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Physiological response of juvenile hop plants to water deficit

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ABSTRACT

This paper evaluates the response on the rate of photosynthesis (P_n), transpiration (E), stomatal conductance (g_s) and water use efficiency (WUE) in 15 genotypes of young hop plants (19 BBCH) grown in greenhouses in the conditions of water deficit for the period of 9 days. On the 9th day, the relative content of water in the experimental plants fluctuated between 70.14–75.20%. The levels of P_n and g_s evidently dropped in the monitored species as a result of the water deficit. The decrease of P_n in the experimental plants compared with the control group was largest in the Saaz Os. cl. 72 (by 77.5%), Magnum (by 73.3%) and Columbus (by 62.3%). To the contrary, the lowest P_n decrease was noted in the case of genotypes Saaz Late (by 15.7%), Vital (by 23.9%) and Premiant (by 24.2%). All genotypes except for cv. H16 showed an evident decrease of E. Judging by the highest values of WUE, the most effective water management was shown by Premiant, Vital and Saaz Late genotypes. A significant stomatal limitation of photosynthesis due to water stress was identified in the most widely used Czech cultivar, Saaz Os. cl. 72, with low values of stomatal conductance, photosynthetic rate and transpiration.

Keywords: *Humulus lupulus* L.; gas exchange; precipitation deficit; period of drought

Water is vital for plant growth and development. Water-deficit stress, permanent or temporary, limits the growth and the performance of cultivated plants more than any other environmental factors. Water-deficit stress can be defined as a situation in which plant water potential and turgor are sufficiently reduced to interface with normal functions (Hsiao 1973, Chaves et al. 2002, Hu et al. 2006).

Water stress is defined as a moderate loss of water, which leads to stomatal closure and limitation of gas exchange. Desiccation is a far more extensive loss of water that can potentially lead to gross disruption of metabolism and cell structure, eventually resulting in the cessation of enzyme catalyzing reactions. Severe water stress may result in the arrest of photosynthesis, disturbance of metabolism, and final death (Bohnert and Jensen 1996).

Shao et al. (2008) divides the responses of plants caused by water deficit as physiological, biochemical and molecular. Among the physiological responses there are recognition of root signals, loss of turgor and osmotic adjustment, reduced leaf-water potential (Ψ), decrease in stomatal conductance to CO_2, reduced intercellular CO_2 concentration (c_i), decline in net photosynthesis and reduced growth rates.

However, photosynthesis is particularly sensitive to water-deficit because the stomata close to conserve water, reducing CO_2 diffusion to the fixation sites in the leaf mesophyll in the vicinity of the enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco). This causes diminished photosynthesis and consequent reduced productivity (Lawlor and Tezara 2009, Galmés et al. 2011).

Water deficit is the major problem in agriculture and the ability to withstand such stress is of immense economic importance. Hop is a plant sensitive to lack of water, particularly to proper distribution of precipitation throughout the vegetation period. Seasons with precipitation deficit show reduced yields and economic losses. Precipitation

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deficit can be solved by various irrigation systems that evidently increase yields and do not affect the quality of the hop-heads (Slavík and Kopecký 1994), while increasing the photosynthetic accumulation of energy-rich matters (Hniličková and Novák 2000).

The main goal of our experiment was to monitor a set of 15 genotypes of hops in juvenile phases of ontogeny and the effects of gradual water deficit on basic physiological parameters such as the rate of net photosynthesis (P_n), transpiration (E), stomatal conductance (g_s) and water use efficiency (WUE). The secondary goal of the study were to acquire new and missing information and thus contribute to other researchers and growers of hop plants.

MATERIAL AND METHODS

Plant material and growth and experimental conditions. The experiment focused on monitoring the effects of water deficit on the physiological parameters in 15 genotypes and new cultivations of young hop plants in phase 19 BBCH scale – 9 and more pairs of leaves unfolded (Rossbauer et al. 1995). The overview of the genotypes is listed in Table 1.

The experiments took place in May of years 2010–2013 in the greenhouse of the Czech University of Life Sciences in Prague. They were conducted in semi-controlled conditions (natural light conditions, air temperature 23 ± 2/18 ± 2°C day/night, relative air humidity 65% min and 85% max). The experimental plants were grown in containers with the volume of 5 dm^3 in garden substrate (pH 5.0–6.5, nutrient content N 80–120 mg/L, P 22–44 mg/L, K 83–124 mg/L) and siliceous sand in the ratio of 2:1.

Table 1. The overview of the hop genotypes

Genotype	Country	Registration
Kazbek	CZ	2008
H16	UK	–
First Gold	UK	1995
Rubín	CZ	2007
Bohemia	CZ	2010
Harmonie	CZ	2004
4914	CZ	2010
4964	CZ	2010
5166	CZ	2011
Saaz Os. cl. 72	CZ	1952
Premiant	CZ	1996
Vital	CZ	2008
Saaz Late	CZ	2010
Columbus	US	1997
Magnum	DE	1993

One plant was grown in each container with a support rod to which two bines were attached. Five experimental plants and five control plants were grown for each genotype. During the experiment, the control plants were watered to the point of full saturation of the substrate. The experimental plants were not watered for nine days. The change of water contents in the substrate were monitored using the WET-2 Sensor/HH2 Moisture Meter (Delta-T Devices, Cambridge, UK). The sensor was calibrated for the substrate used. Using measured the values of the substrate conductance, the values of soil mass wetness w (g/g) were calculated on the basis of the calibration curve and derived equation:

$$y = -0.0397 + 0.0006x \ (r = 0.998; P = 0.0000; r^2 = 0.996) \quad (1)$$

Where: x – reading of the sensor (mV); y – soil-mass wetness (w). The experimental measurements were taken on the first, third, sixth and ninth day of the water deficit (1D, 3D, 6D, and 9D).

Determination of leaf relative water content. The relative water content (RWC) in the leaves was established as:

$$100 \times (FM - DM)/(SM - DM)$$

Where: FM – fresh mass of 10 leaf discs (diameter 6 mm) cut from the 7^{th}–9^{th} pair of bine leaves and immediately weighed on an analytical balance; SM – saturated mass of the same discs after their hydration in the dark for 5 h; DM – dry mass of these discs after they were oven-dried at 105°C for 24 h.

Leaf gas exchange measurements. The net photosynthetic rate, the rate of transpiration, the stomatal conductance and the intercellular CO_2 concentration were measured on the 8^{th} pair of bine leaves *in situ*, using the portable gas exchange system LCpro+ (ADC BioScientific Ltd., Hoddesdon, UK). The gas exchange was measured from 8:00 A.M. to 11:30 A.M., Central European Time.

Irradiance was 650 µmol/m^2/s of photosynthetically active radiation, the temperature in the measurement chamber was 23°C, the CO_2

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concentration was 420 ± 35 vpm (μmol/mol), the air flow rate was 205 ± 30 μmol/s and the duration of the measurement of each sample was a 10 min interval after the establishment of steady-state conditions inside the measurement chamber. The measurement of these parameters took place repeatedly on a single leaf on three plants. The water use efficiency was calculated from the measured parameters of gas exchange. The water use efficiency was calculated, as P_n/E.

Statistical analysis. A statistical evaluation of the experiment was made using the analysis of variance (ANOVA) and the values obtained were compared in further detail, using the Tukey's test at the significance level $P < 0.05$. Statistical analyses were performed using Statistica 9.0 CZ for MS Windows software (Tulsa, USA).

RESULTS AND DISCUSSION

The initial water levels in experimental plants and substrate prior to discontinuing the irrigation (1D) were as follows: RWC on average 89.9% and average soil-mass wetness of the substrate 0.404 g/g (Table 2). Variances in the monitored physiological characteristics were found among all cultivars.

The highest P_n was measured in genotypes Saaz Late (13.85 μmol $CO_2/m^2/s$), Saaz Os. cl. 72 (13.60 μmol $CO_2/m^2/s$), Vital (13.33 μmol $CO_2/m^2/s$) and Premiant (13.06 μmol $CO_2/m^2/s$). The lowest P_n occurred in genotypes Columbus and Magnum (5.10 and 5.36 μmol $CO_2/m^2/s$, respectively). Hejnák et al. (2014) states that in genotype Saaz Os. cl. 72 in phase 21–29 BBCH the photosynthesis rate in field conditions is 4.35 μmol $CO_2/m^2/s$.

In genotypes Columbus and Magnum Kenny (2005) indicates a photosynthetic rate in adult leaves of 18.9 and 15.8 μmol $CO_2/m^2/s$, further indicating that the average photosynthetic rate of 40 genotypes (including cultivars, native North American and native Yugoslavian germplasm, and breeding lines) was 16.2 μmol $CO_2/m^2/s$. The range in photosynthetic rate was between 9.0 and 22.3 μmol $CO_2/m^2/s$.

Higher rates of transpiration occurred in genotypes Vital and Premiant (5.34 and 4.80 mmol $H_2O/m^2/s$, respectively) and the lowest were recorded in genotypes Columbus and Magnum (1.16 and 1.27 mmol $H_2O/m^2/s$, respectively). Significant differences were found in stomatal conductance between genotypes. The highest g_s registered Premiant genotype (1.12 mol $CO_2/m^2/s$) and Vital (0.88 mol $CO_2/m^2/s$), corresponding to their high levels of photosynthesis (Table 2). Kenny (2005) states that the average stomatal conductance was 320 mmol $H_2O/m^2/s$, and the range was between 173 and 477 mmol $H_2O/m^2/s$.

The gradual drying of the substrate of experimental plants from 1D to 9D is apparent from the decreasing values of soil-mass wetness (Table 2), the average soil-mass wetness of the substrate on 9D being 0.105 g/g. Upon interruption of the irrigation, the monitored cultivars showed a decrease of RWC (70.14–75.20%). Normal values of RWC ranged between 90% in turgid and transpiring leaves to about 40% in severely desiccated and dying leaves. In most crop species, the typical RWC at near-wilting is around 60–70%, with exceptions (Lugojan and Ciulca 2011).

The photosynthesis rate decreased in a statistically significant manner in all monitored genotypes due to the water-deficit. The lowest values were measured in genotype Saaz Os. cl. 72. Genotypes Saaz Late, Premiant and Vital showed a smaller drop in photosynthetic rate. At the same time, stomatal conductance decreased in a statistically evident manner throughout all cultivars.

The lowest stomatal conductance on 9D was measured in genotype Saaz Os. cl. 72 and the highest in the new breeding cultivar, 4964 (Table 2). Closing of stomata and decreases of stomatal conductance are the very factors considered to be the main reason for decreased photosynthesis during periods of moderate water stress (Lawlor and Tezara 2009), as well as one of the mechanisms for preventing dehydration through decreasing transpiration (Larcher 2003).

The mutual relationship between photosynthetic rate and stomatal conductance in the individual genotypes on 9D is shown in Figure 1. This graph indicates that the lower photosynthetic rate corresponds with lower values of stomatal conductance (with the exception of genotype Saaz Os. cl. 72). It specifically indicates that the higher values of stomatal conductance correspond with higher photosynthetic rates (Table 2).

The main chemical signal for closing stomata (and subsequent decrease of transpiration) is abscisic acid (ABA), which is transported from the roots through the xylem into the leaves of the plants (Pérez-Alfocea et al. 2011). Korovetska et al. (2014) states that the concentration of ABA increases in

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Table 2. The rate of photosynthesis (P_n; μmol $CO_2/m^2/s$); transpiration (E; mmol $H_2O/m^2/s$), stomatal conductance (g_s; mol $CO_2/m^2/s$), intercellular CO_2 concentration (c_i; μmol CO_2/mol), relative water content (RWC; %) and soil-mass wetness (w; g/g) in the experimental genotypes of hop in the individual dates of measurement (time/day)

Genotype	Time/day	P_n	E	g_s	c_i	RWC	w
Kazbek	1D	10.00^{a}	1.68^{a}	0.132^{a}	266.60	87.52	0.405
	3D	9.80^{a}	1.20^{ab}	0.075^{b}	298.60	82.39	0.293
	6D	9.03^{b}	1.23^{ab}	0.054^{bc}	293.07	79.88	0.165
	9D	8.50^{b}	1.12^{b}	0.042^{c}	295.73	73.26	0.128
H16	1D	9.98^{a}	1.55^{a}	0.083^{a}	248.73	89.62	0.410
	3D	9.28^{ab}	1.76^{a}	0.077^{a}	277.40	83.54	0.321
	6D	8.73^{b}	1.49^{a}	0.064^{ab}	250.33	80.25	0.173
	9D	7.94^{c}	1.32^{a}	0.054^{b}	273.33	72.12	0.125
First Gold	1D	9.55^{a}	2.34^{a}	0.125^{a}	314.80	86.15	0.391
	3D	8.84^{ab}	1.47^{bc}	0.103^{a}	395.53	83.21	0.315
	6D	8.54^{b}	1.34^{bc}	0.071^{b}	326.53	79.66	0.162
	9D	6.74^{c}	1.21^{c}	0.058^{b}	236.53	70.14	0.105
Rubín	1D	9.68^{a}	1.75^{a}	0.086^{a}	256.87	92.15	0.398
	3D	8.96^{ab}	1.22^{a}	0.062^{a}	267.17	85.65	0.296
	6D	8.64^{b}	1.47^{a}	0.074^{a}	209.53	78.12	0.157
	9D	7.67^{c}	0.55^{b}	0.021^{b}	264.13	74.29	0.111
Bohemia	1D	8.89^{a}	2.85^{a}	0.139^{a}	328.33	88.64	0.409
	3D	8.28^{ab}	1.75^{b}	0.093^{b}	469.27	81.18	0.305
	6D	8.08^{bc}	1.60^{b}	0.076^{bc}	331.31	77.25	0.162
	9D	7.85^{c}	1.03^{c}	0.050^{c}	293.80	73.15	0.119
Harmonie	1D	9.16^{a}	3.62^{a}	0.217^{a}	399.53	90.51	0.419
	3D	8.91^{a}	2.22^{b}	0.113^{b}	289.79	86.44	0.289
	6D	8.09^{b}	2.02^{b}	0.103^{b}	354.81	80.73	0.152
	9D	7.83^{b}	0.93^{c}	0.047^{c}	272.07	75.20	0.098
4914	1D	9.47^{a}	3.23^{a}	0.187^{a}	286.07	89.87	0.389
	3D	9.52^{a}	0.67^{b}	0.026^{b}	284.54	86.23	0.308
	6D	9.33^{a}	0.43^{b}	0.017^{b}	379.47	78.16	0.161
	9D	8.65^{b}	0.56^{b}	0.020^{b}	463.20	74.32	0.104
4964	1D	8.80^{a}	2.37^{a}	0.137^{a}	324.67	88.14	0.392
	3D	8.48^{a}	2.14^{a}	0.095^{b}	501.06	83.21	0.275
	6D	7.95^{b}	2.00^{a}	0.091^{b}	275.85	78.91	0.158
	9D	7.52^{b}	1.55^{b}	0.080^{b}	357.07	73.65	0.089
5166	1D	9.16^{a}	2.68^{a}	0.209^{a}	351.27	91.12	0.408
	3D	8.51^{b}	1.84^{b}	0.083^{b}	392.20	85.33	0.295
	6D	8.29^{bc}	0.82^{c}	0.066^{c}	314.33	80.42	0.149
	9D	7.91^{c}	1.34^{b}	0.070^{c}	298.67	74.81	0.099
Saaz Os. cl. 72	1D	13.60^{a}	3.33^{a}	0.265^{a}	349.22	93.55	0.395
	3D	13.32^{a}	2.90^{a}	0.242^{a}	364.76	86.18	0.284
	6D	9.16^{b}	1.51^{b}	0.131^{b}	224.16	79.39	0.152
	9D	2.28^{c}	0.22^{c}	0.012^{c}	371.18	70.55	0.096
Premiant	1D	13.06^{a}	4.80^{a}	1.123^{a}	341.53	91.06	0.425
	3D	12.51^{b}	1.03^{b}	0.068^{b}	283.84	87.43	0.324
	6D	11.96^{b}	0.30^{c}	0.059^{b}	344.39	80.21	0.172
	9D	11.34^{c}	0.25^{c}	0.016^{c}	319.57	75.11	0.126

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Table 2. The rate of photosynthesis (P_n; μmol $CO_2/m^2/s$); transpiration (E; mmol $H_2O/m^2/s$), stomatal conductance (g_s; mol $CO_2/m^2/s$), intercellular CO_2 concentration (c_i; μmol CO_2/mol), relative water content (RWC; %) and soil-mass wetness (w; g/g) in the experimental genotypes of hop in the individual dates of measurement (time/day)

Genotype	Time/day	P_n	E	g_s	c_i	RWC	w
Vital	1D	13.33[a]	5.34[a]	0.883[a]	387.17	89.72	0.399
	3D	12.52[b]	2.39[b]	0.091[b]	277.26	83.22	0.265
	6D	11.96[b]	1.34[c]	0.065[c]	376.35	77.15	0.148
	9D	11.29[c]	0.52[d]	0.034[d]	488.32	74.28	0.083
Saaz Late	1D	13.85[a]	1.91[a]	0.162[a]	418.75	90.67	0.411
	3D	12.63[b]	1.70[a]	0.126[b]	381.20	84.12	0.312
	6D	12.47[b]	0.81[b]	0.048[c]	404.89	78.15	0.141
	9D	11.82[c]	0.56[b]	0.041[c]	343.48	72.49	0.114
Columbus	1D	5.10[a]	1.16[a]	0.052[a]	365.11	89.55	0.382
	3D	4.74[a]	1.05[ab]	0.063[a]	399.58	84.12	0.280
	6D	3.70[b]	0.81[ab]	0.050[a]	280.33	78.11	0.139
	9D	3.40[b]	0.67[b]	0.031[b]	313.20	74.11	0.088
Magnum	1D	5.36[a]	1.27[a]	0.221[a]	295.61	90.19	0.419
	3D	5.16[a]	0.91[b]	0.165[b]	236.94	86.15	0.388
	6D	4.64[b]	0.90[b]	0.110[c]	324.67	79.11	0.155
	9D	3.79[c]	0.45[c]	0.032[ad]	299.06	73.03	0.093

Values within a column marked with the same letter are not significantly different ($P \leq 0.05$)

the xylem in hops during gradual drying of the soil, while the transpiration rate decreases.

There was a statistically evident decrease in transpiration on 9D in 14 genotypes, most notably in genotypes Saaz Os. cl. 72 and Premiant. In the case of the H16 hybrid the decrease in transpiration was not statistically evident. According to Sperry (2000), the decrease of their transpiration rate during water deficits enables plants to survive the lack of water, while at the same time their photosynthetic production is limited. On the contrary, plant cultivars that do not retard gas exchange in cases of moderate water-deficit are able to sustain high productivity, even during short-term fluctuation of water content in the soil.

Figure 2 shows the comparison of photosynthetic rate on 9D in control and experimental plants. In all genotypes there was a statistically evident difference in photosynthetic rates between experimental and control plants. This difference is the most significant in the case of genotypes Saaz Os. cl. 72 (by 77.5%), Magnum (by 73.3%) and Columbus (by 62.3%). The smallest decrease of photosynthetic rate in comparison with the control group was in genotypes Saaz Late (by 15.7%), Vital (by 23.9%) and Premiant (by 24.2%).

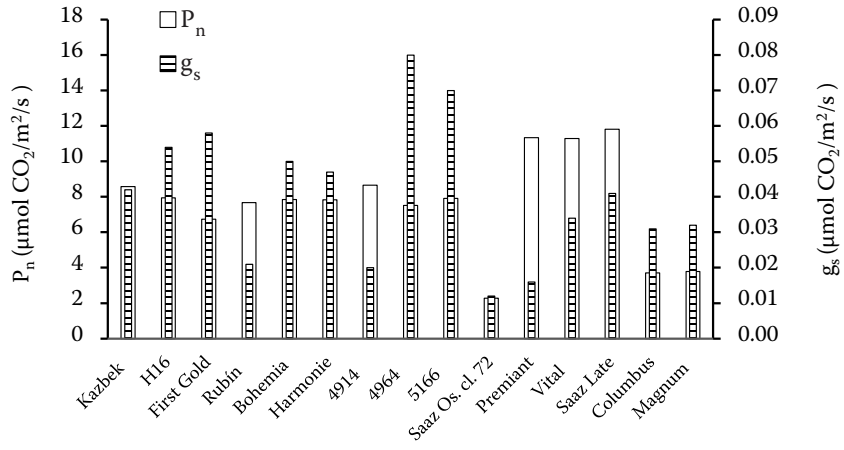

Figure 1. The rate of photosynthesis (P_n), and stomatal conductance (g_s), in ninth day (9D) of the water deficit in experimental plants. The indicated P_n and g_s are average values

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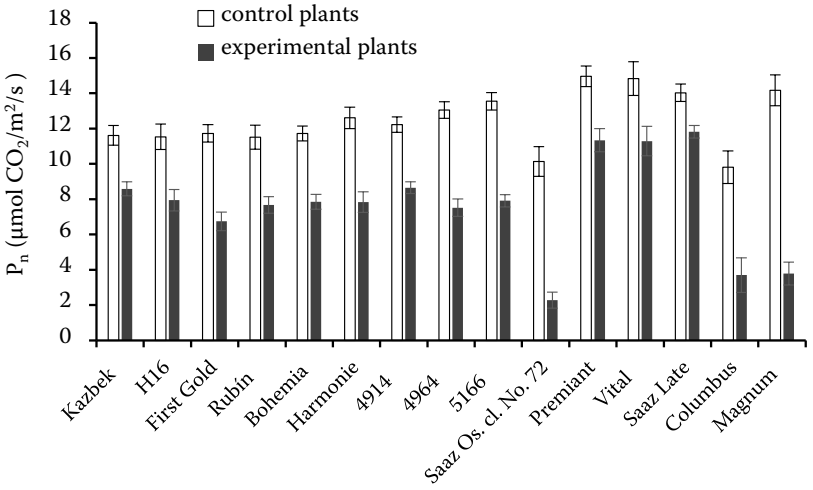

Figure 2. The rate of photosynthesis (P_n) in ninth day (9D) of the water deficit in experimental and control plants. The indicated P_n is an average value ± standard error

Figure 3 indicates values of water use efficiency for stressed plants on 9D. WUE is measured as a ratio of pure photosynthetic rate and the transpiration of leaves given at the time of the photoperiod. This is known as instantaneous water use efficiency and is the characteristic often used as the selection marker for cultivars that can effectively manage water (Condon et al. 2004).

The Premiant genotype had the highest WUE among the set of 15 genotypes (45.36 μmol CO_2/mmol H_2O). Genotypes Vital and Saaz Late had, on average, 21.41 μmol CO_2/mmol H_2O. The new breeding line, 4914 and genotype Rubín showed 14.7 μmol CO_2/mmol H_2O. The average WUE in other genotypes was 6.99 μmol CO_2/mmol H_2O.

The results measured show that despite the fact that, according to the RWC values, this was a moderate water stress and, according to the characteristics detailed by Lugojan and Ciulca (2011), there was an evident decrease of photosynthetic rate in all cultivars. Genotypes Premiant, Vital and Saaz Late showed the most optimal fine-tuning of the two roles of stomatal regulation of gas exchange – those in the strategy of the plant preventing water loss due to water stress and that of a sufficient supply of CO_2 for leaf mesophyll during the course of photosynthesis.

This is evident by both higher values of photosynthesis and higher values of WUE in comparison with other cultivars. Significant stomatal limitation of photosynthesis due to water stress was recorded in the case of the most widely used Czech cultivar, Saaz Os. cl. 72, along with low values of stomatal conductance, photosynthetic rate and transpiration rate.

From the new breeding lines, the highest WUE was shown in 4914, while 4964 and 5166 indicated the highest values of stomatal conductance along with average photosynthetic rates by comparison to other genotypes.

To conclude we can confirm that the parameters of photosynthesis, transpiration, stomatal

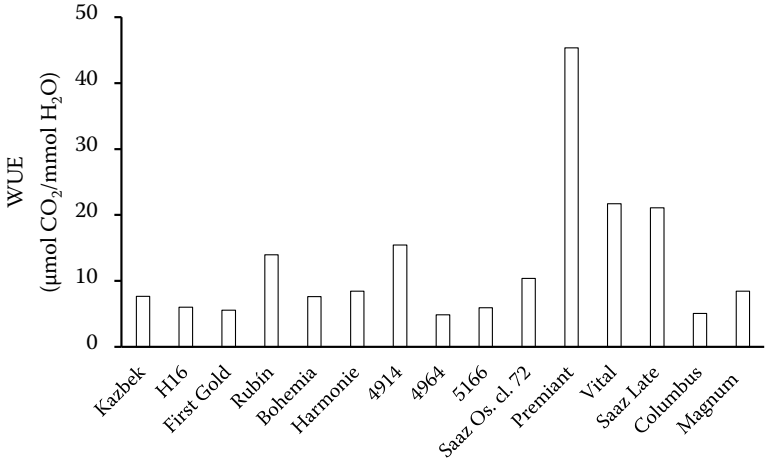

Figure 3. The water use efficiency (WUE) in ninth day (9D) of the water deficit in experimental plants

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conductance and WUE can be used for evaluation of genotypes (and the differences between them) in monitoring the impact of water deficit on the basic physiological functions of hop plants.

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