Photosynthetic activity of selected genotypes of hops (*Humulus lupulus* L.) in critical periods for yield formation

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ABSTRACT

This paper evaluates the influence of genotype on the photosynthetic activity of hops in the period critical for generating yield. Results over three years from measuring the photosynthesis rate statistically show an increase in the photosynthetic activity of hop plants in the flowering stage. The average photosynthetic rates from measurements on the second date (BBA 65) in the years 2007, 2008, and 2009 increased by 17.9%, 45.6%, and 49.2%, respectively. Different photosynthesis curve trends during the final stage of ontogenesis of the plants indicate the maturity level of each hop genotype. As regards the genotypes for which photosynthesis did not reduce significantly, it may be assumed that such plants had not reached technical maturity. The results from the three-year study also show that any promising genotype, with respect to the photosynthesis rate and yield, is the result of breeding of new varieties with greater resistance to drought and high temperatures. Very good results in photosynthetic activity were reached by the new varieties exhibiting high yield and a similar chemical composition to Saaz hop and those sharing the same origins to Saaz, showing a higher content of bitter substances. In 2008 and 2009, all three new forms reached yield levels of 2.35 to 3.12 t/ha of dry hops.

Keywords: hops; photosynthesis rate; varieties; hop cone yield

Photosynthesis is the basic physiological process in plants and one of the important factors in the formation of crop yield (Wullschleger and Oosterhuis 1990, Yu et al. 2001). Many studies examined the relationship between photosynthetic indicators and external natural factors (Changhai et al. 2010). These depend on many external factors and their changes during the development of plants (Kakani et al. 2004, Dogan et al. 2010). Examples include temperature (Traore et al. 2000), the concentration of CO₂ (Coviella et al. 2002), the watering system (Matzke 1990), the methods of fertiliser application and cultivation of the soil (Bruns and Abel 2003). The yield of hops also depends on the hop plant cut quality, not just in a given year, but even in subsequent years (Krofta and Jezek 2010). Reynolds and Delgado (2000) wrote that energy inherent in the biomass of crops is typically less than 5% of the total incident radiation. All hop plant aboveground organs other than fruit are ready for the intensive course of photosynthesis. In hops, the photosynthetic process starts to take place when the plants begin sprouting. The photosynthetic rate gradually increases. The active balance of photosynthesis and respiration processes facilitates elongation growth and thickening of each organ of the hop plant (Rybacek 1980). Larcher et al. (1995) states that the transition from the vegetative to generative phase resulted in significant changes in enzyme activity and shifts in the distribution of assimilates, thereby increasing the intensity of photosynthesis. The dependence of photosynthesis at the level of hop development has several causes. Very young leaves still possess less than the area of fully grown leaves and thus capture smaller amounts of radiation, have less chlorophyll and breathe more intensely. Photosynthetic capacity is particularly high in the generative period of life, i.e. during the flowering and hop cone formation phases (Rybacek 1980). To study the photosynthesis production of higher plants, gasometry methods are mainly used. Applying these methods

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monitors changes of CO₂ concentrations in the vicinity of the measured plant parts or the rate of decrease in the concentration of CO₂ in the air which the plant is exposed to, where necessary. When measuring, the leaf, plant or the part of the plant is enclosed in an air-conditioned assimilation chamber under constant conditions of temperature, humidity, radiation and CO₂ concentration (Sestak and Catsky 1966). In the study of net photosynthesis, Crepinsek (1996) compiled a dynamic model of growth, development and yield of hops. This model simulates the course of net photosynthesis for each hour of the growing season and on this basis can predict the amount of yield. Kenny (2005) reported that older hop leaves have a significantly lower photosynthetic efficiency. This author examined the average rate of photosynthesis in forty genotypes originating from North America and the countries of the former Yugoslavia. The average rate for these varieties was around 16.2 μ mol CO₂/m²/s. The range of photosynthetic efficiency varied between 9 to 23 μ mol CO₂/m²/s. Genotypes with below average photosynthetic efficiency were often sourced from the European varieties. Kenny (2005) stated that the American variety of Willamette at the saturation irradiance of 2000 mol CO₂/m²/s demonstrated an average photosynthetic efficiency of 17.5 µmol $CO_2/m^2/s$. Hnilickova and Hnilicka (2006) studied the influence of water stress and different types of irrigation on the physiological characteristics of the Osvald clone 72 hop. Their values measured under natural light conditions were in the range of 1.65 to 12.23 μ mol CO₂/m²/s. Kenny (2005) measured for the variety of Saaz hops an average photosynthetic rate of 13.7 μ mol CO₂/m²/s.

MATERIALS AND METHODS

This paper aims to assess the photosynthetic capacity of selected genotypes of hop plants in the period critical for production of the yield. The experiment monitored the Saaz and Premiant varieties and newbreedings with the numerical designations Nb. 4237, Nb. 4837, Nb. 4784, and Nb. 4788, of which the first two are genotypes that rank amongst aromatic hops (Nb. 4237 and Nb. 4837). Two other genotypes – Nb. 4784 and Nb. 4788 – are bitter hops with a higher content of alpha bitter acids. The newbreeding numbered Nb. 4237 is a genotype with higher resistance to drought and high temperatures. The content and composition of hop resins and oils are the same as for Saaz. It has a longer growing season, which is very important for division of the peak workload over the hop harvest period. The yield level is above 2 t/ ha. The newbreeding denoted as Nb. 4837 displays the same content and composition of hop resins as found in Saaz. Its main advantage is high yield (up to 3 t/ha). Both Nb. 4784 and Nb. 4788 share almost the same origins as a significant proportion of Saaz. These two genotypes can be classified as bitter hops as alpha acids account for more than 10% of wt. The yield of hop cones is high (above a level of 3 t/ha). Typical values of α - and β -bitter acids of examined hop genotypes are shown in Table 1.

The site of the experiment – Suchdol area (experimental station of university) - lies at the altitude of 280 m. The location is within a moderately warm climate region, more specifically, moderately warm and moderately dry climate district with prevailing mild winters. Table 2 shows the course of weather conditions in 2007, 2008, and 2009 in the period under examination.

The technology utilised for growing the hops followed the normal working pattern for the production of hop gardens.

To measure the rate of photosynthesis, an LC pro+ device was used. LC pro+ (an infrared leaf analyser) can measure basic physiological processes in a leaf without separating it from the plant. This device tracks the physiology of the leaf, which is inserted into the measuring chamber under controlled temperatures and lighting.

Variety	α acids (% w/w)	β acids (% w/w)	α/β ratio
Saaz hop	2.5-4.0	4.0-6.0	0.6-0.9
Premiant	7.0-9.0	3.5-5.5	1.7-2.3
Nb. 4784	10.0-13.0	3.0-5.0	2.5-3.5
Nb. 4788	10.0-13.0	5.0-6.5	2.0-3.0
Nb. 4837	4.0-7.0	5.0-8.0	0.7-1.0
Nb. 4237	4.0-7.0	5.0-7.0	0.5-0.8

Table 1. Typical values of α - and β -bitter acids of examined hop genotypes

Table 2. The course of weather conditions in 2007, 2008 and 2009 in the measurement per	iod
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Year	Period -	N.	VI	٧	/II	V	TII	I	Х
		temp.	precip.	temp.	precip.	temp.	precip.	temp.	precip.
2007	1 st decade	19.5	12.3	16.8	44	19.6	36.4	13.1	25.8
	2 nd decade	21.5	20.5	22.7	2.8	18.9	34.8	13	17.2
	3 rd decade	17	51.5	18.8	29.5	17.7	5.4	12.6	31.1
2008	1 st decade	19.5	21.4	19	28.2	20.8	5.6	18.8	6
	2 nd decade	15.5	3.4	17.7	32.4	18.7	41.1	14.9	4.9
	3 rd decade	20.6	19.9	20.6	20.3	17.8	14.6	10.7	7.3
2009	1 st decade	13.9	4.3	18.7	23.8	20.8	7.8	17.6	8.5
	2 nd decade	15	23.5	18.7	43.8	20.6	11.5	16.9	1.7
	3 rd decade	15.6	68.1	19.1	9	20.3	1.2	16.4	6
2007-2009	VI–IX	17.6	75	19.1	77.9	19.5	52.8	14.9	36.2

The differences in gas concentration and air flow levels inside the chamber form the basis for calculating rates of assimilation and transpiration every 20 s. A small fan in the chamber facilitates mixing of the air around the leaf. Measurement is carried out on an infrared CO_2 gas analyzer (IRGA, ADC, BioScientific Ltd., Great Amwell, UK). The water content in the air is evaluated by moisture sensors. The values measured are automatically saved on to a PCMCIA card. For this experiment, measurements were conducted at a constant temperature of 23°C and 600 nm of irradiation.

An average plant was selected from each genotype of hop and rate of photosynthesis measured on the given date. This was measured in the period critical for formation of hop yield on 3 July (BBA 61), 18 July (BBA 65), 8 August (BBA 69–81) 2007, 1 July (BBA 61), 15 July (BBA 65), 12 August (BBA 69–81) 2008 and 2 July (BBA 61), 16 July (BBA 65) and 6 August (BBA 69–81) 2009. 16 plants were selected from each genotype of hop, they were hand harvested, dried and conditioned at 10% humidity. Then the yields were converted into the area of 1 hectare.

The results of photosynthesis measurement were compared with the yields of dry hops and assessed using the Statgraphic statistics program.

RESULTS AND DISCUSSION

The photosynthesis rates measured for selected genotypes are shown in Figures 1 to 3. In 2007 (Figure 1), for all genotypes, the average photosynthetic rates ranged from 5.21 to 7.82 µmol $CO_2/m^2/s$; in 2008 (Figure 2) the photosynthesis rates were calculated as 4.9 to 7.99 µmol $CO_2/m^2/s$; whereas in 2009 (Figure 3), these varied from 5.65 to 7.3 µmol $CO_2/m^2/s$. Intervals between the measurements of values were quite regular in





Figure 1. Photosynthetic rate measured for selected hop genotypes in 2007

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Figure 2. Photosynthetic rate measured for selected hop genotypes in 2008

length. Figure 4 compares the intensity of photosynthetic rates of two photosynthetically most different hop genotypes in measured terms during the period from 2007 to 2009. There was no statistically significant effect of year (with three critical periods for yield formation during 2007, 2008, and 2009) on the rate of photosynthesis (Figure 5). However, statistically a major difference was found in the effect of a genotype on the rate of photosynthesis (Figure 6). Genotype Nb. 4237 has, at a significant level of $\alpha = 0.05$, the statistically highest photosynthetic rate (7.30 µmol CO₂/m²/s).

In the first period of measurement (3 July 2007), the genotype Nb. 4784 displayed the highest photosynthetic activity, which reached 8.51 μ mol CO₂/ m²/s. The lowest value was recorded for the Nb. 4837 genotype (4.94 μ mol CO₂/m²/s. The trends of changes in the photosynthetic rate were similar for all genotypes. From the first towards the second measurement (when the hops were flowering), a slight increase was recorded, whilst a decreased rate of photosynthesis was discovered in the period leading to the formation of hop cones. These findings were also described by Larcher (1995). He suggests that the transition from vegetative to generative phase of hops is accompanied by changes in metabolism, through increased photosynthetic activity. The reduced values at the end of the measurement period are explained by the transition of the hop plant into the phase of maturity.

On average, for the entire period of 2007, the highest photosynthetic activity was recorded for the Nb. 4788 genotype (7.82 μ mol CO₂/m²/s), whereas the Nb. 4237 genotype displayed high yields of dry cones (1.07 t/ha) as did the Saaz variety (0.95 t/ha). This result is also underscored by the photosynthesis measured. On average over this period, the rates of photosynthesis in both genotypes were among the peak values (7.13 and 7.64 CO₂ μ mol



Terms of measurement

Figure 3. Photosynthetic rate measured for selected hop genotypes in 2009



Figure 4. The comparison of the photosynthetic rates intensity of two photosynthetically most different genotypes of hops (2007–2009)

 $CO_2/m^2/s$). In 2007, all the hop genotypes were only planted the previous year; hence they did not attain the same performance parameters as adult plants. This is most evident in the production indicators (Table 2).

The second year (2008) revealed a very similar trend in the values measured. For the date of measurement (1 July), the Nb. 4237 genotype was the most significant. It had one of the highest measured values of photosynthetic rate (7.83 μ mol CO₂/m²/s) and on average throughout the year it was the most photosynthetically active (7.99 μ mol CO₂/m²/s). This was also confirmed by the second highest yield achieved, which amounted

8 Photosynthesis rate ($\mu mol CO_2/m^2/s$) 7 6 Ι 6.7 6.28 5 6.15 4 3 2 1 0 2007 2008 2009

Figure 5. The effect of years (respectively three critical periods for yield formation in 2007, 2008 and 2009) on the photosynthesis rate of hop plants

to 2.47 t/ha. For all genotypes selected, the flowering of the hops again brought about increases in the photosynthesis rate (15 July 2008). After some more time, approximately 20 days, there was stagnation or decline in the value of photosynthesis. A marked decline occurred in the rather earlier genotypes (e.g. Saaz). Even in this period, the rate of photosynthesis experienced by some genotypes (Nb. 4788 and Nb. 4237) was constant or slightly increased – from 6.54 to 6.72 µmol $CO_2/m^2/s$. The constant value was 8.07 µmol $CO_2/m^2/s$. Therefore, the authors assume they are ready for harvest later than other genotypes.

In 2008, a significantly higher production capability for all the genotypes was observed. The

Table 3. Statistical evaluation of the significance of differences in the yields of selected genotypes in 2007, 2008 and 2009

Variety	2007	2008	2009
Žatecký poloraný červeňák	0.95 ^{cd}	1.51 ^a	1.62ª
Premiant	0.89 ^c	2.20 ^b	2.28 ^b
Nb. 4784	1.01 ^{de}	3.12 ^d	3.01 ^d
Nb. 4788	0.62 ^b	2.35 ^{bc}	2.65 ^c
Nb. 4837	0.45 ^a	2.39 ^{bc}	2.49 ^{bc}
Nb. 4237	1.07 ^e	2.47 ^c	2.98 ^d

^{a-e}differences between average values marked with the same letter are statistically non-significant



Figure 6. The effect of genotype on the photosynthesis rate of hop plants (2007–2009)

highest yield of hop cones was achieved by the Nb. 4784 genotype (3.12 t/ha). In terms of yield, this genotype was followed by Nb. 4237 and Nb. 4837 (2.47 t/ha and 2.39 t/ha, respectively). The measurement of the photosynthetic rate illustrates the resultant yields. On average, these three genotypes were the most active over the period in question (6.44 μ mol CO₂/m²/s, 7.99 μ mol CO₂/m²/s and 7.1 μ mol CO₂/m²/s).

The values of photosynthetic rate measured in 2009 confirmed the data from the two preceding years, i.e. there are increases in photosynthesis during flowering. In 2009, just as in 2008, the most photosynthetically active genotype was Nb. 4237 in average terms (6.8 μ mol CO₂/m²/s). As regards the yield of dry cones, good results were achieved by the Nb. 4784 genotype (3.01 t/ha), then Nb. 4237 (2.98 t/ha) and Nb. 4837 (2.49 t/ha). From the recognized varieties, high yield (1.62 t/ha) was attributed to Saaz.

Statistically significant differences were found among the years 2007, 2008, and 2009 as regards

the yield of dry hops (Figure 7). At the significance level of $\alpha = 0.05$, the statistically significant lowest yield was that in 2007. All the hop genotypes in 2007 were only planted the previous year; hence they did not display the same performance parameters as adult plants.

The measurements of photosynthesis over the three years showed a trend in the hop plants for increased photosynthetic activity in the flowering stage, followed by a decrease in activity in the lead-up to the formation of the qualitative parameters of the hop cone. It was statistically proven that the photosynthetic rate increased every time on the second date of measurement (BBA 65) in the years 2007, 2008, and 2009 (Figure 8). The plants entering into the generative period were changing their metabolism, thereby increasing the activity of photosynthetic apparatus. This was also described by Larcher (1995). Another finding was the differing trend of photosynthesis curves towards the end of the plants ontogeny, which indicates the level of maturity of genotypes. As



Figure 7. The effect of year on the yield of dry hop cones (2007–2009)



Figure 8. The effect of term on the photosynthesis rate of hop plants (2007–2009)

regards the genotypes for which photosynthesis did not reduce significantly (Nb. 4237, Nb. 4837), the authors believe that technical maturity had yet to be reached. The results show that under the photosynthetic curve it is possible to predict the maturation of hop cones.

The results over the three years show that a highly promising genotype, when considering the rates of photosynthesis and yield of dry cones, is the new form of Nb. 4237. Very good results as for the photosynthetic activity were also attained by the Nb. 4837 and Nb. 4784 new forms, which is also attested to by the high yield of cones of these. All three new forms reached in 2008 and 2009 a yield level of between 2.35 to 3.12 t/ha.

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