deficit, plant and soil water loss was measured gravimetrically on a daily basis using a platform scale (FKB 36K0.1, KERN, KERN & SOHN GmbH, Balingen, Germany) with a maximum range of 36 kg and 0.1 g accuracy. Control plants were irrigated daily to 75% available water content (AWC), moderate to 50% AWC, and severe deficit to 25% AWC. Before starting the treatment, AWC was determined for each pot/plant individually by flooding the pots after sunset to avoid transpiration losses. The excess water was able to drain overnight. Before sunrise, pots were weighed to get the maximum pot weight/field capacity. Wilting point was considered as the minimum weight of the pots. Therefore, all pots were dried out until a constant weight was reached and plants started wilting. Plants were rewatered and adjusted to the plant-pot specific weight. The following formula was used to calculate the individual pot weight for every plant in the treatments:

$$\text{Individual Pot Weight} = \text{PotMin} + (\text{PotMax} - \text{PotMin}) \cdot \text{Treatment} \quad (1)$$

Within Formula (1), we used 0.75, 0.5, and 0.25 of the total available water content for the respective treatments (Control (75% AWC), moderate (50% AWC), and severe (25% AWC)).

During 2014 and 2015, pot weight was not adjusted to the increasing plant weight during the water deficit treatment. In 2016, due to additional bunch weight, pot weight for irrigation was modified by including bunch weights at veraison. Therefore, bunch weights were determined individually by a handheld scale and their weight was added to the corresponding pot's weight. Irrigation during water deficit treatment was applied daily, by the gravimetric determination of water used by each plant/pot and manually refilling to the plant specific weight, calculated with Formula (1).

During the water deficit treatment in 2016, temperature and relative humidity were measured in five-minute intervals using a datalogger (TGP-4500, Gemini Data Loggers, Chichester, UK). Mean temperature over the experimental period in 2016 was 21.8 °C and relative humidity was 63.9%

(Figure 1). Vapour-pressure deficit was calculated based on measured values of temperature and relative humidity and ranged between 0.42–1.74 kPa.

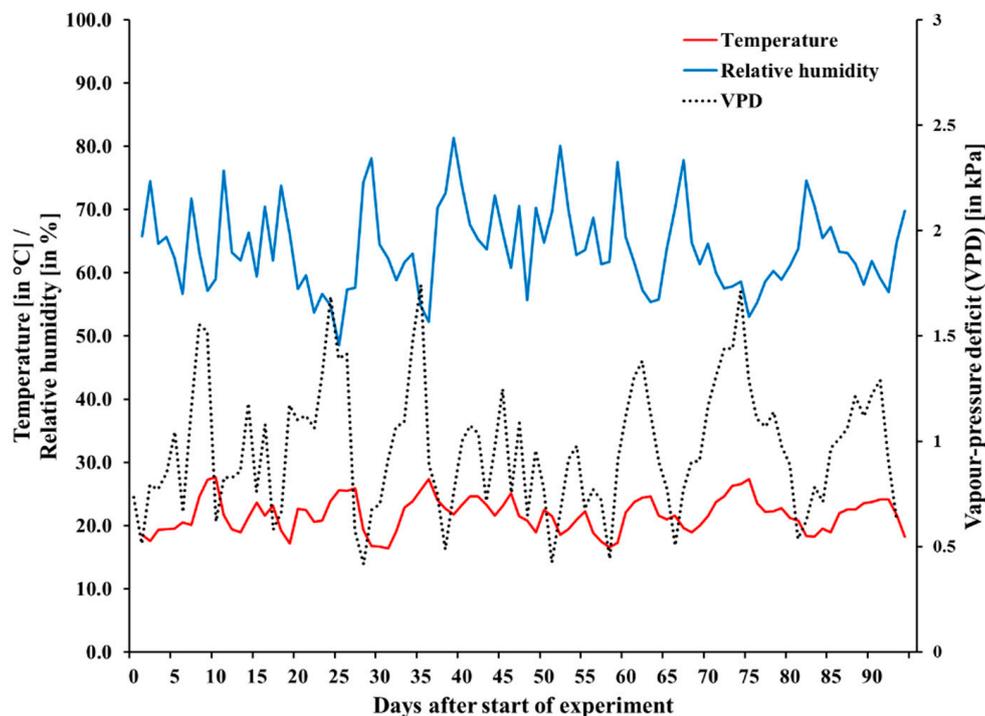


Figure 1. Daily mean values of air temperature, air humidity, and vapour pressure deficit in the open greenhouse during the experimental period (fruit set to harvest) in 2016.

2.2. Plant Water Status

The plant water status was estimated by measuring predawn leaf water potential (Ψ_{pd}) in two consecutive nights before harvest. Measurements were performed with a pressure chamber at harvest, according to the methodology developed by Scholander et al. [26] on one leaf per plant before dawn (03.00 to 06.00 a.m.).

2.3. Gas Exchange Measurements

Net assimilation (A_n), transpiration (E), stomatal conductance (g_s), and intercellular CO_2 (C_i) were measured using the portable gas exchange system GFS 3000 (Walz, Effeltrich, Germany) on one mid plant level leaf of every plant per cultivar–treatment combination. The system was equipped with the Basic System Package, including the Control Unit 3100-C, Standard Measuring Head 3010-S, and LED Light Source 3040-L (90% red and 10% blue light). Measurements were carried out within a timeframe of six days before harvest (10:00 a.m.–06:00 p.m.). Gas exchange was determined on an area of four cm^2 with a flowing rate of $750 \mu mol s^{-1}$ and impeller setting of 7. For the simulation of future climate conditions, a PPFD intensity of $1300 \mu mol m^{-2} s^{-1}$, 400 ppm CO_2 , a temperature of $30^\circ C$, and relative humidity of 50% were configured as the chamber environment.

Instantaneous WUE was calculated by A_n/E and intrinsic WUE by A_n/g_s .

2.4. Plant Dry Weight and Leaf Area

The total leaf area (LA), dry mass (DM) of leaves, stems, and petioles were determined and the number of leaves were counted at harvest for each vine individually. Total leaf area was determined using an LI-3100C Area Meter (LI-COR, Lincoln, NE, USA). Dry mass was measured after drying at $60^\circ C$ until reaching constant weight. Specific leaf area (SLA) ($cm^2 g^{-1}$) was calculated as the ratio of

LA and leaf dry mass and total dry mass water use efficiency (WUE_{DM}) as the ratio of total plant dry mass and water supplied during the experimental period ($g L^{-1}$).

2.5. Statistical Analysis

The physiological response of leaf-level gas exchange, WUE_i and WUE_{inst} , Ψ_{pd} , growth parameters, and WUE_{DM} of six table grape cultivars (cultivars: 6) subjected to three water deficit stress levels (treatments: 3) were analyzed using PROC MIXED (SAS version 9.2., SAS Institute Inc., Cary, NC, USA) with the following model:

$$y_{ijkl} = \mu + t_k + b_{kl} + \tau_i + \varphi_j + (\tau\varphi)_{ij} + e_{ijkl}, \quad (2)$$

where μ is the general effect, t_k and b_{kl} are random block effects for the k th table and the l th block on the k th table, respectively. τ_i , φ_j , and $(\tau\varphi)_{ij}$ corresponds to fixed main effects of the i th cultivar and j th water deficit treatment and their interaction effects, respectively. e_{ijkl} are the error effects of observations y_{ijkl} . Residuals were checked graphically for normality and homogeneity of variances. To reach normality and homogeneity of variances, data of E and g_s needed to be square-root transformed prior to analysis. Data of WUE_i , WUE_{inst} , LA, total DM, WUE_{DM} , and Ψ_{pd} were log-transformed. In case of a significant F-test, multiple comparisons for levels of the corresponding factor were done based on LSD ($\alpha = 0.05$). Significant differences were presented using a letter display created by the SAS macro %mult [27]. Within the letter display, capital letters show significant differences among cultivars in one or for all water deficit treatments. Lower case letters indicate significances among treatments in one cultivar or for all cultivars. If data needed transformation before analysis, statistical analysis are based on the transformed data. However, the same statistical analysis was conducted for transformed and non-transformed data. For the presentation of the results, transformed data were back-transformed (back-transformation: LOG: $y = e^x$; square-root: $y = x^2$). However, the corresponding letter display is based on previously transformed data.

3. Results

3.1. Plant Water Status

Predawn leaf water potential (Ψ_{pd}) showed significant interactions between cultivar and treatment. Ψ_{pd} values for the control treatment ranged between -0.2 to -0.36 MPa, for the moderate treatment between -0.2 to -0.69 MPa, and for the severe treatment between -0.25 to -1.10 MPa (Figure 2). For 'Fanny', all treatments differed significantly from each other and Ψ_{pd} decreased (-0.32 to -1.1 MPa) when water deficit intensified. Differences between the control and severe treatments were observed for 'Palatina' (-0.33 to -0.48 MPa) and 'Crimson Seedless' (-0.27 to -0.36 MPa), while no differences between treatments for 'Nero' and 'Thompson Seedless' were observed. When comparing cultivars within the treatments, 'Thompson Seedless' was the cultivar that differed the most from other cultivars and had the least negative Ψ_{pd} . In contrast, the most negative Ψ_{pd} was observed in 'Fanny' with a moderate (-0.69 MPa) and severe water deficit (-1.1 MPa).

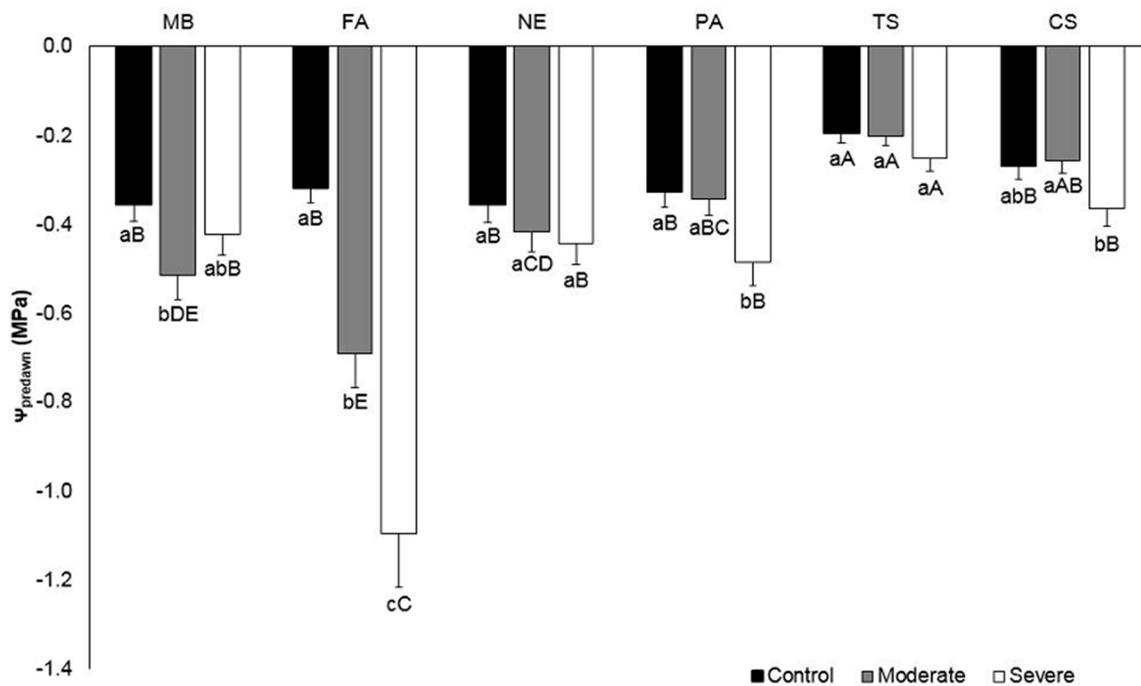


Figure 2. Median values of predawn leaf water potential (Ψ_{pd}) of six table grape cultivars subjected to three water deficit treatments at harvest in 2016. The data represent values of back transformed data. Treatments included: Control: daily irrigation to 75% of available water capacity (AWC), Moderate: daily irrigation to 50% of AWC, and Severe: daily irrigation to 25% of AWC. CS: Crimson Seedless, FA: Fanny, MB: Muscat Bleu, NE: Nero, PA: Palatina, TS: Thompson Seedless; Error bars represent standard errors; Values with identical letters indicate non-significant differences among cultivars (capital letters) and treatments (lower case letters) at $\alpha = 0.05$.

3.2. Gas Exchange Measurement

Gas exchange parameters differed significantly between cultivars and treatments (Table 2). ‘Fanny’ had the highest rate of all cultivars ($10.96 \mu\text{mol m}^{-2}\text{s}^{-1}$), while ‘Muscat Bleu’ ($5.18 \mu\text{mol m}^{-2}\text{s}^{-1}$), ‘Thompson Seedless’ ($5.78 \mu\text{mol m}^{-2}\text{s}^{-1}$), and ‘Crimson Seedless’ ($4.16 \mu\text{mol m}^{-2}\text{s}^{-1}$) were the cultivars with lowest assimilation rates. Similar results were observed for E and g_s , where ‘Thompson Seedless’, ‘Crimson Seedless’, and ‘Muscat Bleu’ had approximately 55 to 60% lower transpiration and 58 to 63% lower stomatal conductance in comparison to ‘Fanny’. The highest C_i was found in ‘Nero’ with $245.48 \mu\text{mol m}^{-2}\text{s}^{-1}$, whereas ‘Palatina’ ($143.91 \mu\text{mol m}^{-2}\text{s}^{-1}$) and ‘Thompson Seedless’ ($161.58 \mu\text{mol m}^{-2}\text{s}^{-1}$) had the smallest C_i values. WUE_{inst} and WUE_i were highest for ‘Palatina’ with $6.42 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$ and $0.16 \mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$ respectively, but did not differ significantly from ‘Thompson Seedless’, ‘Fanny’, and ‘Muscat Bleu’. ‘Nero’, on the other hand, represented the least efficient cultivar at this development stage with 45% lower instantaneous and 47% lower intrinsic WUE compared to ‘Palatina’. Among the treatments, all parameters differed significantly between the control and severe water deficit. Control vines had the highest E ($1.85 \text{ mmol m}^{-2}\text{s}^{-1}$) and g_s ($77.83 \text{ mmol m}^{-2}\text{s}^{-1}$), followed by moderately stressed plants ($E = 1.51 \text{ mmol m}^{-2}\text{s}^{-1}$, $g_s = 62.24 \text{ mmol m}^{-2}\text{s}^{-1}$), and the lowest values were found in plants treated with severe water deficit ($E = 0.94 \text{ mmol m}^{-2}\text{s}^{-1}$, $g_s = 37.6 \text{ mmol m}^{-2}\text{s}^{-1}$). For A_n , C_i , and both leaf-level WUEs, control and moderate treatments did not significantly differ from each other. Vines under severe water deficits had a 22 to 29% lower A_n and 22 to 26% lower C_i , while WUE_i and WUE_{inst} increased by approximately 22 to 30% and 19 to 26%, respectively.

Table 2. Mean values of net assimilation (A_n) and intercellular CO_2 (C_i), and median values of transpiration (E), stomatal conductance (g_s), and leaf-level water use efficiencies (intrinsic: WUE_i and instantaneous: WUE_{inst}) of six table grape cultivars subjected to three water deficit treatments.

Cultivar	Treatment	A_n ($\mu\text{mol m}^{-2}\text{s}^{-1}$)		E ($\text{mmol m}^{-2}\text{s}^{-1}$)		g_s ($\text{mmol m}^{-2}\text{s}^{-1}$)		C_i ($\mu\text{mol m}^{-2}\text{s}^{-1}$)		WUE_{inst} A/E		WUE_i A/ g_s	
Muscat Bleu	Control	4.65	a	0.96	a	39.60	a	218.12	a	3.98	b	0.10	b
	Moderate	5.57	a	1.07	b	43.84	b	203.69	a	4.76	b	0.12	b
	Severe	5.32	b	0.69	c	27.19	c	120.74	b	6.57	a	0.17	a
Fanny	Control	12.30	a	3.28	a	148.08	a	247.20	a	3.74	b	0.08	b
	Moderate	11.86	a	2.45	b	104.30	b	213.00	a	4.23	b	0.10	b
	Severe	8.71	b	1.32	c	53.11	c	149.88	b	6.84	a	0.17	a
Nero	Control	10.67	a	3.14	a	135.63	a	258.41	a	3.25	b	0.08	b
	Moderate	7.54	a	1.93	b	81.64	b	241.87	a	3.67	b	0.09	b
	Severe	7.14	b	1.77	c	75.26	c	236.15	b	3.69	a	0.09	a
Palatina	Control	11.03	a	1.80	a	74.22	a	155.00	a	5.83	b	0.14	b
	Moderate	9.89	a	1.44	b	59.32	b	149.40	a	6.72	b	0.17	b
	Severe	7.80	b	1.03	c	41.17	c	127.33	b	6.75	a	0.17	a
Thompson Seedless	Control	6.64	a	1.29	a	51.29	a	175.67	a	5.15	b	0.13	b
	Moderate	5.88	a	1.14	b	46.38	b	191.45	a	4.87	b	0.12	b
	Severe	4.81	b	0.71	c	27.05	c	117.62	b	7.11	a	0.19	a
Crimson Seedless	Control	5.17	a	1.24	a	49.66	a	225.53	a	4.00	b	0.10	b
	Moderate	5.19	a	1.25	b	48.36	b	220.30	a	4.05	b	0.10	b
	Severe	2.12	b	0.44	c	15.98	c	192.44	b	4.51	a	0.12	a
ANOVA													
	Cultivar (C)	<0.0001		<0.0001		<0.0001		0.0361		0.0355		0.0324	
	Treatment (T)	0.0006		<0.0001		<0.0001		<0.0001		0.0001		<0.0001	
	C*T	0.5774		0.4113		0.3597		0.5151		0.4336		0.3549	

The data represent mean values (A_n , and C_i) and median values of back transformed data (E , g_s , WUE_{inst} , and WUE_i). Treatments included: Control: daily irrigation to 75% of available water capacity, Moderate: daily irrigation to 50% of available water capacity, and Severe: daily irrigation to 25% of available water capacity. Different letters indicate significant differences among cultivars (capital letters) and treatments (lower case letters) at $\alpha = 0.05$. ANOVA: p -values are given for the global F-test of the corresponding factor.

3.3. Growth Parameters, Dry Mass Partitioning, and Plant WUE

Leaf area differed significantly within the cultivars but was not affected by treatments. ‘Crimson Seedless’ was the cultivar that produced the highest LA (1921 cm^2), followed by ‘Thompson Seedless’ (1660 cm^2), ‘Nero’ (1213 cm^2), ‘Palatina’ (1211 cm^2), ‘Fanny’ (1168 cm^2), and lastly ‘Muscat Bleu’ (1116 cm^2) (Table 3). For SLA, significant interactions of treatment and cultivar were observed. Though ‘Fanny’, ‘Palatina’, and ‘Thompson Seedless’ showed no differences between treatments, SLA of ‘Crimson Seedless’ significantly decreased with increasing water limitation. Additionally, ‘Nero’ reached the highest SLA values under severe water deficit conditions (159.73 $\text{cm}^2 \text{g}^{-1}$). Within all levels of treatments, we observed the highest SLA for ‘Fanny’ and ‘Crimson Seedless’. In contrast, the lowest values were found in ‘Palatina’ and ‘Nero’. Differences between cultivars were determined by the number of leaves per plant (Table 3), where ‘Crimson Seedless’ produced the most leaves (20.5) while ‘Fanny’ and ‘Muscat Bleu’ only formed 12 and 9.8 leaves per plant, respectively. However, no differences between the water deficit levels were observed for any of the cultivars studied. Significant effects of treatment and cultivar were found for the total annual DM production and resulting WUE (Table 3). Among all cultivars, ‘Fanny’ had the highest values with a DM of 61.35 g and WUE of 0.08 g L^{-1} . ‘Thompson Seedless’ (30.12 g) produced the least amount of dry mass but did not differ significantly from ‘Crimson Seedless’ (30.45 g). Due to high water usage of both cultivars during the experiment, WUE was 55 to 58% lower than ‘Fanny’. Besides cultivar, deficit treatment led to significant differences in both parameters. Severely stressed vines had 10 to 12% higher annual DM production as well as 19 to 33% higher WUE than the moderate treatment and the control.

Table 3. Mean values of specific leaf area (SLA) and number of leaves and median values of leaf area (LA), total dry mass (Total DM), and total dry mass water use efficiency (WUE_{DM}) of six table grape cultivars subjected to three water deficit treatments.

Cultivar	Treatment	LA		SLA		Total DM		Number of Leaves		WUE _{DM}	
		(cm ²)		(cm ² g ⁻¹)		(g)			(g L ⁻¹)		
Muscat Bleu	Control	1074.27		171.72	a AB	32.54	a	9.88		0.04	c
	Moderate	1151.48	C	152.17	b C	35.95	a CD	10.00	D	0.05	b B
	Severe	1122.71		167.16	a AB	36.08	b	9.38		0.06	a
Fanny	Control	1191.18		168.62	a B	60.33	a	12.75		0.07	c
	Moderate	1228.93	C	171.35	a A	70.98	a A	11.63	C	0.09	b A
	Severe	1087.03		175.67	a A	53.89	b	11.63		0.09	a
Nero	Control	1282.80		152.30	ab C	43.45	a	16.38		0.05	c
	Moderate	1229.79	C	144.03	b C	41.43	a B	15.25	B	0.05	b B
	Severe	1130.14		159.73	a BC	35.79	b	16.25		0.06	a
Palatina	Control	1311.60		152.09	a C	34.06	a	16.25		0.04	c
	Moderate	1206.16	C	153.33	a BC	37.52	a BC	15.25	B	0.05	b B
	Severe	1121.81		149.95	a C	33.65	b	15.25		0.05	a
Thompson Seedless	Control	1766.40		169.15	a B	32.31	a	14.71		0.03	c
	Moderate	1560.87	B	164.10	a AB	29.46	a E	14.88	B	0.03	b C
	Severe	1658.88		161.83	a B	29.37	b	15.13		0.05	a
Crimson Seedless	Control	2185.06		180.90	a A	34.90	a	21.13		0.03	c
	Moderate	1836.10	A	174.25	ab A	31.77	a DE	19.25	A	0.03	b C
	Severe	1767.82		165.01	b AB	25.47	b	21.25		0.04	a
ANOVA											
	Cultivar (C)	<0.0001		<0.0001		<0.0001		<0.0001		<0.0001	
	Treatment (T)	0.0633		0.0448		0.0324		0.8144		<0.0001	
	C*T	0.7734		0.0069		0.4589		0.9975		0.7317	

The data represent mean values (SLA and number of leaves) and median values of back transformed data (LA, Total DM, and WUE_{DM}). Treatments included: Control: daily irrigation to 75% of available water capacity, Moderate: daily irrigation to 50% of available water capacity, and Severe: daily irrigation to 25% of available water capacity. Different letters indicate significant differences among cultivars (capital letters) and treatments (lower case letters) at $\alpha = 0.05$; ANOVA: *p*-values are given for the global F-test of the corresponding factor.

Total annual dry mass production of vines and relative dry mass production of fruit, leaves, stem, and petioles are shown in Tables 3 and 4. Overall, we determined significant differences between cultivars regarding leaves, petioles, and fruit dry mass. Petioles were also affected by the water deficit treatments (Table 4). For stem dry mass, significant interactions between cultivar and treatment have been determined. ‘Fanny’ had the highest fruit dry mass and the lowest DM of leaves, stem, and petioles, while ‘Crimson Seedless’ had the highest dry mass of leaves, and petioles, but no plant of ‘Crimson Seedless’ produced fruit. Lowest dry mass of leaves and petioles were determined for ‘Fanny’ (6.9 g and 1.08 g).

Table 4. Mean values of annual dry mass production of leaf, stem, petioles, and fruit of six table grape cultivars subjected to three water deficit treatments.

Cultivar	Treatment	Leaf DM (g)		Stem DM (g)		Petioles DM (g)		Fruit DM (g)	
Muscat Bleu	Control	6.33		17.99a	AB	1.05	a	21.98	
	Moderate	7.66	D	18.06a	AB	1.04	a	14.81	B
	Severe	6.76		16.06a	A	1.03	b	11.58	
Fanny	Control	7.14		13.46a	C	1.14	a	35.48	
	Moderate	7.27	D	12.51a	C	1.15	a	57.62	A
	Severe	6.27		11.36a	C	0.93	b	37.45	
Nero	Control	8.55		16.83a	B	1.33	a	27.08	
	Moderate	9.12	C	16.31a	B	1.38	a	17.80	B
	Severe	7.27		14.98a	AB	1.09	b	14.62	
Palatina	Control	8.72		17.49a	B	1.63	a	17.55	
	Moderate	7.98	C	17.80a	AB	1.47	a	23.13	B
	Severe	7.69		15.20b	AB	1.33	b	16.74	
Thompson Seedless	Control	10.47		17.47a	B	1.61	a	18.51	
	Moderate	10.01	B	17.27a	AB	1.49	a	10.11	B
	Severe	10.39		16.54a	A	1.46	b	14.03	
CrimsonSeedless	Control	12.11		20.03a	A	2.07	a	n.a.	
	Moderate	11.07	A	18.96a	A	1.85	a	n.a.	n.a.
	Severe	10.90		13.06b	BC	1.62	b	n.a.	
ANOVA									
	Cultivar (C)	<0.0001		<0.0001		<0.0001		<0.0001	
	Treatment (T)	0.1221		<0.0001		0.0003		0.5901	
	C*T	0.6549		0.0191		0.6271		0.4693	

The data represents mean values of leaves, stem, petioles, and fruit dry mass. Treatments included: Control: daily irrigation to 75% of available water capacity, Moderate: daily irrigation to 50% of available water capacity, and Severe: daily irrigation to 25% of available water capacity; n.a.: not available; Different letters indicate significant differences among cultivars (capital letters) and treatments (lower case letters) at $\alpha = 0.05$; ANOVA: p -values are given for the global F-test of the corresponding factor.

4. Discussion

At the end of the water deficit treatments, cultivars showed a high variation in plant water potential when exposed to water limitation. According to Ojeda et al. [28], who defined four levels of water deficit, the cultivar suffering from the most severe water stress was 'Fanny' with about -1.1 MPa at the end of the treatment, while 'Thompson Seedless' had a stress level that ranged between none to weak stress (-0.2 to -0.25 MPa). Differential behaviors and responses of plant water potential to water deficit were described by Costa et al. [29] for the cultivars 'Aragonez' and 'Trincadeira'. In the study of Ojeda et al. [28], they also determined Ψ_{pd} continuously during the experiment and Ψ_{pd} of the stress treatment showed high variations. At some measurements, they could observe only a weak or non-existent stress level. In our study, only minor differences between the levels of water deficit were found for some cultivars. Based on the studies of Ezzahouani and Williams [30] and Wenter et al. [31], who determined decreasing Ψ_{pd} values towards the end of stress/growing season, plants with highest water limitation could have experienced a period with severe water stress (defined by Ojeda et al. [28]) in this study. In order to identify differences in the behavior of different cultivars to water limitation during the experimental period, additional measurements of water potential should be carried out before and during the experimental period.

Even though no clear results were found for Ψ_{pd} , gas exchange measurements and leaf-level WUE showed a definite reaction to water limitation. For g_s , rates decreased when the deficit intensified, which is in accordance with other studies on grapevines [13], table grapes [10], and rootstocks [32,33]. Since stomata closure is the first reaction to water limitations [34], g_s is often used as a non-destructive indicator to detect water stress. Therefore, water stress was classified into three levels. The first level of mild water stress is defined by g_s from 150 to 500 $\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$ ($\hat{=}$ max. g_s), the second

level of moderate water stress by g_s between 50 to 150 $\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$, and the third level of severe water stress by $g_s < 50 \text{ mmol H}_2\text{O m}^{-2}\text{s}^{-1}$ [34,35]. According to these definitions, the control and the moderate treatment had a moderate water stress level at harvest, while vines subjected to severe water deficit had g_s values within the third level of water stress. As a consequence of increasing stomatal closure, we observed a downregulation of A_n when water deficit intensified. Previous studies observed similar results and determined a curvilinear relationship of A_n and g_s [34,35]. Furthermore, the range of A_n and g_s values are in agreement with studies by Chaves et al. [36] and Jara-Rojas et al. [37]. Decreasing C_i values with intensified water limitation, as observed in our study, imply stomatal limitations as the dominant factor for regulation at moderate stress [38,39], while the dominant factors for an upregulation of C_i , at the threshold value of g_s (50 $\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$), are non-stomatal limitations [38]. As we could not determine increasing C_i at the threshold value within our study, stomatal closure may have led to decreasing g_s values. As a result of a higher decrease of g_s and E than A_n , both leaf-level WUEs increased with severity of water deficit. Medrano et al. [34] described similar results, where g_s decreased by 50% while A_n only decreased by 30% when the deficit progressed and led to higher WUE values when the water deficit intensified. Based on the observations for g_s , A_n , E , C_i , and leaf-level WUEs, our results indicate stomatal limitations as the limiting factor for lower A_n values in table grapes exposed to severe water limitation. The stomatal limitation could have been caused by increasing ABA concentration within xylem sap [33,40,41] and/or decrease of hydraulic conductance [33,42,43], as they are considered as main factors regulating stomatal conductance. Besides the effect of water deficit treatment, cultivar selection had a major influence on all gas exchange parameters and WUE_{leaf} . Variations and differences among grapevine cultivars in gas exchange under non-limiting and limiting water conditions were observed in several studies [13,44,45] and the response to water limitation is highly dependent on environmental conditions [45]. However, results obtained by gas exchange measurements could be overestimated, due to the possible occurrence of non-uniform closure of stomata (patchiness) in grapevines, when subjected to water deficit [46]. Furthermore, single leaf WUEs are limited due to high variability of measurements within the canopy, differences in leaf-response to the cumulative daily irradiance and leaf age, as young leaves have a higher gas exchange than older leaves [24]. Within our study, we determined differences among the cultivars for plant-level WUE_{DM} . The result of a high variability of cultivars are conform with other grapevine studies, comparing whole plant WUE (WUE_{WP}) of 19 cultivars under well-watered conditions in a glasshouse [47] or eight cultivars under well-watered and water-stressed conditions [12]. In contrast to our study, Palliotti et al. [44] could not find any differences in the measurement of whole plants $\text{WUE}_{\text{Canopy}}$ with regard to the response to higher water limitation. The comparison of results based on whole plants in relation to water stress is problematic and difficult, as the results are based, among other things, on gas exchange measurements of the canopy [44], biomass growth during the experiment [12], or, as in our study, on the total dry matter of the plant. When comparing leaf and plants WUEs, we observed increasing efficiencies with increasing water deficits, while in other studies no clear relationship was found between leaf and plant WUEs [24,44]. Medrano et al. [24] suggested the analysis of additional physiological parameters to reveal cultivar specific responses.

In most studies investigating the influence of water deficiency on plant growth and the adaptation of plants to the limited availability of soil water, it was observed that leaf area, dry matter, and number of leaves decreased in response to water limitation [19]. In our study, leaf area and the number of leaves were not negatively affected by the water deficit, in contrast to the results of Gomez-del-Campo et al. [20] where less leaf area was produced under water limiting conditions and the number of leaves was lower than under well-watered conditions. Plant growth, indicated by annual dry mass production, decreased, when the deficit was more severe which is in accordance with the study of Toumi et al. [19]. Within the study of Tardieu et al. [48], SLA was reported to decrease, if environmental conditions led to greater reduction of growth than on photosynthesis [48]. Therefore, it is used as a tool for the detection of changes in leaf structure [49,50]. Within our study, response of SLA depended on cultivar-treatment. Only SLA values of 'Crimson Seedless' decreased with increasing water limitation,

indicating a higher influence of water deficit conditions on growth than on photosynthesis. While no clear behavior of the cultivars with regard to water deficit could be determined for SLA, differences could be determined for dry mass. A severe water deficit led to a lower dry mass. Since A_n rates and dry mass production have a close relationship [51], the reduced carbon assimilation, as an effect of closed stomata, could have led to a decrease in dry mass production in severely stressed plants within our study. Reductions of plant dry matter in case of a severe water deficit are in line with other studies [19,33] and indicated reduced plant growth due to a prolonged water deficit during fruit development and ripening. Cultivar differences, as they occurred in this study, were also observed by Gómez del Campo et al. [52,53], where cultivar selection and cultivar–irrigation interactions were the main factors influencing leaf area, number of leaves, SLA, and dry mass production [53–55].

5. Conclusions

Based on the obtained results, we identified gas exchange and water use efficiencies of table grapes to be affected by cultivar and by water deficit treatment. Since high productivity (high A_n) with low water loss (g_s) is a selection criterion for cultivation in water limiting environments, ‘Palatina’ could be a possible cultivar for cultivation under these environmental conditions. In addition, ‘Fanny’ appeared to be the cultivar least influenced by the deficit treatment. Hence, under changing climatic conditions with increasingly limited water availability during the growing period, ‘Palatina’ and ‘Fanny’ seem to be the most promising table grape cultivars of our study. However, further studies in the field under limited water conditions, as well as grafting on different rootstock, are necessary to confirm the ability of these cultivars to cope with water limitations.

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